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Functional and systematic implications of the postcranial anatomy of a Late Miocene feline (Carnivora, Felidae) from Batallones-1 (Madrid, Spain)

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Abstract The Spanish late Miocene locality of Batallones-1 yielded a rich sample of large carnivorans, including saber-toothed felids, amphicyonids, and ailurids, but also of smaller species, with the small cats being especially interesting. Two species are known from Batallones-1, one of them the size of a wildcat, *Felis silvestris*, the other one the size of a caracal, *Caracal caracal*. The former is represented by skulls, mandibles, and postcranial bones, whereas the latter is known from a collection of long bones. Both species are less abundant than their larger relatives, the saber-toothed felids *Promegantereon ogygia* and *Machairodus aphanistus*, but the available sample allows us to assess body proportions and adaptations of the smallest species, and to propose a new genus for this feline, *Leptofelis vallesiensis*. Its limb bones are remarkably gracile compared to fossils of the earlier genera *Pseudaelurus*, *Miopanthera*, and *Styriofelis*, and comparable in cursorial adaptations to the wildcat, very different from extant arboreal cats. While middle Miocene felids were likely semi-arboreal forest dwellers, *L. vallesiensis* would be mostly terrestrial, climbing essentially for protection. This indicates an adaptation to a mosaic of habitats, including relatively open terrain, and may be related to the climatic changes detected in Eurasia during the late Miocene.

Keywords Morphology; Locomotion; Vallesian; *Leptofelis*.

Introduction

Fossils of primitive felids are recorded in several early and middle Miocene sites of Europe, Africa, and North America (Thenius 1949; Viret 1951; Crusafont-Pairó 1952; de Beaumont 1961; Ginsburg 1961a, 1983, 1999, 2002; Crusafont-Pairó and Ginsburg 1973; Rothwell 2001, 2003; Morales et al. 2003; Werdelin et al. 2010). Concerning those showing feline affinities, there are up to four species classically included in the genus *Pseudaelurus* Gervais, 1850: *Ps. romieviensis* Roman and Viret, 1934, from La Romieu (France, MN4), *Ps. turnauensis* (Hoernes, 1882) from Göriach (Germany, MN 5), *Ps. transitorius* Depéret, 1892 and *Ps. lorteti* Gaillard, 1899, both from La Grive-Saint-Alban (France, MN 7/8). All of them are mostly known from cranial and dental fragments, which show a quite similar pattern, but unfortunately, very few postcranial bones are known from these early felines, and thus it is difficult to make inferences about their locomotor adaptations. A fifth species of primitive felid from Sansan (France, MN 6) was also included in *Pseudaelurus* as *Ps. quadridentatus* (Blainville, 1843) (in fact this form is the type species of the genus), but based on its particular features (moderately elongated and laterally flattened upper canines and relatively robust Mc I) it is currently considered as the first known saber-toothed felid, hence the genus *Pseudaelurus* should be included within the subfamily Machairodontinae (de Beaumont 1978; Werdelin et al. 2010; Salesa et al. 2012a; Peigné 2012). Considering this, and the feline dental characters (basically, relatively short upper canines with rounded section) that they displayed, most of the other species of *Pseudaelurus* (i.e., *Ps. lorteti*, *Ps. turnauensis*, and *Ps. transitorius*, the last being a junior synonym of *Ps. turnauensis*) mentioned above were assigned in different genera, *Styriofelis* Kretzoi, 1929, for *Ps. turnauensis*, and *Miopanthera* Kretzoi, 1938, for *Ps. lorteti* (Geraads and Peigné 2016). To summarize, in the middle Miocene at least three different taxa are known in Western Europe: the primitive machairodontine *Ps. quadridentatus*, the lynx-sized feline *M. lorteti*, and the wild cat-sized feline *S. turnauensis*. Nonetheless, we should consider that the scarcity of postcranial bones of these taxa is probably concealing a greater generic diversity and preventing an in-depth taxonomic knowledge of these early Felinae.

Cranial remains of European late Miocene Felinae are much better known than those from the lower and middle Miocene, and several skulls and mandibles are known from different Turolian European localities (Wagner 1857; Schlosser 1924; de Mecquenem 1924; Riabinin 1927; Kretzoi 1951, 1952; de Beaumont 1961; Schmidt-Kittler 1976; Solounias 1981; Forsten and Kaya 1995; Morlo 1997; Ginsburg 1999; Roussiakis 2002; de Bonis 2005). All of them were classically assigned to the wildcat-sized *Felis attica* Wagner, 1857, but separated by Salesa et al. (2012a) into the new genus *Pristifelis* as *P. attica*. Nevertheless, the postcranial skeleton of this animal is as poorly known as those from the earliest Felinae. In fact, few papers including comparative descriptions or functional inferences on the postcranial anatomy of these Miocene felines have been published (de Beaumont 1961, 1986; Salesa et al. 2011). Finally, a new species was described from the Vallesian of Batallones-1 and Batallones-3 (Madrid, Spain) by Salesa et al. (2012a) under the name of *Styriofelis vallesiensis*. This is the smallest of the two species of Felinae known from these Spanish localies. When Salesa et al. (2012a) assigned the small feline from Batallones-1 and Batallones-3 to the genus *Styriofelis* as the new species *S. vallesiensis*, they chose the most conservative taxonomic point of view based on a set of dental similarities between the Batallones sample and the Middle Miocene feline *S. turnauensis*, although in their cladogram these two species are not sister-taxa.

Here, we describe the postcranial anatomy of *S. vallesiensis*, based on a well-documented sample from Batallones. The objective of our study is first to address the generic affinities of the two species of *Styriofelis*: do their postcrania provide an additional support of their close generic relationships? At a wider scale, we also want to address the systematic relationships and postcranial functional anatomy of the small- to medium-sized felines of the middle and late Miocene of Europe mentioned above: *Miopanthera lorteti*, *Styriofelis turnauensis*, *Styriofelis vallesiensis*, and *Pristifelis attica*. We posit that their postcranial anatomy presents marked differences that, in addition to their particular cranio-dental features, supports both their taxonomic distinction and different adaptations and ecology. Thus, in the Systematic Palaeontology section we provide with a proper discussion on this issue, and the proposal of the new genus *Leptofelis* for the species *S. vallesiensis*. In consequence, we will refer throughout the text to the species from Batallones-1 with the new name of *Leptofelis vallesiensis*.

Material and methods

The studied postcranial fossils of *Leptofelis vallesiensis* come from the fossil site of Batallones-1, which is part of the Cerro de los Batallones paleontological complex, located in a low hill of around 700 m of elevation, 30 km south of the city of Madrid (Spain). Up to nine localities have been found since 1991 thanks to the exploitation of the hill as an opencast mine of sepiolite. The sites were formed through a geological process of piping, which consisted in the erosion of the sepiolite levels by water flowing along fractures, causing collapses and the development of karst-like (‘pseudokarst’) topography (Pozo et al. 2004; Calvo et al. 2013). These cavities acted as natural traps for the animals inhabiting the area, mostly carnivorous vertebrates that entered the holes attracted by the carcasses of other previously trapped animals (Antón and Morales 2000; Morales et al. 2000). One of them, Batallones-1, excavated during 1991-2008, has provided an amazing assemblage of Carnivorans, including the ailurid *Simocyon batalleri*, the amphicyonid *Magericyon anceps*, three species of mustelids, the primitive hyaenid *Protictitherium crassum*, the machairodont felids *Machairodus aphanistus* and *Promegantereon ogygia*, and two species of felines (Morales et al. 2000, 2004; Antón et al. 2004; Peigné et al. 2005, 2008; Salesa et al. 2005, 2006a, b, 2008, 2010a, b; Siliceo et al. 2015, 2017). In their revision of the late Miocene felines, Salesa et al. (2012a) proposed the new species *Styriofelis vallesiensis* for the smaller of these two species of Felinae, mainly based on the relative dental similarities of this species with the Middle Miocene *S. turnauensis*. *Leptofelis vallesiensis* is present in two localities of Batallones: Batallones-1 and Batallones-3, separated by no more than one hundred meters, and with their saber-toothed felids populations showing enough morphological differences to support also a temporal separation between them (Monescillo et al. 2014; Siliceo et al. 2014).

The fossils of *L. vallesiensis* described here are housed at the Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain). They were found during the excavation campaigns of 1991-2008 at the late Vallesian locality of Batallones-1 (Torrejón de Velasco, Spain), coordinated by J. Morales. The list of studied material is as follows: BAT-1’06 D4-64a, BAT-1’06 D4-64b and BAT-1’06 D4-64c, L7-L4; B-4968, right humerus; BAT-1’02 D6-58, left humerus; B-2074 (5), right radius; B/S-575, left radius; B-2074 (6), BAT-1’08 C8-24, and BAT-1’06 E5-50, right ulnae; BAT-1’03 D4-239, right Mc I; B-2849, left Mc I; BAT-1’03 D5-162, right Mc II; BAT-1’04 D4-184, right Mc III; BAT-1’03 E4-164, right Mc IV; BAT-1’04 E5-129, right Mc V; BAT-1’04 E5-212, left Mc V; BAT-1’06 D4-66a, left and right coxae; BAT-1’06 D4-66b, sacrum; BAT-1’06 D4-67a, right femur; BAT-1’06 D4-67b, left femur; BAT-1’06 D4-103, right tibia; BAT-1’06 D4-110, left tibia; BAT-1’04 D6-173, right talus; BAT-1’03 D6-300, left talus; BAT-1’04 D6-173 and BAT-1’06 F5-61, right calcanei; BAT-1’04 D6-62 and BAT-1’03 D6-301, left calcanei.

Nine species of small extant Felidae were used for anatomical comparisons: *Caracal caracal* (Schreber, 1776), *Felis silvestris* Schreber, 1775, *Felis lybica* Forster, 1780, *Leopardus wiedii* (Schinz, 1821), *Leopardus geoffroyi* (d’Orbigny and Gervais, 1844), *Leptailurus serval* (Schreber, 1776), *Lynx pardinus* (Temminck, 1827), *Lynx lynx* (Linnaeus, 1758), and *Lynx rufus* (Schreber, 1777). We also used specimens from other families of Carnivora: the viverrids *Genetta genetta* Linnaeus, 1758, and *Civettictis civetta* (Schreber, 1776), and the mustelid *Martes martes* (Linnaeus, 1758). All this material belongs to the collections of the Museo Anatómico, Facultad de Medicina, Universidad de Valladolid (Spain), and the Comparative Anatomy Collections of the Museo Nacional de Ciencias Naturales-CSIC. We also compared the fossils of *Leptofelis vallesiensis* from Batallones-1 with the sample of *Miopanthera lorteti* (Blainville, 1842) from the classical fossil site of Sansan (MN 6, France), belonging to the collections of the Muséum national d’Histoire naturelle (Paris, France); comparisons were also made with published material of *Styriofelis turnauensis* (Gaillard 1899; de Beaumont 1961) and *M. lorteti* (Ginsburg and Antunes 1995; Salesa et al. 2011) and the late Miocene feline *Pristifelis attica* (Roussiakis 2002). The anatomical descriptions follow the terminology used by Barone (2010), Evans (1993), Julik et al. (2012) and the Nomina Anatomica Veterinaria (2012). The measurements were taken with digital calipers, and are shown in Fig. 1 and Tables 1–2.

Abbreviations

Institutional abbreviations: AMPG PA, Athens Museum of Palaeontology and Geology, National and Kapodistrian University of Athens; MAN, Museo Anatómico de la Universidad de Valladolid; MNCN, Museo Nacional de Ciencias Naturales-CSIC; L. Gr. and LGR, La Grive-Saint-Alban, Muséum d'Histoire Naturelle de Lyon; SNSB BSPG, Staatliche Naturwissenschaftliche Sammlungen Bayerns - Bayerischen Staatssammlung für Paläontologie und Geologie.

Anatomical and measurement abbreviations: ah, articular proximodistal height; aw, articular mediolateral width; dw, distal mediolateral width; Mc, metacarpal; Mt, metatarsal; oh, olecranon proximodistal height; pl, proximal craniocaudal length; pw, proximal mediolateral width; tl, total proximodistal length.

Use of cladistic terminology

Unfortunately, and due to the scarcity of postcranial fossils of Miocene felines, no cladistic analysis could be performed in the present study. Nevertheless, the discussed characters are polarized by outgroup comparisons to non-felid Feliformia or Caniformia on one end, and crown-group felids on the other. Given this, and in absence of a proper cladistic analysis, we cannot rule out the possibility that apparently plesiomorphic features are actually reversals, and that features that appear to be derived are convergences with crown taxa (instead of shared derived characters). Only a future cladistic analysis could elucidate these issues, but we have considered of interest to use the terms "primitive" and "derived" in the context of our discussion on functional adaptations.

Data availability Statement

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

Anatomical descriptions and comparisons

In general, the postcranial bones of *L. vallesiensis* from Batallones-1 show a good state of preservation, and practically, all their anatomical structures can be observed. In this section, we describe the most remarkable features of this material.

Lumbar vertebrae

Four articulated lumbar vertebrae of *L. vallesiensis*, the cranial one just preserving its caudal half, are known from Batallones-1 (Fig. 2). The most caudal of these vertebrae has a craniocaudally shorter body and wider caudal articulation processes than the others, which identifies it as the seventh lumbar vertebra, and so the rest are the sixth, the fifth, and a caudal fragment of the fourth lumbar vertebrae (formally, L7-L4). Comparing this lumbar series with those of the comparative sample of extant felines, the L7 of *L. vallesiensis* is relatively shorter than those of the other species, especially those of *F. silvestris*, *F. lybica* and *Lp. geoffroyi*, whereas the L7 of *Le. serval*, *C. caracal*, *Ly. lynx*, *Ly. pardinus*, and *Ly. rufus* are only slightly craniocaudally longer than that of *L. vallesiensis*. The costal processes are severely broken in all the specimens, but the preserved portions show that they were flat and cranially curved. The spinous processes were developed from the cranial to the caudal border of the dorsal surface, and at least in the sixth and fifth vertebrae were triangular (in the seventh lumbar just the base is preserved), although their tips are broken

(Fig. 2a). Both the cranial and caudal articular processes are elliptical and dorsocranially or dorsocaudally oriented, respectively; they show this same morphology and orientation in the rest of the compared species. In the ventral surface of the body, a shallow central ridge is observed in all the compared felines (Fig. 2b).

Humerus

The overall morphology of the humerus of *L. vallesiensis* is similar to that of other small-sized felines. The diaphysis is quite straight in cranial view, whereas in lateral view it is gently craniocaudally curved (Fig. 3). Among the compared felines, only *Le. serval* shows a slightly straighter diaphysis. In proximal view, the proximal epiphysis of *L. vallesiensis* shows an elliptic articular head, slightly laterally flattened, with a smooth greater tubercle developed along the craniolateral margin, and a craniomedially projected lesser tubercle on the medial margin. The greater tubercle of *Lp. geoffroyi* is less cranially expanded onto the articular head than those of *L. vallesiensis* and the other extant compared felines. Also, the articular head is rounded (not elliptic) in *Lp. wiedii*, *C. caracal, Ly. lynx*, *Ly. pardinus,* and *Ly. rufus*. The intertubercular groove of *L. vallesiensis* is well developed and relatively wide, very similar to that of the compared felines.

In medial view, the greater tubercle of *L. vallesiensis*, as well as those of *F. silvestris*, *Le. serval*, *Ly. lynx*, *Ly. pardinus,* and *Ly. rufus* is more proximally projected than those of *Lp. wiedii* and *Lp. geoffroyi*, clearly surpassing the level of the articular head. A right humerus of *S. turnauensis* from La Grive-Saint-Alban illustrated by Galliard (1899), with the catalogue number L. Gr. 1216 shows a reduced greater tubercle, similar to those of *Lp. wiedii* and *Lp. geoffroyi*. In cranial view, the lesser tubercle of *L. vallesiensis* is medially projected (Fig. 3a), with an almost vertical medial border, and a small, round proximal tuberosity that is part of the attachment area of the m. subscapularis, located on the medial surface of the lesser tubercle. *Leopardus wiedii*, *Lp. geoffroyi*, *F. silvestris*, *Le. serval*, *Ly. lynx*, *Ly. pardinus*, and *Ly. rufus* show this pattern, although the lesser tubercle is much more medially projected than in *L. vallesiensis*. Just distally to the lesser tubercle, there is a short crest that barely extends distally onto the diaphysis, similarly developed in all the compared species. The attachment area for the m. subscapularis, which occupies the cranial margin of the lesser tubercle, is much more distally elongated in *L. vallesiensis*, *F. silvestris*, *Le. serval*, *Ly. lynx*, *Ly. pardinus*, and *Ly. rufus* than in *Lp. wiedii*, whereas *Lp. geoffroyi* shows an intermediate pattern. In cranial view, two different orientations of the proximal margin of the greater tubercle can be clearly observed: in *L. vallesiensis*, *F. silvestris*, *Le. serval*, *Ly. lynx*, *Ly. pardinus*, and *Ly. rufus*, this margin is more cranially inclined than those of *Lp. wiedii* and *Lp. geoffroyi*, probably due to the lesser development of the greater tubercle. From the illustration by Gaillard (1899), the primitive *S. turnauensis* shows a close morphology to that of these latter South American felines. The crest of the greater tubercle of *L. vallesiensis* is very gentle, and it extends along the cranial border of the humerus until the middle part of the diaphysis, where a very smooth deltoid tuberosity is developed; this morphology is also observed in *F. silvestris*, *Lp. wiedii*, *Lp. geoffroyi*, *C. caracal*, and *Le. serval*, whereas in *Ly. lynx*, *Ly. pardinus*, and *Ly. rufus* the crest is much more marked, even ridged. This crest is the attachment area for the mm. pectorales (superficialis and profundus) and m. deltoideus, this latter attaching on the deltoid tuberosity (Davis 1964; Evans 1993; Barone 2010; Ercoli et al. 2015).

On the middle of the lateral surface of the greater tubercle of *L. vallesiensis*, there is a marked elliptical scar for the attachment of the m. infraspinatus (Fig. 3b); it has ridged margins, and it is oriented with its proximal border slightly inclined caudally, as in *F. silvestris* and *Le. serval*, and also as in *S. turnauensis*; on the contrary, in *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *Lp. wiedii*, and *Lp. geoffroyi*, the scar is almost rounded and sub-parallel to the diaphysis, although in the two *Leopardus* species, the scar is relatively smaller than those of the other compared felines. In all the compared taxa, the articular head is projected caudally, and the neck is marked, clearly distinguished from the head. The tricipital line of *L. vallesiensis* (for the attachment of the lateral branch of the m. triceps brachii) is marked, slightly ridged, and it develops from the attachment area for the m. infraspinatus, to the distal tip of the deltoid tuberosity. In the compared sample, the line is only absent in *Lp. wiedii*, being especially marked in *Le. serval* and *Ly. pardinus*. In *L. vallesiensis*, just distal to the attachment area for the m. infraspinatus, and on the proximal end of the tricipital line, there is a rough and irregular scar for the attachment of the m. teres minor, similarly marked in *F. silvestris* and *Lp. wiedii*, less evident in *Lp. geoffroyi*, and much more developed, even showing a strong ridge, in *Le. serval*, *Ly. lynx*, *Ly. pardinus*, and *Ly. rufus*. Caudal to this attachment area, *L. vallesiensis* shows a strongly excavated groove for the accessory branch of the m. triceps brachii; this area is shallower in *F. silvestris*, *Lp. wiedii*, and *Lp. geoffroyi*, whereas in *Le. serval*, *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, and *S. turnauensis*, it is more excavated, with a proximal strongly ridged border.

In the distal epiphysis, the medial epicondyle of *L. vallesiensis*, *Le. serval*, and *Ly. lynx* is moderately medially expanded (Fig. 3a), whereas those of *F. silvestris*, *Lp. wiedii*, *Lp. geoffroyi*, *C. caracal*, *Ly. pardinus*, and *Ly. rufus* are much more projected. The fossil species *S. turnauensis* and *M. lorteti* show well-developed medial epicondyles too, much more projected than that of *L. vallesiensis*, as shown by the specimen L. Gr. 1216 (Gaillard 1899) and an almost complete humerus of the larger *M. lorteti* from the Portuguese site of

Quinta das Flamengas (Ginsburg and Antunes 1995); finally, a distal fragment of a left humerus of the Turolian species *Pristifelis attica* (AMPG PA 2803/91) published by Roussiakis (2002) shows a medial epicondyle very similarly developed as that of *L. vallesiensis*. On the other hand, the lateral epicondyle, which shows less projection than the medial one, is clearly less expanded in *L. vallesiensis* than in any of the compared species, which are quite similar in the development of this structure (including *S. turnauensis*, *M. lorteti*, and *P. attica*). There is a well-developed supracondylar foramen in all the compared species, including *L. vallesiensis* and *P. attica*. In cranial view, the trochlea is strongly distally projected in all the species, although less in *Lp. wiedii* and *Lp. geoffroyi*. In medial view, the cranial margin of the trochlea is craniodistally oriented in all the species, but more projected in *Ly. lynx* and *Ly. rufus* than in *L. vallesiensis*, *Lp. wiedii*, *Lp. geoffroyi*, *Le. serval*, *Ly. pardinus*, and *C. caracal*. In *L. vallesiensis*, *Lp. geoffroyi*, and *Le. serval*, the scar for the attachment of the m. pronator teres, located on the distal end of the supracondylar bar, is relatively smaller than those of *F. silvestris*, *Lp. wiedii*, *C. caracal*, *Ly. pardinus*, *Ly. rufus*, and *Ly. lynx*, mainly because in all these latter species it is proximally extended, significantly increasing the attachment surface of this muscle. Just distal to the attachment area for the m. pronator teres there is a similarly sized surface for the attachment of the m. flexor carpi radialis; this surface is relatively larger in *Lp. wiedii* than in the rest of the compared species, including *L. vallesiensis*. In the caudal face of the distal epiphysis, the olecranon fossa of *L. vallesiensis* is deep, with a ridged lateral border, as observed in the rest of the compared taxa. This olecranon fossa is relatively wider in *F. silvestris*, *Ly. rufus*, *Lp. wiedii*, and *Lp. geoffroyi* than in *L. vallesiensis*, *Ly. lynx*, *Ly. pardinus*, *C. caracal*, and *Le. serval*, mostly because the medial margin of the olecranon fossa is much more vertical in the latter group, whereas in the former, it opens distally.

Also in caudal view, *L. vallesiensis* shows a relatively mediolaterally narrower distal epiphysis than those of the compared felines. The caudal surface of the medial epicondyle shows a small round attachment surface for the medial branch of the m. triceps brachii, very similarly developed in all the compared species except in *Ly. lynx*, in which it is very smooth, almost unnoticeable. In the distal tip of the medial epicondyle there are a couple of elliptical and rough attachment surfaces for the m. flexor carpi radialis and m. palmaris longus, which do not show remarkable differences among the studied sample. In the caudal surface of the lateral epicondyle of *L. vallesiensis* there is an excavated groove for the articular capsule, especially marked in *Le. serval*, *Ly. lynx*, *Ly. pardinus*, and *Ly. rufus*. The lateral supracondylar crest of *L. vallesiensis* is slightly ridged, mostly in its distal portion, although it continues proximally to the middle of the diaphysis as a smooth but marked crest; this pattern is observed in *F. silvestris*, *Lp. wiedii*, and *Lp. geoffroyi*, and in the fossil species *S. turnauensis* and *P. attica*, whereas in *Ly. pardinus*, *Ly. rufus*, *C. caracal*, and, especially in *Le. serval*, the crest is expanded forming a bony wall; on the other hand, in *Ly. lynx* the crest, although present does not project from the bone surface, and it is formed more as a cord rather than as a real crest. On the caudal surface of the crest there is a flat and smooth surface for the attachment of the m. anconeus; the size of this surface is related to the different development of the lateral supracondylar crest, and thus it is relatively larger in *Ly. pardinus*, *Ly. rufus*, *C. caracal*, and, especially in *Le. serval*.

Radius

The radius of *L. vallesiensis* is slender, with a straight and strongly craniocaudally flattened diaphysis (Fig. 3c, d). The proximal epiphysis is slightly medially inclined; its proximal articulation facet is concave and elliptical, with a marked notch in the middle of its cranial margin forming a clear capitular eminence; the lateral margin of this facet is ridged, whereas the medial one is inclined distally, developing a smooth and slightly concave surface. This pattern is similar in all the compared species, although in *Le. serval* and *F. lybica* both the cranial notch and capitular eminence are absent, they being less developed in *C. caracal*, *Ly. rufus*, and *Ly. lynx*. The proximal epiphysis is inclined medially in all the compared species, with the medial border markedly medially projected, whereas the lateral one does not stand out from the diaphysis border. The radial tuberosity of *L. vallesiensis* is proximodistally elongated (Fig. 3d), located on the lateral border of the caudal face, and it shows a slightly ridged lateral margin; its development is similar in all the compared species. The diaphysis of *L. vallesiensis*, as that of the other compared species, is craniocaudally flattened, elongated and quite straight, showing few muscular scars on the cranial and caudal faces.

The distal epiphysis of *L. vallesiensis* shows a slightly convex cranial face, developed as a continuation of the diaphysis, and a concave caudal face, separated from the diaphysis by means of a marked ridge; this pattern is also observed in the compared sample of felines. The medial border of the distal epiphysis of *L. vallesiensis* is distally projected in a moderate styloid process, very similarly developed in the rest of the studied species. In *L. vallesiensis*, the lateral facet for articulation with the ulna is elliptical and located in the craniodistal border of this lateral face; the compared felines show this morphology, although in *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *C. caracal*, and *Le. serval*, the facet is laterally projected; also, in the last species, the facet is not elliptical, but round. In *L. vallesiensis*, the medial border of this distal epiphysis has a ridge, as a continuation of the medial margin of the radius, for the attachment of the m. brachioradialis; this ridge is slightly more medially projected in *F. silvestris*, *F. lybica*, and *Lp. geoffroyi*, and much more projected in *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *C. caracal*, and *Le. serval*. The cranial face of the distal epiphysis of *L. vallesiensis* shows a couple of bony ridges, proximodistally oriented, developed for separating the passages of the tendons of several extensor muscles: a central, proximodistally shorter but thicker ridge separates a medial groove for the tendon of the m. extensor carpi radialis from a lateral one for the tendon of the m. extensor digitorum communis, whereas a lateral ridge separates this latter tendon from that of the m. extensor digitorum lateralis, placed into a groove located on the lateral border of the distal epiphysis (Evans 1993; Vollmerhaus and Roos 2001; Barone 2010). The development of these bony ridges shows differences within the studied feline sample: in *F. lybica* and *Le. serval*, the lateral ridge is markedly displaced medially in relation to its position in *L. vallesiensis*, *F. silvestris*, *Ly. lynx*, *Ly. rufus*, *Ly. pardinus*, *C. caracal*, and *Lp. geoffroyi*. The distal articular facet of *L. vallesiensis* is well developed, but it does not occupy the whole distal surface of the epiphysis; it is strongly concave, sub-elliptical, with a marked ridge on its craniolateral margin. This pattern is common to the other felines, although it is remarkable that in *Le. serval* and *F. lybica*, the lateral border of the facet is expanded in both lateral and caudal directions, thus producing an overall slightly larger articular surface for the scapholunar than in the rest of the species.

Ulna

The ulna of *L. vallesiensis* is slender, very similar to that of other felines. The diaphysis shows a gentle caudal convex curvature in its distal half, and it is markedly mediolaterally flattened (Fig. 3e, f). The olecranon of *L. vallesiensis* is well developed, similarly elongated as those of the compared felines; its proximal border, in both lateral and medial views, is clearly caudally inclined, as in *F. silvestris*, *F. lybica*, *Lp. wiedii*, and *Lp. geoffroyi*, whereas in *Ly. lynx*, *Ly. rufus*, *Ly. pardinus*, *C. caracal*, and *Le. serval*, the proximal border of the olecranon is almost horizontal due to the greater proximal projection of its caudal border. The length of the olecranon is similar in all the compared species, although in *Ly. lynx*, *Le. serval*, and *C. caracal*, it is slightly shorter. The olecranon has a pair of proximal tubercles, lateral and medial, that correspond to the attachment areas for two muscles involved in the extension of the forearm: the m. anconeus, which attaches on the lateral tubercle, expanding its attachment surface onto the caudal border of the lateral face of the proximal epiphysis, and the medial branch (caput mediale) of the m. triceps brachii, which attaches on the medial tubercle (Gonyea 1978; Barone 2010; Julik et al. 2012). In *L. vallesiensis, F. silvestris*, *F. lybica*, and *Le. serval*, the medial tubercle is well developed, markedly projected proximally, and surpassing the level of the lateral tubercle. *Lynx pardinus* shows the opposite morphology, with the lateral tubercle much more proximally projected than the medial one, whereas in *Ly. lynx*, *Ly. rufus*, *C. caracal*, *Lp. wiedii*, and *Lp. geoffroyi* both tubercles show a similar proximal projection. In cranial view, the tubercles of *L. vallesiensis*, *F. lybica*, *Lp. wiedii*, *Lp. geoffroyi*, *Le. serval*, *Ly. rufus*, and *Ly. pardinus* are separated by means of a shallow groove, whereas in *F. silvestris*, *Ly. lynx*, and *C. caracal* this groove has a similar width, but it is much deeper.

On the lateral surface of the proximal epiphysis of *L. vallesiensis*, originated from the level of the middle point of the trochlear notch, there is a proximodistally elongated triangular groove for the attachment of the m. extensor digiti I et II (Fig. 3e); the groove continues distally onto the diaphysis by means of a caudal ridge until the distal epiphysis, thus forming an attachment surface for the m. abductor digiti I longus (=m. extensor carpi obliquus) (Barone 2010; Julik et al. 2012); the most proximal portion of this groove is also well marked in *F. lybica*, *F. silvestris*, and *Le. serval*, and much less excavated in *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *C. caracal*, *Lp. wiedii*, and *Lp. geoffroyi*, probably indicating a more powerful m. extensor digiti I et II in the former group. On the medial surface of the proximal epiphysis, close to the beginning of the diaphysis there is a proximodistally elongated scar for the common attachment of the m. brachialis and m. cleidobrachialis, very similarly developed in all the compared species. On the medial surface of the diaphysis there is a caudal proximodistally elongated groove for the attachment of the ulnar branch of the m. flexor digitorum profundus (Fig. 3f); also, in the distal half of the diaphysis, a marked ridge is developed, forming a cranially oriented surface for the attachment of the m. pronator quadratus; this structure does not show differences among the compared felines.

The distal epiphysis of *L. vallesiensis* shows the basic feline morphology: that is mediolaterally flattened with a distocaudally oriented styloid process.

Metacarpal I

The Mc I of *L. vallesiensis* shows similar proportions as in *F. silvestris* and *F. lybica*, which have slenderer Mc I than *Le. serval*, *Lp. wiedii*, *Lp. geoffroyi*, *Ly. lynx*, *Ly. rufus*, and *Ly. pardinus.* A marked, dorsopalmarly developed ridge (Fig. 4a) divides the base into a smooth and dorsally expanded articular surface for the trapezium, and a medial tuberosity for the attachment of the m. abductor digiti I longus and one of the dorsal carpometacarpal ligaments (Fig. 4b). In proximal view, both parts show a similar width in all the compared species. The body is straight and more or less cylindrical in *L. vallesiensis*, *F. silvestris*, and *F. lybica*, and relatively shorter and slightly dorsopalmarly flattened in *Le. serval*, *Lp.*

wiedii, *Lp. geoffroyi*, *Ly. lynx*, *Ly. rufus*, and *Ly. pardinus*. The head is markedly asymmetrical, as the lateral border is much more distally projected than the medial one; on its palmar surface, there is a sharp keel, palmarly projected and similarly developed in all the compared species.

Metacarpal II

The Mc II of *L. vallesiensis* shows similar proportions than those of *Lp. wiedii*, *Lp. geoffroyi*, *C. caracal*, *Ly. lynx*, *Ly. rufus*, and *Ly. pardinus*, whereas *F. silvestris*, *F. lybica*, and *Le. serval* have slenderer Mc II. The overall morphology of this bone is very similar in *L. vallesiensis* and the compared felines. The proximal articular surface has a trapezoid shape, with its dorsal border mediolaterally wider than the palmar one. In dorsal view, the base is clearly laterally inclined, and it shows a groove for the passage of the radial artery. In lateral view (Fig. 4c), the palmar tubercle is large and projected; the groove for articulation with the medial face of the Mc III is proximodorsally located and well excavated. In medial view (Fig. 4d), the round facet for articulation with the trapezium barely surpasses the level of the proximal border in *L. vallesiensis*, *F. lybica*, and *F. silvestris*, whereas in *Lp. wiedii*, *Lp. geoffroyi*, *C. caracal*, *Le. serval*, *Ly. lynx*, *Ly. rufus*, and *Ly. pardinus* the facet is more proximally projected, widely surpassing the level of the proximal border. Distal to this facet, there is a rough tubercle for the attachment of the short interosseous ligament that connects Mc I and Mc II, similarly developed in *L. vallesiensis* and all the compared species. In the palmar border of the base there is a small but distinct scar for the attachment of the m. flexor carpi radialis, slightly more distally extended in *F. silvestris*, *F. lybica*, *Le. serval*, *Ly. lynx*, *Ly. rufus*, *Lp. wiedii*, and *Lp. geoffroyi* than in *L.*

vallesiensis, *Ly. pardinus*, and *C. caracal*. The body is slightly curved in lateral and medial view in all the species, with *Ly. lynx* and *Ly. pardinus* showing the straightest ones. The distal head of *L. vallesiensis*, *Lp. geoffroyi*, *C. caracal*, and *Ly. pardinus* has a well-developed proximopalmarly projected central keel, whereas in *F. silvestris*, *F. lybica*, *Le. serval*, *Ly. lynx*, and *Ly. rufus*, this structure is clearly reduced. Also, the head is relatively smaller in *F. lybica*, *F. silvestris*, and *Le. serval* than in *L. vallesiensis* and the rest of compared species.

Metacarpal III

The Mc III of *L. vallesiensis* shows similar proportions as in *F. silvestris*, *F. lybica*, *C. caracal*, *Ly. rufus*, and *Ly. pardinus*; in this group, the Mc III shows indeed an intermediate robustness between that of the slenderer *Ly. lynx* and *Le. serval* (which show the most gracile Mc III) and that of the more robust *Lp. wiedii* and *Lp. geoffroyi*. In all the compared species, the proximal articular surface is triangular, with a marked notch on its medial border; in dorsal view, the base is clearly laterally inclined. The lateral face of the base shows the articulation surfaces for the Mc IV (Fig. 4e): a large dorsally located groove and a dorsopalmarly elongated facet, located proximally to the former. This facet shows several differences within the compared sample of felines: although it occupies the whole dorsopalmar margin in all the species, in *L. vallesiensis*, *Ly. lynx*, and *Le. serval* it clearly lacks the distal expansion of its palmar end observed in *F. silvestris*, *F. lybica*, *C. caracal*, *Ly. rufus*, *Ly. pardinus*, *Lp. wiedii*, and *Lp. geoffroyi*; all these taxa show a central constriction in the facet, more marked in *F. silvestris*, and absent in *L. vallesiensis*, *Ly. lynx*, and *Le. serval*. The medial face of the base (Fig. 4f) shows two articular facets for the Mc

II, one dorsally and another one palmarly located, widely separated by a rough fossa. These facets show subtle differences within the sample: in *Lp. wiedii*, *Lp. geoffroyi*, *Ly. pardinus*, and *Ly. rufus* the dorsal facet is relatively larger than those of *L. vallesiensis*, *F. silvestris*, *F. lybica*, *C. caracal*, *Le. serval*, and *Ly. lynx*, whereas the palmar facet shows less size differences. Finally, the head is relatively larger in *Lp. wiedii* and *Lp. geoffroyi* than in *L. vallesiensis* and the rest of the compared species.

Metacarpal IV

As in the case of the Mc III, the Mc IV of *L. vallesiensis* shows similar proportions as those of *F. silvestris*, *F. lybica*, *C. caracal*, *Ly. rufus*, and *Ly. pardinus*, which are more robust than those of *Ly. lynx* and *Le. serval*. *Leopardus wiedii* and *Lp. geoffroyi* show a much more robust Mc IV than the rest of the compared sample. All the compared species show a rectangular proximal articular surface, with a medially projected facet for the Mc III; in dorsal view, the proximal border of the base is laterally inclined. The lateral face of the base (Fig. 4g) is occupied by the articulation surfaces for the Mc V: a large and deep central groove and a curved and elongated facet developed along the dorsal, proximal, and palmar margins. Except for its shorter dorsopalmar length in *Le. serval* and *Ly. lynx*, the morphology of this face is very similar in all the compared species. The medial face of the base (Fig. 4h) shows two articular facets for the Mc III, both located near the proximal border, one dorsally and the other one palmarly located, and widely separated by a smooth fossa. Whereas the dorsal facet has a similar development in all the taxa, the palmar facet of *L. vallesiensis* is much less proximodistally expanded, having the shape of a narrow cord, very different from the round to triangle facet seen in the rest of the compared felines.

Finally, the head is relatively larger again in *Lp. wiedii* and *Lp. geoffroyi* than in *L. vallesiensis* and the rest of compared species.

Metacarpal V

The Mc V of *L. vallesiensis* shows similar proportions to those of *F. silvestris*, *F. lybica*, *C. caracal*, *Ly. lynx*, *Ly. rufus*, and *Ly. pardinus*. Once again, the Mc V of *Le. serval* is the most gracile of the sample, whereas those of *Lp. wiedii* and *Lp. geoffroyi* are relatively much shorter and stouter, with the latter being remarkably robust. In proximal view, the Mc V of *L. vallesiensis* shows a semicircular proximal articulation surface that is divided in two parts by means of a marked dorsopalmarly developed groove; this morphology is more or less similar in all the compared species. On the lateral face of the base (Fig. 4i) there is an elliptical attachment surface for the m. extensor carpi ulnaris, dorsopalmarly elongated in *L. vallesiensis* and *Le. serval*, and round and more distally expanded in *F. silvestris*, *F. lybica*, *Ly. lynx*, *Ly. rufus*, *Ly. pardinus*, *C. caracal*, *Lp. wiedii*, and *Lp. geoffroyi*. The medial face of the base (Fig. 4j) shows a central medially expanded and proximodistally elongated bony sheet, surrounded by a smooth facet occupying the proximal and dorsal margins. The head is relatively larger again in *Lp. wiedii* and *Lp. geoffroyi* than in *L. vallesiensis* and the rest of compared species.

Os Coxae

The Batallones-1 sample includes the complete right and left os coxae of a single individual of *L. vallesiensis* (Fig. 5). Their general shape and morphology are very similar to those of the compared felines. The acetabular fossa is rounded and located close to the cranial margin of the obturator foramen. The wing of the ilium of *L. vallesiensis* is slender, craniocaudally elongated, with more or less parallel dorsal and ventral margins and a gently curved cranial border (crest of the ilium). The gluteal fossa is shallow but evident, with a thickened dorsal margin. In *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *F. lybica*, *F. silvestris*, *Lp. wiedii*, and *Lp. geoffroyi*, the body of ilium shows a central constriction due to the ventral projection of the tuber coxae and the marked expansion of the tuber sacrale, whereas in *L. vallesiensis*, *C. caracal*, and *Le. serval*, the corpus of the ilium does not show any constriction. In the cranioventral margin of the wing of *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *F. lybica*, *Le. serval*, and *C. caracal* there is a triangular surface, with ridged margins, for the attachment of the m. sartorius; this surface is very reduced in *L. vallesiensis*, *F. silvestris*, *Lp. wiedii*, and *Lp. geoffroyi*. The ischiatic spine of *L. vallesiensis*, *Le. serval*, and *C. caracal* is located slightly more caudally than in *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *F. lybica*, *F. silvestris*, *Lp. wiedii*, and *Lp. geoffroyi*. In dorsal view, the orientation of the wings of *L. vallesiensis* is very similar to that of the compared species, slightly laterally curved but keeping the dorsoventral plane. In this dorsal view, the acetabular fossa is slightly more laterally projected than in *Le. serval*, *C. caracal*, *F. lybica*, *F. silvestris*, *Lp. wiedii*, and *Lp. geoffroyi*, and similar to that of *Ly. lynx*, *Ly. rufus*, and *Ly. pardinus*. The caudal half of BAT-1’06 D4-66a is damaged, and the actual shape of the obturator foramen cannot be assessed, but it probably was similar to that of the compared species. The ischiatic tuberosity of *L. vallesiensis* and the compared species is rounded and rough, but the ischiatic arch shows some differences within the studied sample: in *L. vallesiensis*, *F. lybica*, *Lp. wiedii*, and *Lp. geoffroyi*, the caudal margin of the ischium is straight, and so the ischiatic arch is small, whereas in *F. silvestris*, *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *Le. serval* and *C. caracal* this margin describes a gentle curvature, producing a wide and larger arch.

Sacrum

A complete sacrum of *L. vallesiensis*, which was articulated to the left and right os coxae described above, is known from Batallones-1. It is composed, as that of other felids, of three fused sacral vertebrae. It is triangular in overall shape, with its maximum mediolateral width at its cranial margin. This morphology is very similar to that of the compared species, although *Ly. lynx, Ly. pardinus, Ly. rufus*, and *C. caracal* show a relatively more elongated sacrum. The available sacrum of *L. vallesiensis* is almost complete, but it lacks the dorsal spines, which only preserve their lower parts, making it impossible to assess their actual development. An intermediate sacral crest, mediolaterally flattened, is preserved in the right side: its cranial portion is cranially oriented, whereas the caudal one is smaller, lower, and vertical (Fig. 6a). This pattern is also observed in *F. silvestris*, *F. lybica*, and *Lp. geoffroyi*, whereas in *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *Le. serval*, and *C. caracal*, the caudal process is absent. In *L. vallesiensis*, the caudal portion of the lateral sacral crest (=transverse process of the last sacral vertebra) is developed as a long and caudally pointed sheet of bone, as in *F. silvestris* and *C. caracal*. In *F. lybica*, *Lp. geoffroyi*, *Ly. lynx, Ly. pardinus*, and *Ly. rufus*, these processes are shorter and less pointed, whereas in *Le. serval* they are extremely thin and slender. This caudal portion of the lateral crest in the Batallones feline shows a central keel, also present, in more or less extent, in the rest of the compared felines. The lateral sacral crest is also laterally projected at the level of the second sacral vertebra in *L. vallesiensis*, *C. caracal*, and *Le. serval*, it being thus much more developed than in *F.*

silvestris, *F. lybica*, *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, and *Lp. geoffroyi*. At least four dorsal sacral formamina are observed in all the compared extant felines, but they are absent in *S. vallesiensis*. On ventral view, the sacrum of *L. vallesiensis* shows four ventral sacral foramina (Fig. 6b), as the rest of the studied felines.

The wings of the sacrum of *L. vallesiensis* are very similar to those of the compared felines, that is, clearly ventrally projected, with a rough lateral surface. Dorsally, the wings contact with the cranial articular surfaces of the sacrum, the articulation area for the last lumbar vertebra. These two cranial articular surfaces are separated by a caudally expanded notch. In *L. vallesiensis*, *C. caracal*, and *Le. serval*, this notch is relatively wider and less caudally expanded than those of *F. silvestris*, *F. lybica*, *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, and *Lp. geofrroyi*.

Femur

The Batallones-1 sample includes two femora of *L. vallesiensis* belonging to the same individual. The femoral head is projected proximomedially by means of a well-developed neck and it is located at the same level of the greater trochanter (Fig. 7); only in *C. caracal* and *Lp. geoffroyi* does the head surpass the level of the greater trochanter. In lateral view, the femur of *L. vallesiensis* has a rough gluteal tuberosity with a strongly ridged cranial margin that contacts proximally with the greater trochanter (Fig. 7a); distal to the gluteal tuberosity, a less marked ridge continues distally on the lateral border, until the middle of the diaphysis. This pattern is seen in the rest of the studied species, and the only remarkable difference is the position of the gluteal tuberosity in *L. vallesiensis* and *Lp. wiedii*, located distal to the lesser trochanter, whereas in the other species it is clearly proximal to this structure. On the proximal tip of the greater trochanter, the attachment areas for the m. gluteus profundus and m. gluteus medius show a similar pattern in all the taxa, with the attachment area for the m. gluteus medius located proximal to that of the m. gluteus profundus, both being restricted to the proximal surface of the greater trochanter. In caudal view (Fig. 7b), the proximal epiphysis of *L. vallesiensis* shows a deep trochanteric fossa, a ridged and relatively short intertrochanteric crest, and a caudally projected lesser trochanter; in the Batallones feline, as well as in *F. lybica*, *Ly. lynx*, *Ly. pardinus*, *Ly. rufus* and *Lp. geoffroyi*, the lesser trochanter is located close to the medial margin, but laterally displaced in relation to its position in *F. silvestris*, *Le. serval*, *C. caracal*, and *Lp. wiedii*. This different position of the lesser trochanter is also related to the orientation of the attachment area for the m. iliopsoas, which is more or less caudally oriented in the former group of felines, and medially faced in the latter.

In the distal epiphysis of *L. vallesiensis*, the lateral condyle is mediolaterally wider than the medial one. In caudal view (Fig. 7b), the medial condyle is vertical, parallel to the proximodistal axis of the femur, whereas the lateral one is slightly laterally inclined, with its proximolateral vertex showing a proximolaterally oriented expansion. Although *F. silvestris*, *Lp. wiedii*, and *Lp. geoffroyi* show this pattern, in *Le. serval*, *F. lybica*, *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, and *C. caracal*, the medial condyle is slightly but clearly laterally inclined. Also, in *L. vallesiensis, F. silvestris*, *F. lybica*, *Lp. wiedii*, and *Lp. geoffroyi*, both condyles reach the same level distally, whereas in *Le. serval*, *Ly. lynx, Ly. rufus*, *Ly. pardinus*, and *C. caracal,* the medial condyle distally surpasses the level of the lateral one. In caudal view, the intercondyloid fossa of *L. vallesiensis* is well developed and shows a similar mediolateral width than those of the other compared felines. In distal view, all the compared taxa show a medial condyle slightly more caudally projected than the lateral one.

In lateral and medial views, both the craniocaudal length of the distal epiphysis, and the curvature of the femoral trochlea of *L. vallesiensis* are very similar to those of the other compared felines. The trochlea of *L. vallesiensis* is more proximally extended than those of any of the compared feline species (Fig. 7a), which indicates a greater range of patellar extension, as has been suggested for other carnivorans (Siliceo 2015).

Tibia

The two tibiae of *L. vallesiensis* from Batallones-1 are complete but strongly laterally compressed, thus preventing a clear assessment of some of their characters. It is slender in overall view, with a more or less straight diaphysis and a caudally curved proximal epiphysis (Fig. 7c–e). The proximal epiphysis of *L. vallesiensis* shows a triangular-shaped proximal surface, with the two articular condyles (medial and lateral) separated by a rough and narrow intercondyloid area. In cranial or caudal views, the lateral condyle in *L. vallesiensis* is located slightly more proximal than the medial one (Fig. 7c), mainly due to the ridged medial margin of the lateral condyle (the intercondyloid eminence); this pattern is observed in all the compared felines. In proximal view, the cranial border is strongly cranially projected, with a marked notch on its lateral margin for the passage of the tendon of the m. extensor digitorum longus (Fig. 7e). The medial condyle of *L. vallesiensis* is clearly less caudally projected than the lateral one, as in the rest of the compared felines. The tibial tuberosity has a smooth proximal surface separated by a ridge from the cranial border, which runs distally until the middle of the cranial margin of the diaphysis.

The diaphysis of *L. vallesisensis* and the compared felines is strongly mediolaterally flattened on its proximal half, whereas the distal half has a square section. Also, the proximal half is laterally inclined in cranial view and caudally in both lateral and medial views; the distal half is quite straight. The morphology of the diaphysis is similar in all the compared species, except for the development of a strong ridge, proximodistally developed, on the caudal face of the diaphysis of the tibia of *L. vallesiensis* (Fig. 7c) and *Lp. geoffroyi*. Interestingly, this ridge has been also observed by de Beaumont (1986) in the Asian golden cat (*Catopuma temminckii*) and the fossil feline *Pristifelis attica,* whereas it is absent in the tibia of *S. turnauensis* figured by de Beaumomt (1961) and that of *M. lorteti* figured by Salesa et al. (2011). Among the studied sample of carnivorans, it is absent in *Genetta genetta, Martes foina, Gulo, gulo, Meles meles, Ailurus fulgens,* and *Canis lupus*, and present in *Ursus americanus.* This ridge seems to have separated in life the m. flexor digitorum lateralis and m. flexor digitorum medialis + m. tibialis caudalis, whose tendons run together along the same groove (Barone 2010). These muscles originate on the proximal epiphysis of the tibia, and are very closely disposed on the caudal surface of the diaphysis (Fisher et al. 2008; Ercoli et al. 2012). Both muscles have strong and long distal tendons, but the relation between the fleshy part and the tendon varies among the Carnivora, with felids and canids having in general longer tendons (and then shorter fleshy parts) than ailurids, ursids, procyonids, or mustelids (Davis 1964; Feeny 1999; Vollmerhaus and Roos 2001; Fisher et al. 2008; Ercoli et al. 2012). Thus, the described ridge in the caudal face of the tibia of *L. vallesiensis* and *Lp. geoffroyi*, which in the former reaches the proximal border of the distal epiphysis, would be actually forming a groove for the accommodation of the tendons of both muscles, m. flexor digitorum medialis + m. tibialis caudalis on the medial side of the ridge, and m. flexor digitorum lateralis on its lateral side.

The distal epiphysis of *L. vallesiensis* strongly resembles that of the compared felines, with no feature showing significant differences.

Talus

The overall morphology and proportions of the talus of *L. vallesiensis* are quite similar to those of the compared felines. The trochlea is wide, with a shallow central groove that divides it into two asymmetrical lips (Fig. 8a), as the medial one is narrower than the lateral one; the distal border of the lateral lip projects distally surpassing the level of the medial one, which does not expand onto the neck. In proximal view, the lateral lip is more dorsally projected than the medial one in *L. vallesiensis* and all the compared felines. The proximal surface of the trochlea of *L. vallesiensis* shows a transversal shallow groove and a small, medially located talar foramen for the posterior tibial artery, as in *F. silvestris*, *F. lybica*, *Le. serval*, *Lp. wiedii*, *Ly. pardinus*, and *Ly. rufus*, whereas in *C. caracal*, *Lp. geoffroyi*, and *Ly. lynx* it is absent. In plantar view (Fig. 8b), a relatively narrow sulcus tali separates two large articular facets for the calcaneus: the lateral facet is rectangular and strongly concave, whereas the medial one is elliptical, convex, and occupies most of the plantar surface of the neck, joining the distal articular surface of the talus head by means of a narrow projection; this morphology is observed in most of the compared species, although in *F. silvestris*, *F. lybica*, *C. caracal*, and *Le. serval* the medial facet is not connected to the distal facet for the navicular. The neck of *L. vallesiensis* is as long as those of *F. silvestris*, *F. lybica*, *C. caracal*, *Le. serval*, *Lp. wiedii*, and *Lp. geoffroyi*, and longer than those of *Ly. lynx*, *Ly. pardinus*, and *Ly. rufus*. The head of the talus in all the species is well distinguished from the neck as it has a gently ridged dorsal margin; in distal view, the head is elliptical in *L.*

vallesiensis, with the lateral border being slightly orientated dorsally relative to the medial one; this orientation is more or less the same in the compared felines, although the head is round rather than elliptical in all the species.

Calcaneus

The calcaneus of *L. vallesiensis* and the compared feline species shows a very similar morphology and relative proportions. In dorsal view (Fig. 8c), the fibular tubercle (distolateral expansion for the attachment of the ligament calcaneofibular or collaterale tarsi laterale longum) shows little lateral projection, and is located close to the distolateral border; its morphology is very similar in all the compared species. The sustentaculum tali is well medially projected in all the compared species, showing a rounded medial talar facet that continues distally through a narrow and long talar facet until the distomedial border of the talar surface; this facet is almost dorsally oriented in *L. vallesiensis*, *Lp. wiedii*, *Lp. geoffroyii*, *F. silvestris*, and *F. lybica*, whereas in *C. caracal*, *Le. serval*, *Ly. lynx*, *Ly. rufus*, and *Ly. pardinus*, it is clearly dorsomedially oriented. The tuber calcanei is relatively slender and mediolaterally flattened in all the compared species. Also, the medial tubercle of the tuber is more proximally projected than the lateral one, although in *Le. serval* and *Ly. rufus* the difference is not so marked. In plantar view (Fig. 8e) the sustentaculum tali shows a similar medial projection in all the compared felines, although in *C. caracal* and *Le. serval*, this structure is slightly more proximally located; the groove for the tendon of the m. flexor digitorum lateralis is similarly marked in all the species. On the distal end of this plantar face, a scar for the ligament plantare longum is observed. In lateral view, the fibular tubercle of *L. vallesiensis* is located very close to the distal border of the lateral margin, it showing a marked oblique groove, also seen in *F. silvestris*, *F. lybica*, *C. caracal*, *Le. serval*, and *Ly. lynx*. Plantar to this tubercle, there is a shallow depression with fairly ridged plantar and dorsal margins for the attachment of the m. quadratus plantae (Fig. 8e); in *L. vallesiensis* and *Lp. geoffroyii*, this attachment area is proximally developed until the level of the coracoid process, whereas in *Lp. wiedii* and *F. silvestris*, it is even more proximally elongated, reaching the middle point of the tuber calcanei; on the contrary, the attachment surface is reduced in *F. lybica*, *C. caracal*, *Le. serval*, *Ly. lynx*, *Ly. rufus*, and *Ly. pardinus*, as it barely surpasses the level of the fibular tubercle. In proximal view, the tuber calcanei shows an elliptical shape, dorsoplantarly elongated, with the medial tubercle larger than the lateral one. In distal view, the articular facet for the cuboid is almost round in all the compared feline species.

Comparative anatomy and biomechanical implications

Lumbar vertebrae

Both the overall morphology and relative proportions of the L7-L5 of *L. vallesiensis* are very similar to those of the compared felines: in all of them the L7 is shorter than the rest of the lumbar vertebrae, with *F. silvestris, F. lybica*, and *Lp. geoffroyi* showing the relatively longest L7 (Fig. 9). In felids and other carnivorans, the extension and flexion movements of the lumbar region (and the vertebral column in general) are very important in galloping (Hildebrand 1959; Goslow et al. 1973; Gambaryan 1974; Taylor 1978; English 1980; Alexander and Jayes 1981). These movements of the column basically contribute to stride length and limb speed through the action of the epaxial and abdominal muscles (Hildebrand

1959; Goslow et al. 1973; English 1980). Thus, a great flexibility of the lumbar series in felines is necessary for increasing both stride length and limb speed, something critical in cursorial species such as *Acinonyx jubatus* (Hildebrand 1959; Gambaryan 1974). A relatively short L7 is typical of arboreal viverrids and mustelids, such as *G. genetta* or *Martes foina*, animals that do not move primarily on the ground, but the relative length of this vertebra in *A. jubatus* is very similar to that of these carnivorans, and slightly shorter than those of *F. silvestris, F. lybica*, and *Lp. geoffroyi*. In consequence, there are only subtle differences in the relative length of L7 among the compared sample of felines, and the significance of a relative short L7 in *L. vallesiensis* (Fig. 9), similar to those of viverrids (but also mustelids) should be considered as a primitive feature with no clear functional implications.

Humerus

The differences in the lateral width of the humeral head observed among our sample of felines have been previously described in other carnivorans; for example, Taylor (1974) already noticed it in his study on herpestids and viverrids, with the more terrestrial species having mediolaterally flattened heads and a relatively limited range of movement in the shoulder, both in the craniocaudal and mediolateral planes. Argot (2001), and Argot and Babot (2011) proposed that a similar lateral compression of the humeral head observed in Paleocene and Eocene marsupials suggested that movements of the glenohumeral articulation were restricted to flexion/extension, indicative of terrestrial habits. This would be the case of *L. vallesiensis*, which has a less rounded humeral head than other compared felines, a probable indication of a mostly terrestrial way of life. Other humeral structures have been revealed as good indicators of terrestrial versus arboreal habits in several groups of mammals, including the development of the greater tubercle (Jolly 1967; Taylor 1974; Fleagle and Simons 1982; Ciochon 1986; Larson and Stern 1989; Gebo and Rose 1993; Siliceo et al. 2015). All these authors concluded that the more arboreal species had less projected tubercles than those moving mainly on the ground. Focusing on the sample of Felinae studied here, *Lp. wiedii* and *Lp. geoffroyi* show greater tubercles that are less proximally projected than that of *L. vallesiensis* and those extant species with typically terrestrial lifestyles, such as the lynxes and the wildcat **(**Fig. 10**)**; this is interesting, as *Lp. wiedii* is one of the most arboreal felines, and although *Lp. geoffroyi* occupies a great diversity of habitats, it is often found in woodlands (Sunquist and Sunquist 2009). The greater tubercle is the attachment area for the m. supraspinatus, which originates on the supraspinous fossa of the scapula (Barone 2010; Julik et al. 2012), extending the humerus and rotating it laterally (Taylor 1974; Barone 2010; Ercoli et al. 2015). The proximal expansion of the greater tubercle produces the lengthening of the moment arm of the m. supraspinatus at the glenohumeral articulation (Jolly 1967; Larson and Stern 1989) and it has been interpreted in baboons as a way of achieving a more economical locomotion on the ground (Jolly 1967); on the contrary, a less projected greater tubercle produces a shorter lever arm for the m. supraspinatus, which favours fast (although weak) flexion of the humerus during arboreal locomotion (Jolly 1967; Larson and Stern 1989). It is remarkable that the middle Miocene feline *S. turnauensis* resembles *Lp. wiedii* and *Lp. geoffroyii* in this feature, suggesting an important arboreal component in its locomotor behavior. On the contrary, the development of the greater tubercle of the late Miocene *L. vallesiensis* indicates a primarily terrestrial locomotion, in a similar way to other extant felines. These different locomotor adaptations would reflect the climate changes at the beginning of the late Miocene in Europe, which produced the predominance of drier, less structured landscapes than those from the more humid middle Miocene (Agustí and Moyà-Solà 1990; Agustí et al. 1997; Fortelius and Hokkanen 2001; Hernández-Fernández et al. 2006).

Among the Carnivora, the medial epicondyle of the humerus is the attachment area for several pronator and flexor muscles of the forearm and carpus (Davis 1964; Barone 1967, 2010; Taylor 1974; Salesa et al. 2008; Fisher et al. 2009; Julik et al. 2012; Ercoli et al. 2015). The degree of medial projection of this humeral structure is an indicator of the development of these muscles in fossil carnivorans, and thus it has been used to infer several aspects of their paleoecology: those species with reduced medial epicondyles show smaller flexor muscles, and have slender limbs, are cursorial hunters, and use to live in open, low-structured habitats, whereas those with well-developed medial epicondyles have more robust proportions, hunt by ambush, and inhabit highly-structured environments, such as woodlands (Argot 2001, 2004; Salesa et al. 2008; Argot and Babot 2011). Thus, the smaller development of the medial epicondyle of *L. vallesiensis* (Fig. 11a) (similar to those of *Le. serval* and *Ly. lynx*) suggests that this feline was a capable runner, occupying the less structured, more open patches of the mixed landscape inferred for the Batallones sites (Antón and Morales 2000; Salesa et al. 2006a, 2008; Morales et al. 2008). The extant feline *F. silvestris*, a species of similar size and proportions as *L. vallesiensis*, occupies a great diversity of habitats, including grasslands and more or less dense woodlands (Nowak 2005; Sunquist and Sunquist 2009), but it has a more developed medial epicondyle than the Batallones feline and the Turolian *P. attica*. This implies that these two latter species had a more limited range of preferred habitats than *F. silvestris*, favoring more open habitats than their extant relative. On the contrary, the much more projected medial epicondyles of the middle Miocene species *S. turnauensis* and *M. lorteti* suggest their preference for the densely-wooded habitats that predominated during that time. Besides this, the presence of a strongly projected medial epicondyle of the humerus has been also associated in Felidae to the capture of relatively large prey (Meachen-Samuels and Van Valkenburgh 2009); following this interpretation, *L. vallesiensis* would take small prey, whereas the middle Miocene *S. turnauensis* and *M. lorteti* would prey upon relatively larger ones.

Other features observed in the humerus of *L. vallesiensis* also seem to be related to its running abilities, such as the mediolaterally narrower distal epiphysis (Fig. 12), and especially, the narrower olecranon fossa than those of *F. silvestris*, *Ly. rufus*, *Lp. wiedii*, and *Lp. geoffroyi*. This feature groups *L. vallesiensis* with taxa showing more cursorial postcranial skeletons, such as *Ly. lynx*, *Ly. pardinus*, *C. caracal*, and *Le. serval*, but also with the Turolian *P. attica*, whose narrow olecranon fossa was described by Roussiakis (2002). A narrower olecranon fossa prevents the lateral and medial torsion of the ulna in mainly terrestrial primates and carnivorans when moving on the ground (Gonyea 1978; Brundrett 2002; Argot and Babot 2011), hence the presence of this feature in the humerus of *S. vallesiensis* is an additional evidence supporting an efficient terrestrial locomotion in this species.

Radius

The radii of the compared sample of felines, included *L. vallesiensis*, are similar in proportions and morphology. In fact, the most remarkable difference, the absence of notch and capitular eminence on the proximal facet, is only shown by *Le. serval* and *F. lybica*, without a clear functional explanation. Davis (1964) suggested that the capitular eminence limits the rotatory mobility of the radius, but Gebo and Rose (1993) noticed its presence in arboreal carnivorans (such as the procyonid *Potos flavus*), suggesting that this structure could not be an impediment for the pronation-supination movements of the forearm when climbing. Nevertheless, Heinrich and Rose (1997) suggested that the capitular eminence might stabilize the radius when the elbow is flexed, and then its absence in terrestrial forms such as *Le. serval* and *F. lybica*, which tend to maintain extended limb articulations, would be more understandable.

The other difference observed within the studied sample of radii is the larger lateral and medial development of the distal facet for the scapholunar, again seen only in *Le. serval* and *F. lybica*. This mediolateral elongation of the facet produces a less rounded facet, and thus a restriction in the rotational movements of the scapholunar on the radius, and a predominance of the wrist flexion and extension actions. It is not surprising that the two species that show this morphology are mostly terrestrial animals that move fast on the ground, and it is not strange either that the primitive morphology, a more rounded facet, is observed in *L. vallesiensis*, most of the compared felines, and *G. genetta*.

Ulna

The caudal border of the olecranon (attachment area for the long branch of the m. triceps brachii) is clearly more inflated (proximally projected) in *Ly. lynx*, *Ly. rufus*, *Ly. pardinus*, *C. caracal*, and *Le. serval* than in *L. vallesiensis*, *F. silvestris*, *F. lybica*, *Lp. wiedii*, and *Lp. geoffroyi* (Fig. 13). In Viverridae, a greater development of this caudal vertex is indicative of a relatively larger long branch of the m. triceps brachii (Taylor 1974). Thus, in the lynxes and lynx-like felines, this muscle should be relatively larger than those of *L. vallesiensis*, *F. silvestris*, *F. lybica*, *Lp. wiedii*, and *Lp. geoffroyi*. Among extant felids, the cursorial species have relatively greater long branches of the m. triceps brachii than those species with more robust proportions, as shown by Gambaryan (1974). Nevertheless, although our observations seem to indicate a difference in the cursorial capacities of the analyzed felines, the group showing more inflated caudal part of the olecranon is composed by the largest taxa, and so the observed differences could be strongly influenced by allometry. Anyway, the larger size of the long branch of the m. triceps brachii in *Ly. lynx*, *Ly. rufus*, *Ly. pardinus*, *C. caracal*, and *Le. serval* is also suggested by the presence, in the cranial part of the olecranon, of a marked groove for the passage of the tendon of this muscle; this feature is typical of terrestrial viverrids, and is lacking in the most arboreal forms (Taylor 1974; Feeney 1999).

The degree of proximal projection of the olecranon tuberosities seems to be closely related to the development of the lateral and medial branches of the m. triceps brachii in fossil and extant Felidae (Gonyea 1978; Salesa et al. 2010a, 2011). In *L. vallesiensis*, *F. silvestris*, *F. lybica*, and *Le. serval* (Fig. 14a, d), the lateral tuberosity is much less proximally projected than the medial one, a morphology also observed in canids and the cursorial felid *Acinonyx jubatus* (Gonyea 1978); these two latter carnivorans have larger medial branches of the m. triceps brachii than those species with larger lateral tuberosities in the ulna (Gambaryan 1974; Gonyea 1978). Interestingly, the lateral tuberosity is more proximally projected than the medial one in those felids inhabiting woodland habitats, and they have significantly larger lateral branches of the m. triceps brachii than those felids that occupy low-structured, open landscapes (Gambaryan 1974; Gonyea 1978). Nevertheless, Gonyea (1978) also found that several species occupying both open and close environments (such as *C. caracal*, *Panthera leo*, *Ly. lynx*, or *Ly. rufus*) had olecranon tuberosities of similar size. All these observations made Gonyea (1978) suggest that the development of the tuberosities was actually an indicator of the degree of deviation of the anterior limb from the parasagittal plane during locomotion, with those felids having larger lateral tuberosities exhibiting the greatest parasagittal deviation of the elbow during locomotion, and those with larger medial tuberosities having little deviation of the forelimb from a 'pendulum-like' motion, and thus exhibiting high cursorial abilities, such as *A. jubatus* and large canids. *Felis silvestris*, *F. lybica* and *Le. serval* also belong to this latter group, and all have a mostly terrestrial way of life, climbing primarily as an escape mechanism (Sunquist and Sunquist 2009; Julik et al. 2012). Considering its olecranon morphology, *L. vallesiensis* would fit well within the group of mostly terrestrial and gracile felines, and probably its lifestyle was not very different from that of the small species of the genus *Felis*. The same morphology is observed in the middle Miocene, more primitive felines such as *M. lorteti* (Salesa et al. 2011). Nevertheless, this pattern might be the plesiomorphic for Felidae, as it is also present in the most primitive felid, *Proailurus lemanensis*, and the earliest members of the saber-toothed subfamily, *Pseudaelurus quadridentatus* and *Promegantereon ogygia* (Salesa et al. 2010a, 2011).

The attachment groove for the m. extensor digiti I et II is more excavated in *L. vallesiensis*, *F. lybica*, *F. silvestris*, and *Le. serval* than in the other species. This muscle extends the thumb and assists the m. extensor digitorum communis in extending the carpus and the digit II (Davis 1964; Barone 2010; Julik et al. 2012). The attachment surface is much shallower in *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *C. caracal*, *Lp. wiedii*, and *Lp. geoffroyi*, and also in large felids such as *Puma concolor*, *Panthera pardus*, or the cursorial *A. jubatus* This similar morphology in felids with differing locomotor adaptations prevents the proposal of any functional interpretation explaining the development of the muscle. In fact, an ulna of *M. lorteti* from Sansan illustrated by Salesa et al. (2011) shows a similar pattern to that of *L. vallesiensis*, and thus a marked groove for the m. extensor digiti I et II might be the primitive condition for the Felinae.

Metacarpal I

The Mc I of *L. vallesiensis*, *F. silvestris*, and *F. lybica* are slenderer than those of the smaller species *Lp. wiedii* and *Lp. geoffroyi*, the larger felines *Le. serval*, *Ly. lynx*, *Ly. rufus*, and *Ly. pardinus*, and the middle Miocene species *S. turnauensis* and *M. lorteti* (Peigné 2012; Salesa et al. 2012). The main function of the Mc I in Felidae is grasping when climbing and hunting, thanks to the abduction of the thumb from the second finger (Barone 1967; Gonyea and Ashworth 1975; Gonyea 1978; Akersten 1985; Taylor 1989; Anyonge 1996; Turner and Antón 1997; Julik et al. 2012). As a result of its slenderness, the thumb of *L. vallesiensis*, *F. silvestris*, and *F. lybica* would be able to withstand smaller forces than those of the rest of the compared felines, which has interesting implications for their climbing abilities and their ability to subdue prey. For example, if *L. vallesiensis* preyed upon smaller animals that those killed by its middle Miocene counterparts (as the morphology of its humerus suggests), it would not be necessary to have the robust Mc I observed in the latter species. The extant felines *F. silvestris* and *F. lybica* hunt mostly small prey (Smithers 1971; Kingdon 1977; Roberts 1977; Sharma 1979; Palmer and Fairall 1988; Sunquist and Sunquist 2009) using head shaking movements that kill them very fast (Leyhausen 1973, 1979; Pellis and Officer 1987). Thus, both species exemplify the ecological role that *L. vallesiensis* probably played in the late Miocene faunas of Europe. On the contrary, the middle Miocene primitive saber-toothed felid *Pseudaelurus quadridentatus* had a robust Mc I (Ginsburg 1961a; Salesa et al. 2010a; Peigné 2012), even more than the extant large pantherin felines (Salesa et al. 2010a), in accordance with the huge dewclaw and robust forelimbs present in Machairodontinae, traits developed for achieving the rapid immobilization of prey (Gonyea 1976a; Emerson and Radinsky 1980; Akersten 1985; Rawn-Schatzinger 1992; Turner and Antón 1997; Salesa et al. 2005, 2006a, 2010a, 2014). The small Mc I of *L. vallesiensis* would also help in reducing the weight of the forelimb, and thus the energy employed when moving on the ground.

Metacarpals II-V

The Mc II-V of *L. vallesiensis* are very similar to those of the compared felines, with minor differences mainly related to their robustness. In general, the metacarpals II-V of *L. vallesiensis* are more robust than those of the most cursorial felines, such *Ly. lynx* and *Le. serval*, but slenderer than those of the most arboreal and forest-dwelling felines *Lp. wiedii* and *Lp. geoffroyi*. But, while this observation provides an overall view of the locomotor abilities of the hand, there are some features that deserve a more detailed discussion, as they seem primitive traits rather than a reflection of functional adaptations. For example, in the Mc II, the dorsomedial facet for the trapezium is not proximally projected in *L. vallesiensis*, *F. lybica*, and *F. silvestris*, whereas in the rest of the compared species it is strongly projected. The viverrids *C. civetta* and *G. genetta*, with different locomotor adaptations, have non-projected facets, thus probably illustrating the primitive morphology. Another probable primitive feature observed in the Mc IV of *L. vallesiensi* is the palmar facet for the Mc III, which is much less proximodistally expanded than in the compared felines, showing the same morphology seen in the Mc IV of *G. genetta*. Interestingly, in the terrestrial viverrid *C. civetta*, this palmar facet is larger, resembling those of the majority of the compared felines. The presence of a large facet between Mc III and IV produces a more stable and controlled articulation, an adaptation seen in several cursorial mammals (Rasmussen and Simons 2000; Stevens et al. 2009), so its presence in most of the felines as well as in terrestrial viverrids fits well with this idea, and would suggest a very primitive state in *L. vallesiensis*, similar to arboreal viverrids. Finally, the facet for the attachment of the muscle extensor carpi ulnaris, on the lateral face of the head of the McV, is less distally expanded in *L. vallesiensis* and *Le. serval* than in *F. silvestris*, *F. lybica*, *Ly. lynx*, *Ly. rufus*, *Ly. pardinus*, *C. caracal*, *Lp. wiedii*, and *Lp. geoffroyi*. This muscle, despite its name, is a flexor of the carpus and an external rotator of the forearm, being developed from the lateral epicondyle of the humerus to the base of the Mc V (Evans 1993; Barone 2010). Thus, the distal expansion of the attachment surface on the Mc V observed in some species slightly increases the length of the tendon, which given the actual size of the muscle, would suggest a larger range of carpus flexion rather than a larger muscle.

Os Coxae

The absence of constriction in the ilium of *L. vallesiensis*, *C. caracal*, and *Le. serval* is a consequence of the lesser dorsoventral expansion of the wing in relation to those species with a more or less developed greater ischiatic notch and an expanded spina alaris (*Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *F. lybica*, *F. silvestris*, *Lp. wiedii*, and *Lp. geoffroyi*) (Fig. 15). This difference affects the attachment area of the m. sartorius, which in felids originates as a thin strip on the ventral border of the iliac crest, inserting onto the medial surface of the patella, the tibial crest, and the medial condyle of the tibia (Reighard and Jennings 1901; Barone 2010; Carlon and Hubbard 2012). Its main function is to adduct and rotate the femur, and to extend the tibia (Reighard and Jennings 1901; Evans 1993; Barone 2010; Carlon and Hubbard 2012). Thus, in *L. vallesiensis*, *C. caracal*, and *Le. serval*, this muscle would have a more dorsal origin than in *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *F. lybica*, *F. silvestris*, *Lp. wiedii*, and *Lp. geoffroyi*. This configuration could imply a longer muscle, as its origin is more dorsally located, but the difference, when comparing in detail the coxae of *L. vallesiensis* and *F. silvestris* (very similar in size) seems really small. In any case, the more dorsally located origin of the m. sartorius could improve the flexion of the femur during the recovery phase of the locomotion, when the limb is preparing for foot-strike, and this bone is carried cranially by the contraction of the m. iliopsoas and m. sartorius (Argot 2002). Besides this, in *L. vallesiensis*, the attachment area of the m. sartorius is not a rough and dorsally ridged area, such as those of *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *Le. serval*, and *C. caracal*, but a thin bony sheet along the ventrocranial border of the ilium wing. This probably implies a relatively weaker m. sartorius, at least regarding its insertion on the wing. Nevertheless, this seems to be related to size, given the differences between small and large species within the compared sample, and the largest species would need a relatively stronger m. sartorius.

Another interesting difference in the coxal morphology of *L. vallesiensis* and the compared felines is the position of the ischiatic spine. In the Batallones feline, as well as in *Le. serval* and *C. caracal*, this structure is more caudally located than in *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *F. lybica*, *F. silvestris*, *Lp. wiedii*, and *Lp. geoffroyi* (Fig. 15). In felids, the ischiatic spine is the origin surface for the m. gemellus cranialis, whereas the m. gemellus caudalis originates on the dorsal border of the ischium between the ischiatic spine and the cranial border of the ischiatic tuberosity; both muscles, developed as two small flattened fleshy masses, attach into the trochanteric fossa of the femur (Barone 2010;

Carlon and Hubbard 2012). Their function is to help the m. obturatorius internus in abducting and rotating the femur (Reighard and Jennings 1901; Evans 1993; Barone 2010). The more caudal position of the ischiatic spine in *L. vallesiensis*, *Le. serval*, and *C. caracal* produces a shorter area for the attachment of the m. gemellus caudalis, and thus a smaller muscle. But also, it implies relatively longer fibers in the m. gemellus cranialis in relation to those of *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *F. lybica*, *F. silvestris*, *Lp. wiedii*, and *Lp. geoffroyi*. In fact, in these latter species, the origin and insertion areas of this muscle are located in such a way that the fibers of the muscle are more or less perpendicular to the craniocaudal axis of the os coxae. The relative caudal migration of the origin area in *L. vallesiensis*, *Le. serval*, and *C. caracal* would make the fibers longer, as well as increasing the range of rotation of the femur. Although both mm. gemelli are relatively small in felids (Reighard and Jennings 1901), the described difference in their disposition might have an important impact on their function as assistant to the m. obturatorius internus. In primitive viverrids such as *Genetta genetta*, the ischiatic spine is as caudally located as in *L. vallesiensis*, *Le. serval*, and *C. caracal*, and although this could point towards well-developed arboreal capacities (because of the greater rotation range of the femur), it could be also reflecting a retained, primitive state for this character.

The shape of the ischiatic arch clearly distinguishes two groups, one with more or less straight caudal margin of the ischium (*L. vallesiensis*, *F. lybica*, *Lp. wiedii*, and *Lp. geoffroyi*) and another one with a curved margin, developing a marked ischiatic arch (*F. silvestris*, *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *Le. serval*, and *C. caracal*). Once again, *Genetta genetta* shares the pattern observed in the former group. Feeny (1999) related the presence of ischiatic arch, with a reduction in the area for the origin of the m. biceps femoris, m. semitendinosus, and m. semimembranosus, and an increase in the area for the origin of the

m. adductor femoris (=m. adductor magnus et brevis). This muscle adducts and extends the coxofemoral articulation (Reighard and Jennings 1901; Evans 1993; Barone 2010). Argot (2002) has noticed that the adductor muscles of the thigh are essential in stabilizing the foot against the medially lying surface in arboreal forms using a wide range of femoral abduction. This means that a strong development of these muscles would point towards arboreal capacities, and that fits with the presence of a reduced ischiatic arch in *G. genetta* as well as *L. vallesiensis*, *F. lybica*, *Lp. wiedii*, and *Lp. geoffroyi*. It is remarkable that *Lp. wiedii* is one of the most arboreal felids (Alderton 1998), but the presence of a similar morphology in *L. vallesiensis* could be indicating the retention of a primitive morphology in a species that is not an ecological equivalent of the extant *Lp. wiedii*.

Sacrum

The sacrum of *L. vallesiensis* is quite similar to that of other felines. It shows some differences, but they do not seem to have a relevant importance. An exception is the wider and less caudally expanded notch separating the cranial articular surfaces and by the great lateral projection of the lateral sacral crest, both features observed also in *C. caracal* and *Le. serval*, although to a lesser degree (Fig. 16). The presence of this wider cranial notch in the sacrum of these species suggests an also wider range of lateral movements between the sacrum and the lumbar series, something that is evident when these bones are articulated experimentally (personal observation). The sacrum of *G. genetta* shows a relatively narrower notch than those of *L. vallesiensis*, *C. caracal*, and *Le. serval* (Fig. 16g), whereas other arboreal carnivorans, such as *Martes foina*, exhibit a relatively wide notch (Fig. 16i), with its cranial articular surfaces separated in a similar way to those of these former felines.

A cranial fragment of sacrum of *M. lorteti* from Sansan, described by Salesa et al. (2011) strongly resembles *L. vallesiensis* in the development of the notch. Unfortunately, no additional sacra of early and middle Miocene felines are known, so we lack data on the primitive morphology of this group. It is interesting that both *L. vallesiensis* and *M. lorteti* show the morphology of the sacral cranial articulation seen in an arboreal mustelid, instead of resembling that of semiarboreal viverrids such as *G. genetta*. In the phylogeny of the Carnivora, the families Viverridae and Felidae are closely related, whereas the Mustelidae are included in another clade (Gaubert and Veron 2003; Gaubert and Cordeiro-Estrela 2006; Wolsan and Sato 2010). Thus, the similar sacral morphology observed in *M. martes*, *L. vallesiensis*, and *M. lorteti* probably indicates a convergent adaptation for increasing the lumbosacral mobility rather than a phylogenetic relationship.

Besides this, the sacrum of *L. vallesiensis*, *C. caracal*, and *Le. serval* shows a strong lateral projection of the lateral sacral crest (Fig. 16b, d), a bony sheet serving as attachment surface for the dorsal sacroiliac ligaments and the m. piriformis (Evans 1993; Ercoli et al. 2013). This might be related with the great lateral mobility of the sacrum of these three species, inferred from the morphology of the cranial articular surface, which would need relatively stronger ligaments stabilizing this region.

Some features of the sacrum of mammals can be associated to their tail length; for example, Russo and Shapiro (2011) and Russo (2016) found that long-tailed species of cercopithecoid primates and felids had significantly more circularly shaped caudal articular surfaces, more acute sacrocaudal articulation angles, and more laterally expanded transverse processes of the last sacral vertebra. Interestingly, the relative length of the sacrum has not been found to be a good indicator of the tail length (Ankel 1965, 1972; Ward et al. 1991; Nakatsukasa et al. 2004), although *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, and

C. caracal show relatively elongated and narrower sacra when comparing to those of *L. vallesiensis*, *Le. serval*, *F. silvestris*, *F. lybica*, and *Lp. geoffroyi*.

The development of the intermediate sacral crest (bearing two mammillo-articular processes) of *L. vallesiensis* is also observed in *F. silvestris*, *F. lybica*, and *Lp. geoffroyi*, species with relatively long tails, whereas in *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, *Le. serval*, and *C. caracal*, species with relatively short tails, the caudal process is absent. These processes are part of the attachment areas for the mm. intertransversarii dorsales caudae, one of the main caudal muscular groups (Evans 1993; Ercoli et al. 2013), and thus a reduction of these structures would be expected when the tail is short. Given this, the presence of well-developed mammillo-articular processes in extant species with long tails would suggest the inclusion of *L. vallesiensis* in this group. Russo and Shapiro (2011) on their study on primates, found that the development of the caudal transverse process of the sacrum separated “long” and “tailless” groups from the “short”/“very short” groups, although the study did not distinguish “short” and “very short” groups (Tojima 2013). In the case of our compared sample of felines, there is no clear relationship between the morphology of the caudal transverse process and the length of the tail, as for example *Le. serval* shows an extremely thin and slender process, more developed than those of *F. lybica* and *Lp. geoffroyi*, which have longer tails. Nevertheless, given the morphology of the other discussed features of the sacrum, a relatively long tail can be inferred for *L. vallesiensis*.

Femur

The femur of *L. vallesiensis* fits very well within the feline pattern, although it shows some differences when compared to those of other felines. The gluteal tuberosity, for instance, is located, like in *Lp. wiedii*, clearly distal to the lesser trochanter, whereas in the rest of the compared species of Felinae it is clearly proximal to this structure (Fig. 17). This configuration relates to the relative length of the m. gluteus superficialis, which originates on the iliac crest and sacrocaudal aponeurosis, and attaches, after partial fusion with the m. gluteofemoralis, onto the gluteal tuberosity (Fisher et al. 2008; Barone 2010; Ercoli et al. 2013). Given these origin and insertion areas, the distal displacement of the gluteal tuberosity in *L. vallesiensis* and *Lp. wiedii* would increase the relative length of an important part of the fibers of the m. gluteus superficialis. The cranial fibers of the m. gluteus superficialis flex and weakly abduct the hip joint, while the caudal ones weakly extend and abduct the hip joint (Fisher et al. 2008). Basically, the pattern observed in *L. vallesiensis* and *Lp. wiedii* could be reflecting a relatively longer m. gluteus superficialis in relation to other felines, and its importance in the flexion and extension of the hind limb during locomotion. The m. gluteus superficialis is relatively larger in those mammals that need a powerful flexion of the hip joint (Endo et al. 2006), and thus, it is especially developed in otters and other aquatic species (Gambaryan 1974; Endo et al. 2006). Nevertheless, among the sample of large extant felids dissected by Gambaryan (1974), there were no significant differences in the relative weight of the m. gluteus superficialis with the exception of the jaguar (*Panthera onca*), which showed a relatively smaller muscle (2.7% vs. more than 4.0% in the rest). Thus, the relatively longer m. gluteus superficialis of *L. vallesiensis* and *Lp. wiedii*, rather than suggesting the presence of a heavier muscle would indicate a capacity for rapid movements, as relatively longer muscles produces faster contractions (Kardong 2002).

The position of the lesser trochanter also affects the function of other important muscle, the m. iliopsoas, which basically flexes the coxofemoral articulation, drawing the pelvic limb forward (Evans, 1993; Barone, 2010). *Leptofelis vallesiensis*, *F. lybica*, *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, and *Lp. geoffroyi* show a lesser trochanter located close to the medial margin of the femur, but laterally displaced in relation to its position in *F. silvestris*, *Le. serval*, *C. caracal*, and *Lp. wiedii* (Fig. 17). As has been noted, a laterally-located lesser trochanter produces lateral rotation as well as flexion at the coxofemoral articulation during the contraction of the m. iliopsoas (Howell 1944; Munthe 1989). On the contrary, in those carnivorans with more medially placed lesser trochanters, such as canids and hyaenids, the pull of the m. iliopsoas is produced primarily in the sagittal plane (Munthe 1989). According to this, *F. silvestris*, *Le. serval*, *C. caracal*, and *Lp. wiedii* would be favouring those movements of the femur in the sagittal plane, whereas the others, including *L. vallesiensis*, would be able of a higher rank of femur movements. Within the first group, *F. silvestris*, *Le. serval*, and *C. caracal* are slender animals, with relatively long limbs and terrestrial habits (Nowak 2005; Sunquist and Sunquist 2009), whereas *Lp. wiedii* has, on the contrary, a more robust proportions and strong climbing abilities (Alderton 1998; Sunquist and Sunquist 2009). Nevertheless, if the medially located lesser trochanter were indicative of a m. iliopsoas acting close to the sagittal plane and producing strong jumping impulse, the observed morphology would fit well with the ecology of *F. silvestris*, *Le. serval*, *C. caracal*, and *Lp. wiedii*, all of them proficient jumpers (Alderton 1998; Sunquist and Sunquist 2009). At this respect, it is remarkable that the semiarboreal viverrid *Genetta genetta*, also a good jumper (Jennings and Veron 2009) shows a medially located lesser trochanter, as *F. silvestris*, *Le. serval*, *C. caracal*, and *Lp. wiedii*. The feline from Batallones would exhibit a morphology also observed in other extant felines, but derived from that of the more primitive viverrids. The same pattern observed in *L. vallesiensis* is present in the femora of *S. turnauensis* from La Grive-Saint-Alban (LGR 4042) and *M.*

lorteti from Sansan (SAN 879), thus indicating that this character derived as early in the evolution of Felinae as the middle Miocene.

One of the few differences observed in the distal epiphysis of the femur is the orientation of the medial condyle in caudal view, rather vertical in *L. vallesiensis*, *F. silvestris*, *Lp. wiedii*, and *Lp. geoffroyi*, and slightly laterally inclined in *Le. serval*, *F. lybica*, *Ly. lynx*, *Ly. pardinus*, *Ly. rufus*, and *C. caracal*. Also, in all these latter species, except *F. lybica*, the medial condyle distally surpasses the level of the lateral one. When the tibia flexes on the femur, both the inclination and the distal projection of the medial condyle makes the tibia rotate laterally when it flexes on the femur, which all at once makes the talus be placed in a more parasagittal position, and so the foot; on the contrary, when both the lateral and medial femoral condyles reach the same level distally, the talus is located in a more lateral position when the tibia flexes on the femur, which makes the foot be rotated laterally. The position of the foot has an enormous importance when running, so the observed differences would be separating more cursorial felids from those inhabiting more closed environments, and thus retaining full climbing abilities. The morphology of the femoral condyles in *G. genetta*, similar to those of *L. vallesiensis* strongly supports this interpretation.

But maybe the most striking feature in the femur of *L. vallesiensis* is the proximodistal development of the trochlea, greater than that of any other of the compared felines (Fig. 18). Argot (2003) noticed that the femoral trochlea of canids was proximodistally higher than those of other carnivorans including ursids, mustelids, and felids, a feature that, following this author, reflected the great range of excursion of the patella in cursorial forms. Previously, Howell (1944) had stated that jumping and cursorial mammals required stronger extensor muscles of the tibia and have a well-developed trochlea, with high marginal ridges. Arboreal viverrids such as *G. genetta* also show a proximodistally high femoral trochlea, very similar to that of *L. vallesiensis*, which probably indicates a good ability for jumping in both species. Nevertheless, the femoral trochlea of the first known felid, the early Miocene *Proailurus lemanensis* from Saint Gérand-le-Puy (MN 2), although being proximodistally higher than those of extant felines, it is mediolaterally much wider than that of *L. vallesiensis*. If this is the primitive morphology for Felidae, the pattern seen in extant felines had been achieved by reducing the proximodistal height of the trochlea. The middle Miocene felines *M. lorteti* from Sansan (MN 6) and *S. turnauensis* from La Grive-Saint-Alban (MN 7/8) (de Beaumont 1961; Salesa et al. 2011), both show a proximodistally shorter trochlea than that of *L. vallesiensis*. Thus, these former species, older than the Batallones feline, already show a modern femoral trochlea, very similar to that of extant felines.

Tibia

The tibia of *L. vallesiensis* shows a similar morphology and proportions to those of other compared felines, except for the remarkable development of a strong bony ridge on the caudal face of the diaphysis (Fig. 7c, 19a). This structure seems to separate the attachment surfaces for the belly masses of the m. flexor digitorum lateralis and m. flexor digitorum medialis + m. tibialis caudalis, and it could be helpful in increasing their area (as the sagittal crest in the skull increases the attachment area for the m. temporalis), as well as stabilizing the muscles by forming a groove to accommodate them. Although the main function of both the m. flexor digitorum lateralis and m. flexor digitorum medialis is to flex the foot phalanges (Evans 1993; Barone 2010) and, although the latter is an accessory of the former, both have an important participation in the propulsion of the body (Barone 2010). If these two muscles were relatively larger in *L. vallesiensis* than in other felines, they would have produced stronger propulsive forces in the hind limb. Among our studied sample of felines, this ridge is also present in *Lp. geoffroyi* (Fig. 19b), but de Beaumont (1986) described it also in *Pristifelis attica* and in the Asian golden cat (*Catopuma temminckii*), which means that at least two species of extant felines that do not have either a close relationship nor marked ecological differences (Ximenez 1975; Johnson and Franklin 1991; Mattern and McLennan 2000; Sunquist and Sunquist 2009) do retain this feature exhibited by these two late Miocene felines. The sharing of this character by *L. vallesiensis* and *P. attica*, and its absence in the middle Miocene *Styriofelis turnauensis* (Fig. 19c) and *Miopanthera lorteti* poses an interesting question of the phylogenetic relationships of these taxa (see Taxonomic Discussion section). The caudal crest is also present, although much less marked, in ursids (Fig. 19e), which agrees with the great development in this group of the attachment area for the m. flexor digitorum medialis + m. tibialis caudalis, something that has been associated to plantigrady (Ginsburg 1961b). Nevertheless, when considering its presence in some extant species of Felinae whose locomotion probably does not differ from that of other species, the developed caudal crest of the tibia of *L. vallesiensis* cannot be considered as an indication of plantigrady in this feline, moreover when the rest of the hind limb elements are relatively slender.

Calcaneus

The dorsal orientation of the talar facet of the sustentaculum tali in *L. vallesiensis*, *Lp. wiedii*, *Lp. geoffroyii*, *F. silvestris*, and *F. lybica* is an important feature (Fig. 20), as it would theoretically imply a greater restriction in the lateral movements of the talus when articulating with the calcaneus, an expected feature of the most cursorial species. Nevertheless, when calcaneus and talus are experimentally articulated in our sample of felines, there are not marked differences in the relative orientation of the talus, as in those species having a dorsally oriented talar facet (*L. vallesiensis*, *Lp. wiedii*, *Lp. geoffroyii*, *F. silvestris*, and *F. lybica*), the matching facet on the talus is less excavated than in felines having a dorsomedially oriented talar facet in the sustentaculum tali (*C. caracal*, *Le. serval*, *Ly. lynx*, *Ly. rufus*, and *Ly. pardinus*). The dorsal orientation of the facet is observed in both terrestrial and arboreal small felines, as well as in *L. vallesiensis*, whereas the most cursorial taxa, *C. caracal*, *Le. serval*, *Ly. lynx*, *Ly. rufus*, and *Ly. pardinus*, show a more dorsomedial orientation. Interestingly, *G. genetta* shows a similar pattern to that observed in the former group, as well as the primitive felids *Proailurus lemanensis* from Saint Gerand-Le-Puy (SG 3532), *Promegantereon ogygia* from Batallones-1 (B/S-341) (Siliceo et al. 2014), and the taxa from Sansan *Pseudaelurus quadridentatus* (Sa 2427) (Peigné 2012), *S. turnauensis* (Sa744) (Peigné 2012), and *M. lorteti* (Sa 671) (Salesa et al. 2011) thus suggesting that this is the primitive condition for Felidae, which later derived in larger felines.

The attachment area for the m. quadratus plantae shows its greatest size in *L. vallesiensis*, *Lp. geoffroyii*, *Lp. wiedii*, and *F. silvestris*, suggesting the presence of a large and fully operative muscle (Fig. 20e, h), whereas it would be reduced (given the development of its attachment area) in *F. lybica*, *C. caracal*, *Le. serval*, *Ly. lynx*, *Ly. rufus*, and *Ly. pardinus* (Fig. 20f, g). In several mammals, the m. quadratus plantae is a wide band arising from the lateral surface of the calcaneus, and extending obliquely across the sole to its insertion on the tendinous sheet of the mm. flexores digitorum profundi, formed by the

m. flexor digitorum medialis and m. flexor digitorum lateralis (Davis 1964; Barone 1967; Ercoli et al. 2013), thus constituting an accessory of it. The m. quadratus plantae has two main functions: adjusting the oblique pull of the mm. flexores digitorum profundi, and flexing the foot without the involvement of this latter muscle (Reighard and Jennings 1901; Barone 1967; Turner and Antón 1997; Vollmerhaus and Roos 2001; Benjamin et al. 2008). Ginsburg (1961b) linked the great development of this muscle with plantigrady, but in the case of felids, which are digitigrade carnivorans, the presence of a well-developed m. quadratus plantare is clearly a primitive feature most likely related to the retention of the grasping function of the hind limb (Turner and Antón 1997), and a reduced capacity for pedal inversion but powerful flexion capability of the distal phalanges of the foot (Cifelli 1983). A well-developed depression for the attachment of the m. quadratus planate is found in many fossil felids, such as *P. lemanensis*, *Ps. quadridentatus*, *M. lorteti*, *Pr. ogygia*, and *Metailurus major* (Ginsburg 1961a; Salesa et al. 2011, 2012b; Siliceo et al. 2014) indicative of a relative large muscle. Thus, these fossil species did probably exhibit a good climbing ability, with the m. quadratus plantae muscle providing extra force and precision to the flexion of the foot during this activity (Turner and Antón 1997). In more cursorial felids, such as *F. lybica*, *C. caracal*, *Le. serval*, *Ly. lynx*, *Ly. rufus*, and *Ly. pardinus*, both the necessity for decreasing the weight of the distal elements of the limbs and the restriction of the lateral movements of the foot (Sooriakumaran and Sivananthan 2005) probably explain the reduction in the size of the m. quadratus plantae (Ginsburg 1961b). Then, in these cursorial felids, the mm. flexores digitorum profundi (m. flexor digitorum medialis and m. flexor digitorum lateralis) became primarily flexors of the toes in relation to the tibia, their function then changing from grasping to propulsion (Turner and Anton 1997).

Taxonomic discussion on "*Styriofelis*" *vallesiensis*

When Salesa et al. (2012a) assigned the small feline from Batallones-1 and Batallones-3 to the genus *Styriofelis* as the new species *S. vallesiensis*, they chose the most conservative taxonomic alternative based on a set of dental similarities between the Batallones sample and the middle Miocene feline *S. turnauensis*, although their cladogram did not imply a generic identity between both taxa. Nevertheless, the present new study reveals important morphological differences in the postcranial skeleton of *S. vallesiensis* and *S. turnauensis*, strongly suggesting a generic separation between these two Miocene felines. These features are: 1) the humerus of *S. turnauensis* and *M. lorteti* has a less proximally projected greater tubercle, and a much more medially projected medial epicondyle than those of *S. vallesiensis*, both features indicating a strong difference in the locomotion of these felines, with the two former species being much less cursorial than the feline from Batallones; 2) the Mc I of *S. vallesisensis* is slenderer than those of *S. turnauensis* and *M. lorteti*; 3) both *S. turnauensis* and *M. lorteti* have proximodistally shorter femoral trochleae than that of *S. vallesiensis*, a feature that links the former species with the extant felines, whereas the Batallones feline shows the same morphology observed in some extant viverrids; 4) in *S. turnauensis* and *M. lorteti*, the attachment area of the m. quadratus plantae is much more proximally extended than in *S. vallesiensis*, suggesting a much larger muscle, typical of arboreal felids inhabiting vegetated ecosystems; and 5) the caudal face of the tibiae of *P. attica* and *S. vallesiensis* shows a marked proximodistally developed ridge, a feature completely absent in *S. turnauensis* and *M. lorteti*.

All these differences, besides suggesting a different lifestyle (with *S. vallesiensis* being a more cursorial animal) support the separation of these felines in different genera.

Recently, Geraads and Peigné (2016) have discussed the status of the genus *Styriofelis*, proposing the inclusion of the species *lorteti* in the genus *Miopanthera*, which would also include the late Miocene *Felis pamiri* as *M. pamiri*. This increases the previously assumed diversity of the felids from the middle Miocene, as at least three different taxa were present at this time: the primitive machairodontine *Pseudaelurus quadridentatus*, the lynx-sized feline *Miopanthera lorteti*, and the wild cat-sized feline *Styriofelis turnauensis*. Of these three lineages, at least the first two had a continuity in the late Miocene, with *Promegantereon ogygia* (a primitive saber-toothed felid very similar to *Ps. quadridentatus*) and *M. pamiri*, which would be very close to the pantherin felid clade (Geraads and Peigné 2016). In both cases, several dental and skeletal similarities support a phylogenetic relationship between those forms included in the same lineage (de Beaumont 1975; Ginsburg 1983; Salesa et al. 2010b, 2012; Peigné 2012; Geraads and Peigné 2016), but the assumption of *S. vallesiensis* as being part of the *S. turnauensis* lineage is quite doubtful, as now it is clear that both species represent two different felid models characterized by a combination of unique dental and skeletal features. Besides this, the other late Miocene feline known in the European faunas, the larger *P. attica* shows a more derived dentition than that of *S. vallesiensis*, which points towards a different generic status (Salesa et al. 2012). In the present study, we have shown the existence of shared features in the postcranial skeleton of *P. attica* and *S. vallesiensis* (such as the proximodistally developed ridge in the caudal face of the tibia), but there are also some others that distinguish both late Miocene felines (such as the smaller projection of the lateral epicondyle of the humerus in *S. vallesiensis*). In absence of a proper cladistic analysis (unapproachable due to the scarcity of fossils), these similarities and differences are difficult to assess, but combining the results of the phylogenetic tree proposed by Salesa et al. (2012) with the observations of the present study, it seems quite probable that *S. vallesiensis* and *P. attica* belonged to the same lineage of terrestrial felines, although representing two different genera. For example, the presence of a P2 in *P. attica*, whereas *S. vallesiensis* retains two small upper deciduous premolars, D1 and D2 (see discussion in Salesa et al. 2012) gives an idea of the marked phylogenetic separation existing between both taxa. In consequence, a different generic name should be proposed for *S. vallesiensis* in order to separate it from the primitive and much more robust *S. turnauensis*, and from the contemporary and more derived *P. attica*. In absence of any available name, we propose the new genus *Leptofelis*, with the following diagnosis:

Order Carnivora Bowdich, 1821

Suborder Feliformia Kretzoi, 1945

Family Felidae Fischer, 1817

Subfamily Felinae Fischer, 1817

Genus *Leptofelis*, new genus

Leptofelis vallesiensis (Salesa, et al., 2012)

Holotype: BAT-3'09 1576, an almost complete skull from Batallones-3.

Type locality: Batallones-3 (late Miocene, Vallesian, MN 10) (Madrid, Spain).

Other localities: Maragheh (MN 11–12, Iran), and Batallones-1 (MN 10, Madrid).

Etymology: from the Greek *λεπτός* (*leptós)*, meaning “slender”, and from the Latin *felis*, cat.

Diagnosis: That provided by Salesa et al. (2012) and also, postcranial skeleton with a combination of primitive and derived features: humerus with a well proximally projected greater tubercle and an almost non-projected medial epicondyle; medial tubercle of the ulna well developed, markedly proximally projected, and surpassing the level of the lateral tubercle; slender Mc I, much less robust than those of middle Miocene felines such as *S. turnauensis* and *M. lorteti*; mediopalmar facet of the Mc IV base relatively less proximodistally expanded than in most felines; relatively short L7; dorsal sacral foramina absent; relatively proximodistally elongated femoral trochlea; relatively reduced attachment area for the m. quadratus plantae on the lateral face of the calcaneus; presence of a marked proximodistally developed ridge on the caudal face of the tibia.

Differential diagnosis: Only postcranial features are considered. Compared to *S. turnauensis* and *M. lorteti*, humerus with a more proximally projected greater tubercle, and a much less medially projected medial epicondyle; Mc I slenderer; proximodistally longer femoral trochlea; attachment area of the m. quadratus plantae much less proximally extended; caudal face of the tibiae with a marked proximodistally developed ridge. Compared to *P. attica*, lesser projection of the lateral epicondyle of the humerus.

Palaeobiology of *Leptofelis vallesiensis*

The postcranial anatomy of the late Miocene small feline *Leptofelis vallesiensis* is characterized by a combination of derived and primitive characters, a good example of the mosaicism typically exhibited by the intermediate forms of several groups of Carnivora. In this case, whereas the forelimb of *L. vallesiensis* is relatively modern, resembling that of some extant felines, its hind limb shows a set of primitive features in the pelvis, femur, and calcaneus, some of them shared with arboreal extant viverrids, and absent in the living felines. This unique combination of traits is different from that seen in the extant members of Felinae, but also from that present in the middle Miocene earliest felines.

Leptofelis vallesiensis had a body mass of around 7–9 kg (see Appendix 1), that is, a little larger than the extant *F. silvestris* and *F. lybica*, and particular proportions, as its brachial index (BIn) was within the range of *C. caracal* and *Lp. geoffroyi*, its crural index (CIn) is close to those of *F. silvestris* and *Ly. lynx*, and its intermembral index (IIn) is similar to that of *C. caracal* and *G. genetta* (Table 3). These indexes provide information on the locomotor adaptations (see Appendix 2), with the most cursorial species of Carnivora having relatively longer radii and tibiae than the corresponding humerii and femora (Taylor 1974, 1989; Gonyea 1978; Van Valkenburgh 1985, 1987; Anyonge 1996), that is, they show BIn and CIn higher or close to 100. In the case of felids, the BIn has also been related to habitat complexity, with those species inhabiting highly structured habitats, with dense vegetational cover, having relatively shorter forearms (and thus BIn between 80–90) than those occupying low structured habitats (and showing BIn close to 100) (Gonyea 1976a, b, 1978). Considering this, *L. vallesiensis* would have inhabited highly structured habitats, which does not always mean dense-vegetated areas, but a landscape composed of relatively open areas mixed with densely-vegetated patches (Fig. 21). This kind of environments allows greater species diversity than less structured habitats, by reducing predation efficiency and enabling predator/prey coexistence, and by increasing the number of available niches (Menge and Sutherland 1976; Petren and Case 1998). This would be an optimal habitat for a small feline such as *L. vallesiensis*, where it could find both refuge and a high diversity of available prey.

On the other hand, the IIn provides information on the relative length of the limbs, and in most felids, whose hind limb is longer than the forelimb, this index shows values below 100. A lower IIn (between 70–80) indicates a particularly long hind limb (Fig. 21), which has been related to jumping capacities (Howell 1944; Gonyea 1976b; Taylor 1976). The IIn of *L. vallesiensis* is almost 81, which supports a well development of its jumping capacities, as inferred from the morphology of its pelvic limb (see above).

In summary, *L. vallesiensis* was very likely a mostly terrestrial species, as shown by the morphology and proportions of its forelimb, but retained both primitive knee and ankle, associated with efficient jumping, an ability that was probably essential for eluding the large carnivorans that inhabited Batallones, such as saber-toothed felids, amphicyonids, ursids, ailurids, etc., all of them much larger than *L. vallesiensis*. This feline would forage on the ground, preying upon relatively small vertebrates, and occupying patched areas with moderate to dense vegetational cover, which provided the necessary protection to avoid detection by other predators, as well as allowing the stalking and hunting of prey. In this respect, its adaptation for jumping could improve the ability of *L. vallesiensis* for capturing fast animals, including birds, which would be caught by way of a powerful leap, thus resembling the sophisticated hunting method of extant servals and caracals (Sunquist and Sunquist 2009).

References

Agustí J, Cabrera L, Garcés M, Parés JM (1997) The Vallesian mammal succession in the Vallés-Penedés basin (northeast Spain): paleomagnetic calibration and correlation with global events. Palaeogeogr Palaeoclimatol Palaeoecol 133: 149–180

Agustí J, Moyà-Solà S (1990) Mammal extinctions in the Vallesian (upper Miocene). Lect Notes Earth Sc 30: 425–432

Akersten WA (1985) Canine function in *Smilodon* (Mammalia; Felidae; Machairodontinae). Contrib Sci 356: 1–22

Alexander RMcN, Jayes AS (1981) Estimates of the bending moments exerted by the lumbar and abdominal muscles of some mammals. J Zool 194: 291–303

Alderton D (1998) Wild Cats of the World. Blandford, London

Ankel F (1965) Der Canalis sacralis als Indikator für die Länge der Caudalregion der Primaten. Folia Primatol 3: 263–276

Ankel F (1972) Vertebral morphology of fossil and extant primates. In: Tuttle R (ed) The Functional and Evolutionary Biology of Primates. Aldine, Chicago, pp 223–240

Antón M, Morales J (2000) Inferencias paleoecológicas de la asociación de carnívoros del yacimiento de Cerro Batallones. In: Morales J, Nieto M, Amezua L, Fraile S, Gómez E, Herráez E, Peláez-Campomanes P, Salesa MJ, Sánchez IM, Soria D (eds) Patrimonio Paleontológico de la Comunidad de Madrid. Madrid: Serie "Arqueología Paleontología y Etnografía," Monográfico 6. Consejería de Educación, Comunidad de Madrid, pp 109–201

Antón M, Salesa MJ, Morales J, Turner A (2004) First known complete skulls of the scimitar-toothed cat *Machairodus aphanistus* (Felidae, Carnivora) from the Spanish late Miocene site of Batallones-1. J Vertebr Paleontol 24: 957–969

Anyonge W (1993) Body mass in large extant and extinct carnivores. J Zool 231: 339–350

Anyonge W (1996) Locomotor behaviour in Plio-Pleistocene sabre-tooth cats: a biomechanical analysis. J Zool 238: 395–413

Argot C (2001) Functional-adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. J Morphol 247: 51–79

Argot C (2002) Functional-adaptive analysis of the hindlimb anatomy of extant marsupials and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. J Morphol 253: 76–108

Argot C (2003) Functional adaptations of the postcranial skeleton of two Miocene borhyaenoids (Mamalia, Metatheria), *Borhyaena* and *Prothylacinus*, from South America. Palaeontology 46: 1213–1267

Argot C (2004) Evolution of South American mammalian predators (Borhyaenoidea): anatomical and palaeobiological implications. Zool J Linn Soc 140: 487–521

Argot C, Babot J (2011) Postcranial morphology, functional adaptations and palaeobiology of *Callistoe vincei*, a predaceous metatherian from the Eocene of Salta, north-western Argentina. Palaeontology 54: 447–480

Barone R (1967) La myologie du lion (*Panthera leo*). Mammalia 31: 459–516

Barone R (2010) Anatomie comparée des Mammifères domestiques, tome second, Arthrologie et Myologie (Quatrième édition). Éditions Vigot, Paris

Beaumont G de (1961) Recherches sur *Felis attica* Wagner du Pontien eurasiatique avec quelques observations sur les genres *Pseudaelurus* Gervais et *Proailurus* Filhol. Nouv Arch Mus Hist nat Lyon 6: 17–45

Beaumont G de (1975) Recherches sur les Félidés (Mammifères, Carnivores) du Pliocène inférieur des sables à *Dinotherium* des environs d'Eppelsheim (Rheinhessen). Archs. Sci. Genève 28: 369–405

Beaumont G de (1978) Notes complémentaires sur quelques félidés (Carnivores). Archs Sci Genève 31: 219–227

Beaumont G de (1986) La patte postérieure de *Felis attica* Wagn. (Mammifère, Carnivore) du Turolien de Grèce. Archs Sci Genève 39: 377–386

Benjamin M, Kaiser E, Milz S (2008) Structure-function relationships in tendons: a review. J Anat 212: 211–228

Bonis L de (2005) Carnivora (Mammalia) from the late Miocene of Akkasdagi, Turkey. Geodiversitas 27: 567–589

Brundrett KT (2002) Functional morphology of the forelimb in *Victoriapithecus* and its implications for phylogeny within the Catarrhini. Dissertation, University of Chicago, Chicago

Calvo JP, Pozo M, Silva PG, Morales J (2013) Pattern of sedimentary infilling of fossil mammal traps formed in pseudokarst at Cerro de los Batallones, Madrid Basin, central Spain. Sedimentology 60: 1681–1708

Carlon B, Hubbard C (2012) Hip and thigh anatomy of the clouded leopard (*Neofelis nebulosa*) with comparisons to the domestic cat (*Felis catus*). Anat Rec 295: 577–589

Cifelli RL (1983) Eutherian tarsals from the late Paleocene of Brazil. Am Mus Novitates 2761: 1–31

Ciochon RL (1986) The cercopithecoid forelimb: anatomical implications for the evolution of African species. Dissertation, University of California, Berkeley

Crusafont-Pairó M (1952) La presencia del Félido *Pseudaelurus tournauensis* (Hoernes) en el Mioceno de Hostalets de Pierola y Sabadell (Vallés-Penedés). Not Com Inst Geol Min España 28: 1–15

Crusafont-Pairó M, Ginsburg L (1973) Les Carnassiers fossiles de Los Valles de Fuentidueña. Bull Mus natl Hist nat 131: 29–45

Davis DD (1964) The giant panda: a morphological study of evolutionary mechanisms. Fieldiana Zool Mem 3: 1-339

Depéret C (1892) La faune de Mammifères miocènes de la Grive-Saint-Alban (Isère) et de quelques autres localités du basin du Rhône. Archs Mus Hist nat Lyon 5: 1–93

Emerson SB, Radinsky L (1980) Functional analysis of sabertooth cranial morphology. Paleobiology 6: 295–312

Endo H, Yonezawa T, Rakotondraparany F, Sasaki M, Hasegawa M (2006) The adaptational strategies of the hindlimb muscles in the Tenrecidae species including the aquatic web-footed tenrec (*Limnogale mergulus*). Ann Anat 188: 383–390

English AWM (1980) The functions of the lumbar spine during stepping in the cat. J Morphol 165: 55–66

Ercoli MD, Álvarez A, Stefanini MI, Busker F, Morales MM (2015) Muscular anatomy of the forelimbs of the lesser grison (*Galictis cuja*), and a functional and phylogenetic overview of Mustelidae and other Caniformia. J Mammal Evol 22: 57–91

Ercoli MD, Echarri S, Busker F, Álvarez A, Morales MM, Turazzini GF (2013) The functional and phylogenetic implications of the myology of the lumbar region, tail, and hind limbs of the lesser grison (*Galictis cuja*). J Mammal Evol 20: 309–336

Evans HE (1993) Miller's Anatomy of the dog (3rd edition). Saunders, Philadelphia

Feeny S (1999) Comparative osteology, myology, and locomotor specializations of the fore and hind limbs of the North American foxes *Vulpes vulpes* and *Urocyon cinereoargenteus*. Dissertation, University of Massachusetts, Amherst

Fisher RE, Adrian B, Barton M, Holmgren J, Tang SY (2009) The phylogeny of the red panda (*Ailurus fulgens*): evidence from the forelimb. J Anat 215: 611–635

Fisher RE, Adrian B, Elrod C, Hicks M (2008) The phylogeny of the red panda (*Ailurus fulgens*): evidence from the hindlimb. J Anat 213: 607–628

Fleagle JG, Simons EL (1982) The humerus of *Aegyptopithecus zeuxis*: a primitive anthropoid. Am J Phys Anthropol 59: 175–193

Forsten A, Kaya T (1995) The hipparions (Mammalia, Equidae) from Gülpinar (Canakkale, Turkey). Paläont Z 69: 491–501

Fortelius M, Hokkanen A (2001) The trophic context of hominoid occurrence in the later Miocene of western Eurasia – a primate-free view. In: de Bonis L, Koufos G, Andrews P (eds) Phylogeny of the Neogene Hominoid Primates of Eurasia. Cambridge University Press, Cambridge, pp 19–47

Gaillard C (1899) Mammifères miocènes de La Grive-Saint-Alban (Isère). Archs Mus Hist nat Lyon 7: 1–41

Gambaryan PP (1974) How Mammals Run. Anatomical Adaptations. Wiley, New York

Gaubert P, Cordeiro-Estrela P (2006) Phylogenetic systematics and tempo of evolution of the Viverrinae (Mammalia, Carnivora, Viverridae) within feliformians: implications for faunal exchanges between Asia and Africa. Mol Phylogenet Evol 41: 266–278

Gaubert P, Veron G (2003) Exhaustive sample set among Viverridae reveals the sister-group of felids: the Linsangs as a case of extreme morphological convergence within Feliformia. P Roy Soc Lond B Bio 270: 2523–2530

Gebo DL, Rose KD (1993) Skeletal morphology and locomotor adaptation in *Prolimnocyon atavus*, an early Eocene hyaenodontid creodont. J Vertebr Paleontol 13: 125–144

Geraads D, Peigné S (2016) Re-appraisal of '*Felis*' *pamiri* Ozansoy, 1959 (Carnivora, Felidae) from the Upper Miocene of Turkey: the earliest pantherin cat? J Mammal Evol doi:10.1007/s10914-016-9349-6

Gervais P (1850) Zoologie et paléontologie françaises. Nouvelles recherches sur les animaux vertébrés dont on trouve les ossements enfouis dans le sol de la France et sur leur comparaison avec les espèces propres aux autres regions du globe. Arthus Bertrand, Paris

Ginsburg L (1961a) La faune des Carnivores miocènes de Sansan (Gers). Mem Mus Nat Hist Nat, Nouv Ser, C 9: 1–190

Ginsburg L (1961b) Plantigradie et digitigradie chez les carnivores fissipedes. Mammalia 25: 1–21

Ginsburg L (1983) Sur les modalités d'évolution du genre néogène *Pseudaelurus* Gervais (Felidae, Carnivora, Mammalia). Colloq Internatl CNRS 330: 131–136

Ginsburg L (1999) Order Carnivora. In: Rössner GE, Heissig K (eds) The Miocene Land Mammals of Europe. Verlag Dr Friedlich Pfeil, Munich, pp 109–148

Ginsburg L (2002) Les carnivores fossiles des sables de l'Orléanais. Ann Paleontol 88: 115–146

Ginsburg L, Antunes MT (1995) Les carnivores du Miocène de Lisbonne (Portugal). Ann Paleontol 81: 125–165

Gonyea WJ (1976a) Behavioral implications of saber-toothed felid morphology. Paleobiology 2: 332–342

Gonyea WJ (1976b) Adaptative differences in the body proportions of large felids. Acta Anat 96: 81–96

Gonyea WJ (1978) Functional implications of felid forelimb anatomy. Acta Anat 102: 111–121

Gonyea W, Ashworth R (1975) The form and function of retractile claws in the Felidae and other representative carnivorans. J Morphol 145: 229–238

Goslow GE, Reinking RM, Stuart DG (1973) The cat step cycle: hind limb joint angles and muscles lengths during unrestrained locomotion. J Morphol 141: 1–42

Heinrich RE, Rose KD (1997) Postcranial morphology and locomotor behaviour of two early Eocene miacoid carnivorans, *Vulpavus* and *Didymictis*. Palaeontology 40: 279–305

Hernández-Fernández M, Cárdaba JA, Cuevas-González J, Fesharaki O, Salesa MJ, Corrales B, Domingo L, Élez J, López-Guerrero P, Sala-Burgos N, Morales J, López-Martínez N (2006) The deposits of middle Miocene vertebrates of Somosaguas (Pozuelo de Alarcon, Madrid): paleoenvironment and paleoclimate implications. Estud Geol-Madrid 62: 263–294

Hildebrand M (1959) Motions of the running cheetah and horse. J Mammal 40: 481–495

Hoernes VR (1882) Säugetier-Reste aus der Braunkohle von Göriach bei Turnau in Steiermark. Jahrb K K Geol Reichs 32: 153–164

Howell AB (1944) Speed in Animals: Their Specialization for Running and Leaping. University of Chicago Press, Chicago

Hunt RM Jr (2009) Long-legged pursuit carnivorans (Amphicyonidae, Daphoeninae) from the early Miocene of North America. Bull Am Mus Nat Hist 318: 1–95

International Committee on Veterinary Gross Anatomical Nomenclature (2012) Nomina Anatomica Veterinaria (5th edition, revised version). World Association of Veterinary

Anatomists (W.A.V.A.), Hannover (Germany), Columbia MO (U.S.A.), Ghent (Belgium), Sapporo (Japan)

Iwaniuk AN, Pellis SM, Whishaw IQ (1999) The relationships between forelimb morphology and behavior in North American carnivores (Carnivora). Can J Zool 77: 1064–1074

Jennings AP, Veron G (2009) Family Viverridae (civets, genets and oyans). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World, Vol. 1, Carnivores. Lynx Edicions, Barcelona, pp 174–232

Johnson WE, Franklin WL (1991) Feeding and spatial ecology of *Felis geoffroyi* in southern Patagonia. J Mammal 72: 815–820

Jolly CJ (1967) The evolution of the baboons. In: Vagborg H (ed) The Baboon in Medical Research. Vol II. University of Texas Press, Austin, pp 23–50

Julik E, Zack S, Adrian B, Maredia S, Parsa A, Poole M, Starbuck A, Fisher RE (2012) Functional anatomy of the forelimb muscles of the ocelot (*Leopardus pardalis*). J Mammal Evol 19: 277–304

Kardong KV (2002) Vertebrates: Comparative Anatomy, Function, Evolution. McGraw-Hill, Boston

Kingdon J (1977) East African Mammals: An atlas of Evolution in Africa, vol. 3 (A). Carnivores. Academic Press, New York

Kretzoi M (1929) Feliden-Studien. Föld Intezet Haziny 24: 1–22

Kretzoi M (1951) The *Hipparion*-fauna from Csákvár. Föld Közl 81: 402–417

Kretzoi M (1952) Die Raubtiere der Hipparionfauna von Polgárdi. Jahrb Ung Geo Anstalt 40: 1–42

Larson SG, Stern JT (1989) Role of supraspinatus in the quadrupedal locomotion of vervets (*Cercopithecus aethiops*): implications for interpretation of humeral morphology. Am J Phys Anthropol 79: 369–377

Leyhausen P (1973) On the function of the relative hierarchy of moods. In: Lorenz K, Leyhausen P (eds) Motivation of Human and Animal Behavior: An Ethological View. Van Nostrand, New York, pp 144–247

Leyhausen P (1979) Cat Behavior. The Predatory and Social Behavior of Domestic and Wild Cats. Garland STPM Press, New York

Mattern MY, McLennan DA (2000) Phylogeny and speciation of felids. Cladistics 16: 232–253

Meachen-Samuels J, Van Valkenburgh B (2009) Forelimb indicators of prey-size preference in the Felidae. J Morphol 270: 729–744

Mecquenem R. de (1924) Contribution à l’étude des fossiles de Maragha. Ann Paleontol 13: 135–160

Menge BA, Sutherland JP (1976) Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Am Nat 110: 351–369

Morales J, Alcalá L, Álvarez-Sierra MA, Antón M, Azanza B, Calvo JP, Carrasco P, Fraile S, García-Paredes I, Gómez E, Hernández Fernández M, Merino L, Van Der Meulen A, Martín Escorza C, Montoya P, Nieto M, Peigné S, Pérez B, Peláez-Campomanes P, Pozo M, Quiralte V, Salesa MJ, Sánchez IM, Sánchez-Marco A, Silva PG, Soria MD, Turner A (2004) Paleontología del sistema de yacimientos de mamíferos miocenos del Cerro de los Batallones, Cuenca de Madrid. Geogaceta 35: 139–142

Morales J, Alcalá L, Amezua L, Antón M, Fraile S, Gómez E, Montoya P, Nieto M, Pérez B, Salesa MJ, Sánchez IM (2000) El yacimiento de El Cerro de los Batallones. In: Morales J, Nieto M, Amezua L, Fraile S, Gómez E, Herráez E, Peláez-Campomanes P, Salesa MJ, Sánchez IM, Soria D (eds) Patrimonio Paleontológico de la Comunidad de Madrid. Editorial de la Comunidad de Madrid, Madrid, pp 179–190

Morales J, Pickford M, Fraile S, Salesa MJ, Soria D (2003) Creodonta and Carnivora from Arrisdrift, early middle Miocene of southern Namibia. Mem Geol Surv Namibia 19: 177–194

Morales J, Pozo M, Silva PG, Domingo MS, López-Antoñanzas R, Álvarez Sierra MA, Antón M, Martín Escorza C, Quiralte V, Salesa MJ, Sánchez IM, Azanza B, Calvo JP, Carrasco P, García-Paredes I, Knoll F, Hernández Fernández M, Van Den Hoek Ostende L, Merino L, Van Der Meulen AJ, Montoya P, Peigné S, Peláez-Campomanes P, Sánchez-Marco A, Turner A, Abella J, Alcalde GM, Andrés M, DeMiguel D, Cantalapiedra JL, Fraile S, García Yelo BA, Gómez Cano AR, López Guerrero P, Oliver Pérez A., Siliceo G (2008) El sistema de yacimientos de mamíferos miocenos del Cerro de los Batallones, Cuenca de Madrid: estado actual y perspectivas. Palaeontol Nova 8: 71–114

Morlo M (1997) Die Raubtiere (Mammalia, Carnivora) aus dem Turolium von Dorn-Dürkheim 1 (Rheinhessen). Teil. 1: Mustelida, Hyaenidae, Percrocutidae, Felidae. Cour Forsch Senck 197: 11–47

Munthe K (1989) The skeleton of the Borophaginae (Canidae). Univ Calif Publ Geol Sci 133: 1–115

Nakatsukasa M, Ward C, Walker A, Teaford M, Kunimatsu Y, Ogihara N (2004) Tail loss in *Proconsul heseloni*. J Hum Evol 46: 777–784

Nowak RM (2005) Walker’s Carnivores of the World. The Johns Hopkins University Press, Baltimore

Palmer R, Fairall N (1988) Caracal and African wild cat diet in the Karoo National Park and the implications thereof for hyrax. S Afr J Wildl Res 18: 30–34

Peigné S (2012) Les Carnivora de Sansan. In: Peigné S, Sen S (eds) Mammiféres de Sansan. Mém Mus natl Hist nat Paris 203: 559–660

Peigné S, Salesa MJ, Antón M, Morales J (2005) Ailurid carnivoran mammal *Simocyon* from the late Miocene of Spain and the systematics of the genus. Acta Palaeontol Pol 50: 219–238

Peigné S, Salesa MJ, Antón M, Morales J (2008) A new amphicyonine (Carnivora: Amphicyonidae) from the upper Miocene of Batallones-1, Madrid, Spain. Palaeontology 51: 943–965

Pellis SM, Officer RCE (1987) An analysis of some predatory behaviour patterns in four species of carnivorous marsupials (Dasyuridae), with comparative notes on the eutherian cat *Felis catus*. Ethology 75: 177–196

Petren K, Case TJ (1998) Habitat structure determines competition intensity and invasion success in gecko lizards. P Natl Acad Sci USA 95: 11739–11744

Pozo M, Calvo JP, Silva P, Morales J, Peláez-Campomanes P, Nieto M (2004) Geología del sistema de yacimientos de mamíferos miocenos del Cerro de los Batallones, Cuenca de Madrid. Geogaceta 35: 143–146

Rasmussen DT, Simons EL (2000) Ecomorphological diversity among Paleogene hyracoids (Mammalia): a new species of cursorial browser from the Fayum, Egypt. J Vertebr Paleontol 20: 167–176

Rawn-Schatzinger V (1992) The scimitar cat *Homotherium serum* Cope: osteology, functional morphology, and predatory behavior. Illinois St Mus Rep Inv 47: 1–80

Reighard J, Jennings HS (1901) Anatomy of the Cat. Henry Holt and Company, New York

Riabinin A (1927) Faune de mammifères de Taraklia. 1. Carnivora vera, Rodentia, Subungulata. Trav Mus Géol Leningrad 5: 75–134

Roberts TJ (1977) The Mammals of Pakistan. Ernest Benn, London

Rodríguez J (1997) Análisis de la estructura de las comunidades de mamíferos del Pleistoceno de la Sierra de Atapuerca. Revisión de Metodologías. Dissertation, Universidad Autónoma de Madrid, Madrid

Roman F, Viret J (1934) La faune de mammifères du Burdigalien de La Romieu (Gers). Mém Soc géol France 21: 1–67

Rothwell T (2001) A partial skeleton of *Pseudaelurus* (Carnivora: Felidae) from the Nambé Member of the Tesuque Formation, Española Basin, New Mexico. Am Mus Novitates 3342: 1–31

Rothwell T (2003) Phylogenetic systematics of North American *Pseudaelurus* (Carnivora: Felidae). Am Mus Novitates 3403: 1–64

Roussiakis SJ (2002) Musteloids and feloids (Mammalia, Carnivora) from the late Miocene locality of Pikermi (Attica, Greece). Geobios 35: 699–719

Russo GA (2016) Comparative sacral morphology and the reconstructed tail lengths of five extinct primates: *Proconsul heseloni*, *Epipliopithecus vindobonensis*, *Archaeolemur edwardsi*, *Megaladapis grandidieri*, and *Palaeopropithecus kelyus*. J Hum Evol 90: 135–162

Russo GA, Shapiro LJ (2011) Morphological correlates of tail length in the catarrhine sacrum. J Hum Evol 61: 223–232

Salesa MJ (2002) Estudio Anatómico, Biomecánico, Paleoecológico y Filogenético de *Paramachairodus ogygia* (Kaup, 1832) Pilgrim, 1913 (Felidae, Machairodontinae) del yacimiento vallesiense (Mioceno superior) de Batallones-1 (Torrejón de Velasco, Madrid). Dissertation, Universidad Complutense de Madrid, Madrid

Salesa MJ, Antón M, Morales J, Peigné S (2011) Functional anatomy of the postcranial skeleton of *Styriofelis lorteti* (Carnivora, Felidae, Felinae) from the middle Miocene (MN 6) locality of Sansan (Gers, France). Estud Geol-Madrid 67: 223–243

Salesa MJ, Antón M, Morales J, Peigné S (2012a) Systematics and phylogeny of the small felines (Carnivora, Felidae) from the late Miocene of Europe: a new species of Felinae from the Vallesian of Batallones (MN 10, Madrid, Spain). J Syst Palaeontol 10: 87–102

Salesa MJ, Antón M, Peigné S, Morales J (2006b) Evidence of a false thumb in a fossil carnivore clarifies the evolution of pandas. P Natl Acad Sci USA 103: 379–382

Salesa MJ, Antón M, Peigné S, Morales J (2008) Functional anatomy and biomechanics of the postcranial skeleton of *Simocyon batalleri* (Viret, 1929) (Carnivora, Ailuridae) from the late Miocene of Spain. Zool J Linn Soc 152: 593–621

Salesa MJ, Antón M, Siliceo G, Pesquero MD, Alcalá L (2014) First evidence of pathology in the forelimb of the late Miocene saber-toothed felid *Promegantereon ogygia* (Machairodontinae, Smilodontini). Anat Rec 297: 1090–1095

Salesa MJ, Antón M, Turner A, Alcalá L, Montoya P, Morales J (2010b) Systematic revision of the late Miocene sabre-toothed felid *Paramachaerodus* in Spain. Palaeontology 53: 1369–1391

Salesa MJ, Antón M, Turner A, Morales J (2005) Aspects of the functional morphology in the cranial and cervical skeleton of the sabre-toothed cat *Paramachairodus ogygia* (Kaup, 1832) (Felidae, Machairodontinae) from the late Miocene of Spain: implications for the origins of the machairodont killing bite. Zool J Linn Soc 144: 363–377

Salesa MJ, Antón M, Turner A, Morales J (2006a) Inferred behaviour and ecology of the primitive sabre-toothed cat *Paramachairodus ogygia* (Felidae, Machairodontinae) from the late Miocene of Spain. J Zool 268: 243–254

Salesa MJ, Antón M, Turner A, Morales J (2010a) Functional anatomy of the forelimb in *Promegantereon ogygia* (Felidae, Machairodontinae, Smilodontini) from the late Miocene of Spain and the origins of the sabre-toothed felid model. J Anat 216: 381–396

Salesa MJ, Pesquero MD, Siliceo G, Antón M, Alcalá L, Morales J (2012b) A rich community of Felidae (Mammalia, Carnivora) from the late Miocene (Turolian, MN 13) site of Las Casiones (Villalba Baja, Teruel, Spain). J Vertebr Paleontol 32: 658–676

Schlosser M (1924) Tertiary vertebrates from Mongolia. Palaeontol Sin 1: 1–133

Schmidt-Kittler N (1976) Raubtiere aus dem Jungtertiär Kleinasiens. Palaeontogr Abt A 155: 1–131

Sharma IK (1979) Habits, feeding, breeding and reaction to man of the desert cat *Felis lybica* (Gray) in the Indian Desert. J Bombay Nat Hist Soc 76: 498–499

Siliceo G (2015) Anatomía functional y paleobiología de *Magericyon anceps* (Amphicyonidae, Carnivora) del complejo de yacimientos vallesienses (Mioceno superior, MN 10) del Cerro de los Batallones (Torrejón de Velasco, Madrid). Dissertation, Universidad de Alcalá, Alcalá de Henares

Siliceo G, Salesa MJ, Antón M, Monescillo MGF, Morales J (2014) *Promegantereon ogygia* (Felidae, Machairodontinae, Smilodontini) from the Vallesian (late Miocene, MN 10) of Spain: morphological and functional differences in two noncontemporary populations. J Vertebr Paleontol 34: 407–418

Siliceo G, Salesa MJ, Antón M, Pastor JF, Morales J (2015) Comparative anatomy of the shoulder region in the late Miocene amphicyonid *Magericyon anceps* (Carnivora): functional and paleoecological inferences. J Mammal Evol 22: 243–258

Siliceo G, Salesa MJ, Antón M, Peigné S, Morales J (2017) Functional anatomy of the cervical region in the late Miocene amphicyonid *Magericyon anceps* (Carnivora, Amphicyonidae): implications for its feeding behaviour. Palaeontology 60: 329–347

Smithers RHN (1971) The Mammals of Botswana. The Trustees of the National Museums of Rhodesia, Salisbury

Solounias N (1981) The Turolian fauna from the Island of Samos, Greece. Contrib Vertebr Evol 6: 1–232

Sooriakumaran P, Sivananthan S (2005) Why does man have a quadratus plantae? A review of its comparative anatomy. Croat Med J 46: 30–35

Stevens NJ, O’Connor PM, Roberts EM, Gottfried MD (2009) A hyracoid from the late Oligocene red sandstone group of Tanzania, *Rukwalorax jinokitana* (gen. and sp. nov.). J Vertebr Paleontol 29: 972–975

Sunquist ME, Sunquist FC (2009) Family Felidae (Cats). In: Wilson DE, Mittermeier RA (eds) Handbook of the Mammals of the World, Vol. 1, Carnivores. Lynx Edicions, Barcelona, pp 54–169

Taylor CR (1978) Why change gaits? Recruitment of muscles and muscle fibers as a function of speed and gait. Am Zool 18: 153–162

Taylor ME (1974) The functional anatomy of the forelimb of some African Viverridae (Carnivora). J Morphol 143: 307–336

Taylor ME (1976) The functional anatomy of the hindlimb of some African Viverridae (Carnivora). J Morphol 148: 227–254

Taylor ME (1989) Locomotor adaptations by carnivores. In: Gittleman J (ed) Carnivore Behavior, Ecology and Evolution. Springer, New York, pp 382–409

Thenius E (1949) Die Carnivoren von Göriach (Steiermark). S-B öst Akad Wiss math-nat Kl Abt 158: 695–762

Tojima S (2013) Tail length estimation from sacrocaudal skeletal morphology in catarrhines. Anthropol Sci 121: 13–24

Turner A, Antón M (1997) Big Cats and Their Fossil Relatives: An Illustrated Guide to Their Evolution and Natural History. Columbia University Press, New York

Van Valkenburgh B (1985) Locomotory diversity within past and present guilds of large predatory mammals. Paleobiology 11: 406–428

Van Valkenburgh B (1987) Skeletal indicators of locomotor behavior in living and extinct carnivores. J Vertebr Paleontol 7: 162–182

Viret J (1951) Catalogue critique de la faune des mammifères miocènes de La Grive Saint-Alban (Isère). Nouv Arch Mus Hist nat Lyon 3: 1–103

Vollmerhaus B, Roos H (2001) Konstruktionsprinzipien an der Vorder- und Hinterpfote der Hauskatze (*Felis catus*). III. Mitteilung: Muskulatur. Anat Histol Embryol 30: 89–105

Wagner A (1857) Neue Beiträge zur Kenntniss der fossilen Säugthier-Ueberreste von Pikermi. Abh K Bayerische Akad Wissen 8: 111–158

Ward C, Walker A, Teaford M (1991) *Proconsul* did not have a tail. J Hum Evol 21: 215–220

Werdelin L, Yamaguchi N, Johnson WE, O'Brien SJ (2010) Phylogeny and evolution of cats (Felidae). In: Macdonald DW, Loveridge AJ (eds) Biology and Conservation of Wild Felids. Oxford University Press, Oxford, pp 59–82

Wolsan M, Sato JJ (2010) Effects of data incompleteness on the relative performance of parsimony and Bayesian approaches in a supermatrix phylogenetic reconstruction of Mustelidae and Procyonidae (Carnivora). Cladistics 26: 168–194

Ximenez A (1975) *Felis geoffroyi*. Mammal Species 54: 1–4

Figure captions

Fig. 1. Measurements for each studied postcranial element. **a**, **b**, left humerus in (**a**) cranial and (**b**) lateral views. **c**, lateral view of a right ulna. **d**, cranial view of right femur. **e**, lateral view of a left coxal. **f**, dorsal view of a right calcaneus. **g**, dorsal view of a right talus. **h**, ventral view of a sacrum. Abbreviations: ah, articular proximodistal height; aw, articular mediolateral width; dw, distal mediolateral width; oh, olecranon proximodistal height; pl, proximal craniocaudal length; pw, proximal mediolateral width; tl, total proximodistal length.

Fig. 2. Caudal part of a lumbar region of *Leptofelis vallesiensis* from Batallones-1 (BAT-1'06 D4-64a, BAT-1'06 D4-64b and BAT-1'06 D4-64c) in left lateral (**a**), and ventral (**b**) views. From left to right, L7, L6, L5 and caudal fragment of L4. Scale bar = 20 mm.

Fig. 3. Long bones of *Leptofelis vallesiensis* from Batallones-1. **a**, **b**, BAT-1'02 D6-58, left humerus in cranial (**a**), and lateral (**b**) views. **c**, **d**, B-2074 (5), right radius in cranial (**c**), and caudal (**d**) views. **e**, **f**, Right ulna B-2074 (6) in lateral (**e**), and medial (**f**) views. Scale bar = 20 mm.

Fig. 4. Metacarpals of *Leptofelis vallesiensis* from Batallones-1. **a**, **b**, BAT-1'03 D4-239, right metacarpal I in dorsal (**a**), and medial (**b**) views. **c**, **d**, BAT-1'03 D5-162, right Mc II in lateral (**c**), and medial (**d**) views. **e**, **f**, BAT-1'04 D4-184, right Mc III in lateral (**e**), and medial (**f**) views. **g**, **h**, BAT-1'03 E4-164, right Mc IV in lateral (**g**), and medial (**h**) views. **i**, **j**, BAT-1'04 E5-129, right Mc V in lateral (**i**), and medial (**j**) views. Scale bar = 20 mm.

Fig. 5. BAT-1'06 D4-66a, pelvis of *Leptofelis vallesiensis* from Batallones-1 in left lateral (**a**) and ventral (**b**) views. Scale bar = 20 mm.

Fig. 6. BAT-1'06 D4-66b, sacrum of *Leptofelis vallesiensis* from Batallones-1 in dorsal (**a**) and ventral (**b**) views. Scale bar = 20 mm.

Fig. 7. Long bones of *Leptofelis vallesiensis* from Batallones-1. **a**, **b**, BAT-1'06 D4-67a, right femur of in cranial (**a**), and caudal (**b**) views. **c**–**e**, BAT-1'06 D4-110, left tibia in caudal (**c**), medial (**d**), and lateral (**e**) views. Abbreviations: cr, caudal ridge. Scale bar = 20 mm.

Fig. 8. Tarsals of *Leptofelis vallesiensis* from Batallones-1. **a**, BAT-1'04 D6-173, right talus in dorsal view (digitally separated from the articulated calcaneum BAT-1'04 D6-174). **b**, BAT-1'03 D6-300, left talus in plantar view. **c**–**e**, BAT-1'06 F5-61, right calcaneus in dorsal (**c**), medial (**d**), and plantar (**e**) views. Scale bar = 10 mm.

Fig. 9. Ventral view of articulated caudal part of the lumbar region (L7 to L4) of different species of Carnivora shown at the same size for a better comparison. **a**, *Genetta genetta*. **b**, *Martes foina*. **c**, *Leptofelis vallesiensis* from Batallones-1. **d**, *Felis silvestris*. **e**, *Leopardus geoffroyi*. **f**, *Leptailurus serval*.

Fig. 10. Lateral view of the proximal epiphysis of the left humerus of different species of Felidae, shown at the same size for a better comparison. **a**, BAT-1'02 D6-58, *Leptofelis*

vallesiensis from Batallones-1. **b**, *Leopardus geoffroyi*. **c**, *Lynx lynx*. Abbreviations: gt, greater tubercle.

Fig. 11. Cranial view of the distal epiphysis of the left humerus of different species of Felidae, shown at the same size for a better comparison. **a**, BAT-1'02 D6-58, *Leptofelis vallesiensis* from Batallones-1. **b**, *Leopardus geoffroyi*. **c**, *Lynx lynx*. Abbreviations: me, medial epicondyle.

Fig. 12. Caudal view of the distal epiphysis of the left humerus of different species of Felidae, shown at the same size for a better comparison. **a**, BAT-1'02 D6-58, *Leptofelis vallesiensis* from Batallones-1. **b**, *Leopardus geoffroyi*. **c**, *Lynx lynx*. Abbreviations: le, lateral epicondyle.

Fig. 13. Lateral view of the proximal epiphysis of the right ulna of different species of Felidae, shown at the same size for a better comparison. **a**, B-2074 (6), *Leptofelis vallesiensis* from Batallones-1. **b**, *Leopardus geoffroyi*. **c**, *Lynx lynx*. **d**, *Felis lybica*. **e**, *Leopardus wiedii*. **f**, *Leptailurus serval*. Abbreviations: ltb, attachment area for the lateral branch of m. triceps brachii.

Fig. 14. Cranial view of the proximal epiphysis of the right ulna of different species of Felidae, shown at the same size for a better comparison. **a**, BAT-1'06 E5-50, *Leptofelis vallesiensis* from Batallones-1. **b**, *Leopardus geoffroyi*. **c**, *Lynx lynx*. **d**, *Leptailurus serval*. Abbreviations: lt, lateral tuberosity; mt, medial tuberosity.

Fig. 15. Lateral view of the left coxae of different species of Felidae, shown at the same size for a better comparison. **a**, BAT-1'06 D4-66a, *Leptofelis vallesiensis* from Batallones-1. **b**, *Caracal caracal*. **c**, *Lynx pardinus*. Abbreviations: gsn, greater ischiatic notch; sa, spina alaris; is, ischiatic spine.

Fig. 16. Sacra of different species of Felidae and Viverridae, shown at the same size for a better comparison. **a**, **b**, BAT-1'06 D4-66b, *Leptofelis vallesiensis* from Batallones-1 in cranial (**a**) and ventral (**b**) views. **c**, **d**, *Caracal caracal* in cranial (**c**) and ventral (**d**) views. **e**, **f**, *Felis silvestris* in cranial (**e**) and ventral (**f**) views. **g**, **h**, *Genetta genetta* in cranial (**g**) and ventral (**h**) views. **i**, **j**, *Martes foina* in cranial (**i**) and ventral (**j**) views. Abbreviations: cas, cranial articular surface; lsc, lateral sacral crest.

Fig. 17. Caudal view of the right femur of different species of Felidae, shown at the same size for a better comparison. **a**, BAT-1'06 D4-67a, *Leptofelis vallesiensis* from Batallones-1. **b**, *Felis silvestris*. **c**, *Caracal caracal*. **d**, *Leopardus geoffroyi*. **e**, *Lynx lynx.* Abbreviations: gt, gluteal tuberosity; lt, lesser trochanter.

Fig. 18. Cranial view of the right femur of different species of Felidae and Viverridae, shown at the same size for a better comparison. **a**, BAT-1'06 D4-67a, *Leptofelis vallesiensis* from Batallones-1. **b**, *Felis silvestris*. **c**, *Caracal caracal*. **d**, *Genetta genetta.* Arrows indicate the proximal margin of the throclea.

Fig. 19. Caudal view of the left tibia of different species of Felidae. **a**, BAT-1'06 D4-110, *Leptofelis vallesiensis* from Batallones-1. **b**, *Leopardus geoffroyi*. **c**, SNSB-BSPG 1937 II

12806, *Styriofelis turnauensis* from Wintershof-West. **d**, *Genetta genetta*. **e**, *Ursus americanus*. Abbreviations: cr, caudal ridge. Scale bar 1 (for A–D) = 20 mm Scale bar 2 (for E) = 40 mm.

Fig. 20. Calcanei of different species of Felidae, shown at the same size for a better comparison. **a**, **e**, BAT-1'06 F5-61, *Leptofelis vallesiensis* from Batallones-1 in medial (**a**) and lateral (**e**) views. **b**, **f**, *Lynx lynx* in medial (**b**) and lateral (**f**) views. **c**, **g**, *Caracal caracal* in medial (**c**) and ventral (**f**) views. **d**, **h**, *Leopardus wiedii* in medial (**d**) and lateral (**h**) views. Abbreviations: fst, talar facet of the sustentaculum tali; gqp, groove for the m. quadratus plantae (arrows indicate the proximal margin of this groove).

Fig. 21. Skeletal (**a**) and life reconstruction (**b**) of *Leptofelis vallesiensis*, based on the specimens from Batallones-1 (scale bar = 10 cm). The shown hypothetical coat colour pattern is congruent with the phylogenetic inferences about coat pattern evolution in felids proposed by Werdelin et al. (2010) (artwork by M. Antón).

Table captions

Table 1. Measurements of the postcranial bones of *L. vallesiensis* from Batallones-1.

Table 2. Measurements of the postcranial bones of *L. vallesiensis* from Batallones-1.

Table 3. Brachial, Crural, and Intermembral indices of *L. vallesiensis* and several species of Felidae and Viverridae. Data taken from Salesa (2002).

APPENDIX 1

Body mass estimation in *Leptofelis vallesiensis*

For the estimation of the body mass of *L. vallesiensis* we used the specific formulae for the family Felidae of Rodríguez (1997) and Anyonge (1993), both based on the following measurements of the appendicular skeleton: proximal width of the tibia (PW) and width of the femoral head (FHW) (Rodríguez, 1997), and distal articular (condylar) area of femur (FDA) (Anyonge, 1993). The results are:

For the proximal width of the tibia (PW), the formula is: Log Body Mass = 2.8581 (log PW) - 0.0786. The PW of the tibia BAT-1'06 D4-110 is 25.32 mm, which results in a body mass of 8.5 kg.

For the width of the femoral head (FHW), the formula is: Log Body Mass = 2.9968 (log FHW) + 0.5668. The FHW of the femur BAT-1'06 D4-67a is 12.54 mm, which results in a body mass of 7.21 kg.

For the femoral distal articular (condylar) area (FDA) the formula is: Log Body Mass = 1.32 (log FDA) – 2.16. The FDA was calculated following the methodology of Anyonge (1993) for the femora BAT-1'06 D4-67a and BAT-1'06 D4-67b, obtaining areas of 222.63 mm^2 and 229.168 mm^2, respectively. This results in a body mass of 8.68 kg from the femur BAT-1'06 D4-67a, and 9.02 kg from the specimen BAT-1'06 D4-67b.

Thus, the estimated body mass of *L. vallesiensis* from Batallones-1 is between 7.21 and 9.02 kg. The published data on the body weight of extant felines shows wider ranges, as they take into account the size variation within each species, mostly due to sexual dimorphism. Anyway, the estimated body weight of *L. vallesiensis* is close to the maximum weights of several species of extant small felines such as *Felis silvestris*, *F. chaus*, *Leopardus geoffroyi* and *Puma yaguarondi* (Sunquist and Sunquist, 2009).

APPENDIX 2

Body proportions in *Leptofelis vallesiensis*

The body proportions of the feline from BAT-1 have been calculated using the brachial, crural and intermembral indexes (Gonyea, 1976a, 1976b; Taylor, 1976; Anyonge, 1996; Iwaniuk *et al*., 1999). The formulae for these indexes are:

Brachial index (BIn) = (Length radius/Length humerus) x 100.

Crural index (CIn) = (Length tibia/ Length femur) x 100.

Intermembral index (IIn) = (Length thoracic limb/ Length pelvic limb) x 100.

The corresponding measurement were taken on the following bones of *L. vallesiensis* from Batallones-1: Femora (BAT-1’06 D4-67a and BAT-1’06 D4-67b), Tibiae (BAT-1’06 D4-110 and BAT-1’06 D4-103), Humeri (BAT-1’02 D6–58 and B-4968) and Radii (B/S-575 and B-2074(5)).

The results of the different indexes for *L. vallesiensis* are as follows: BIn: 89.16–91.13; CIn: 103.01–104.04; IIn: 80.23–80.93.

Figure 1

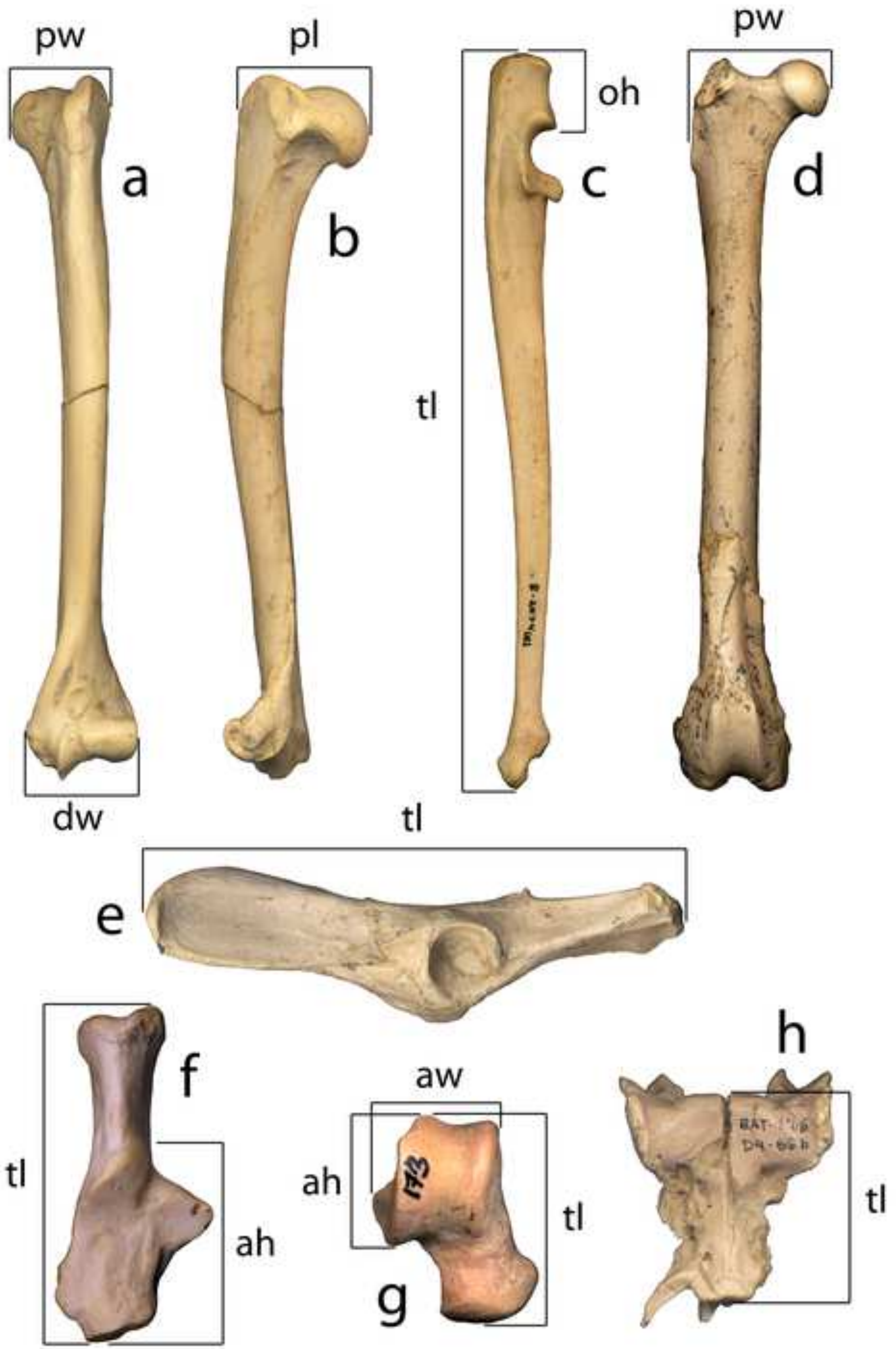


Figure 2

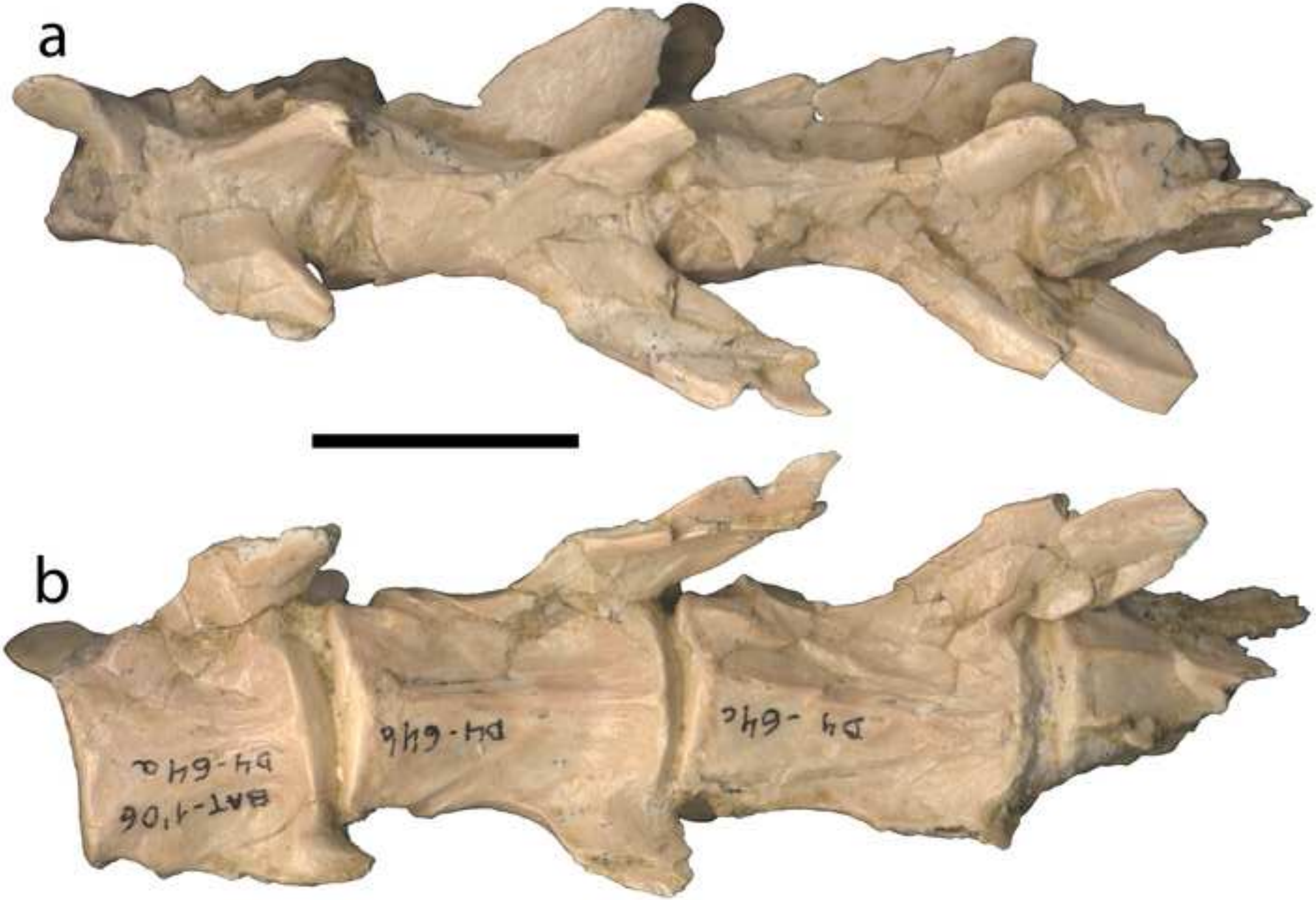


Figure 3

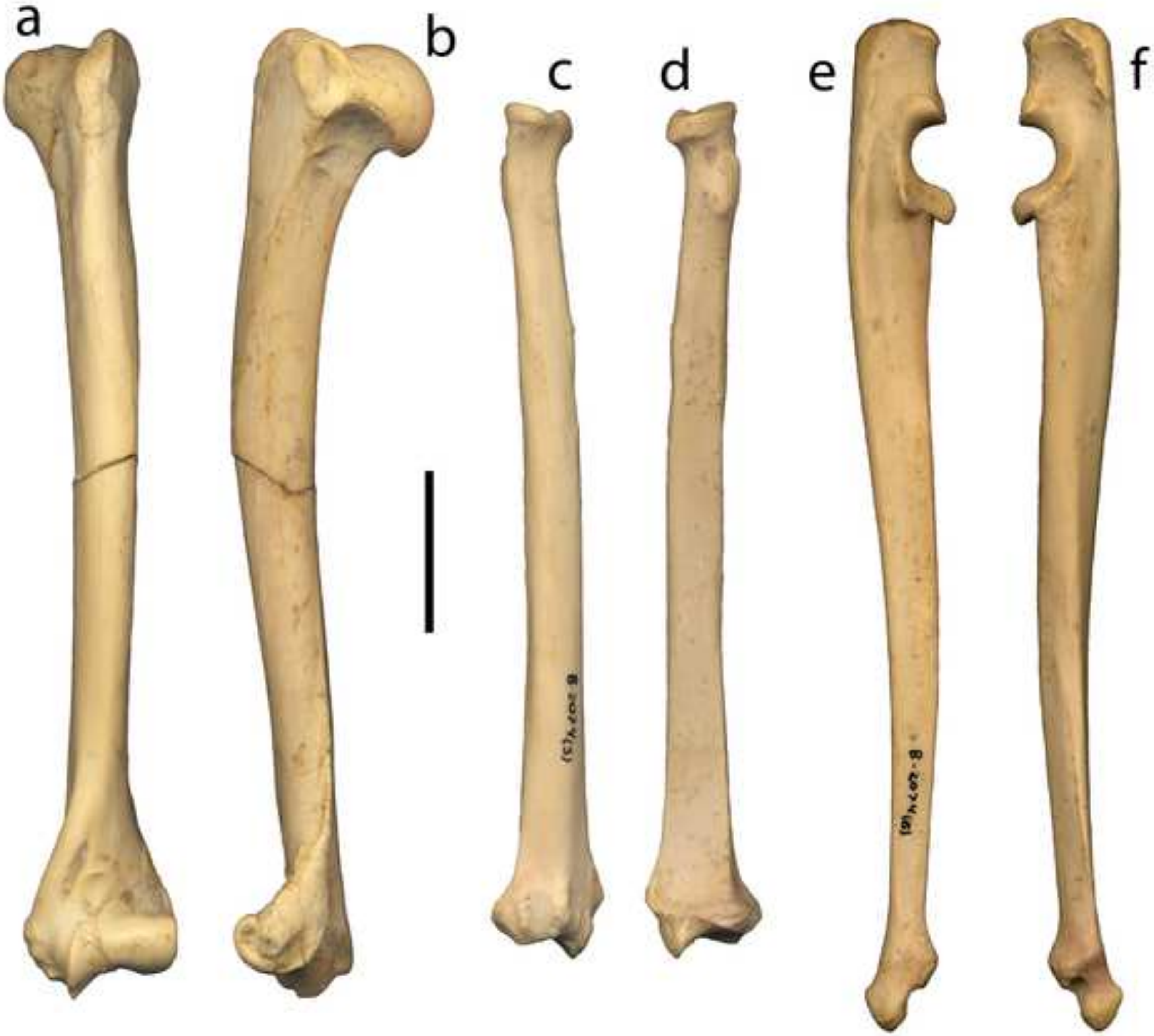
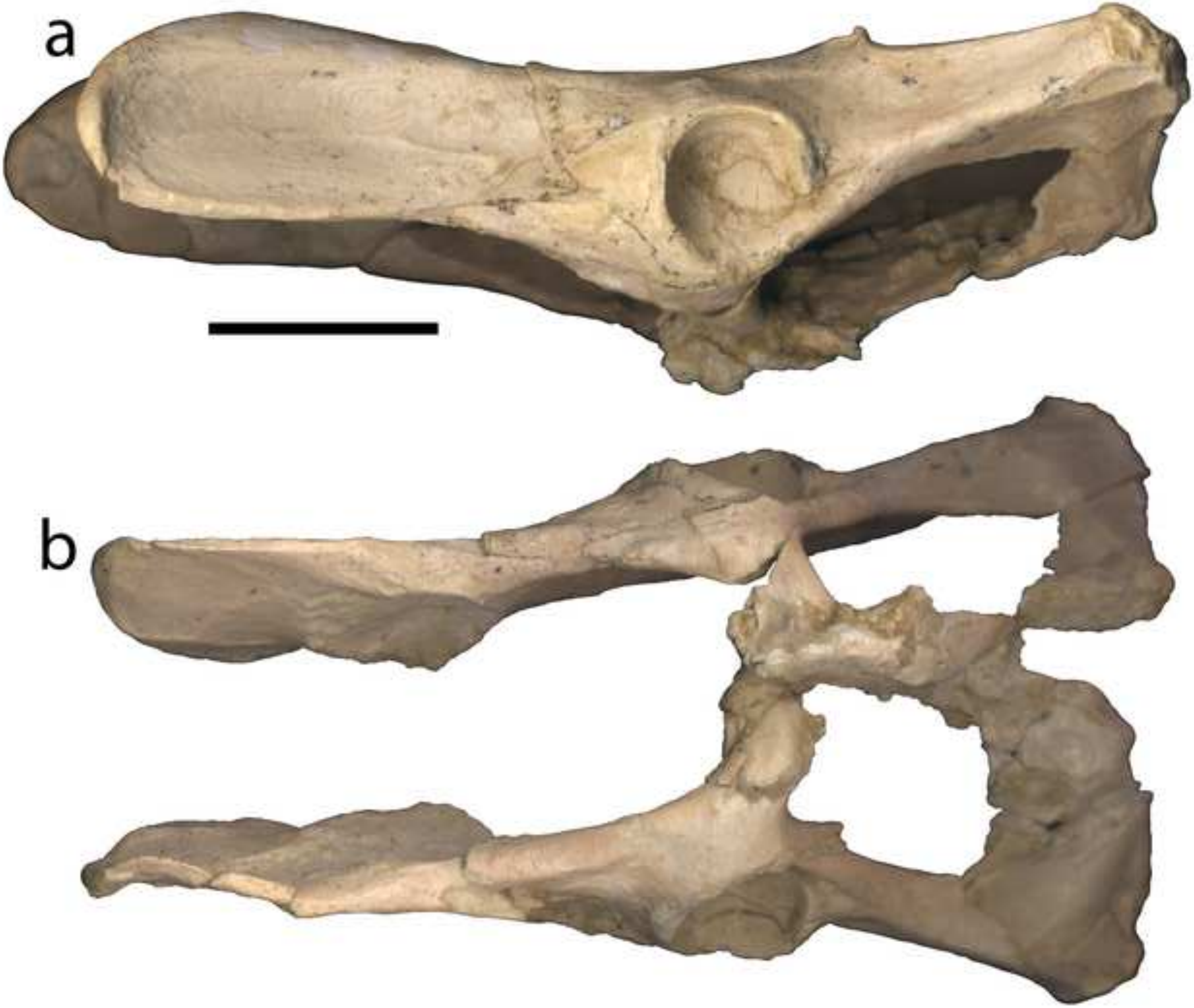


Figure 4

Figure 5



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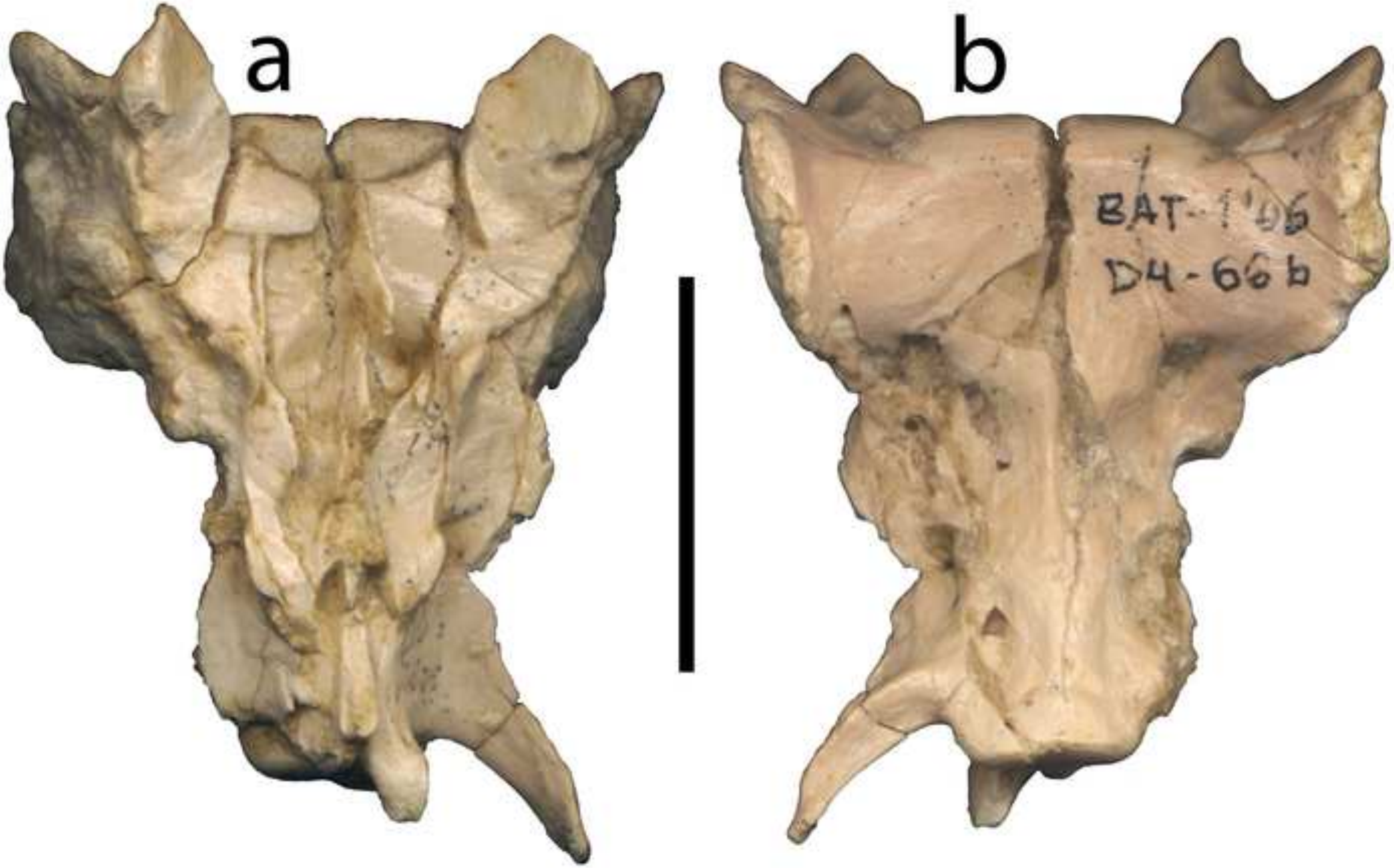


Figure 7

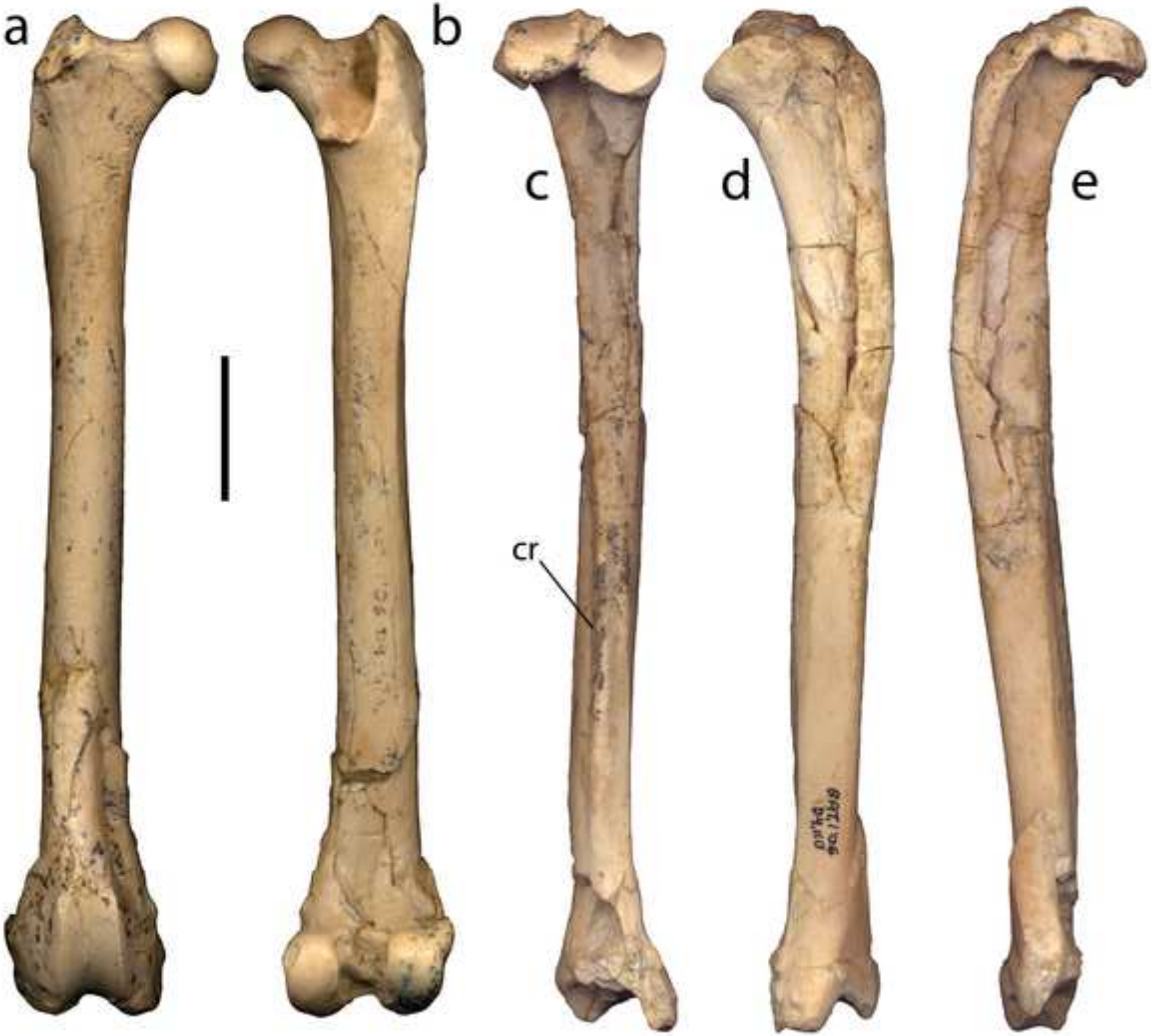


Figure 8

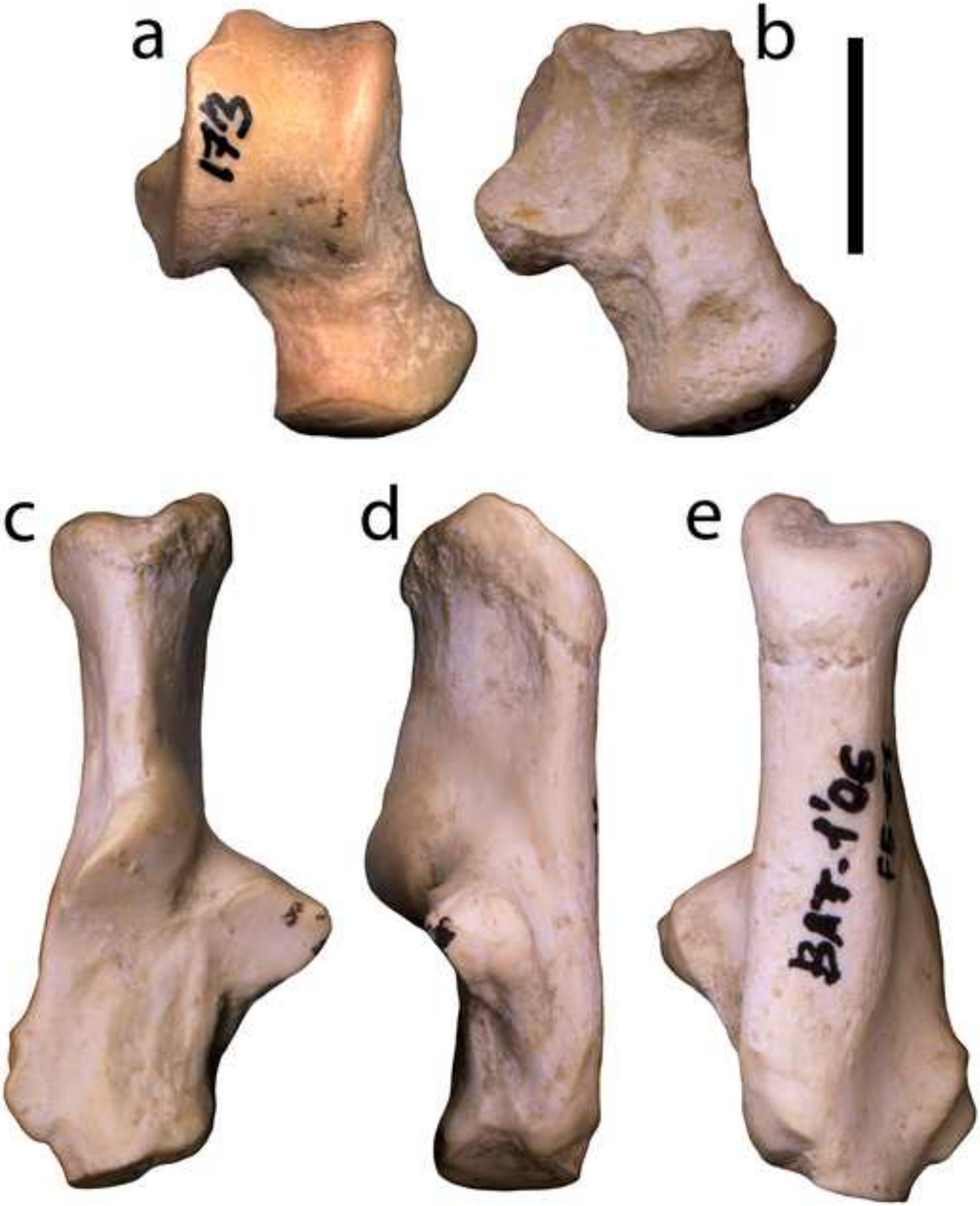
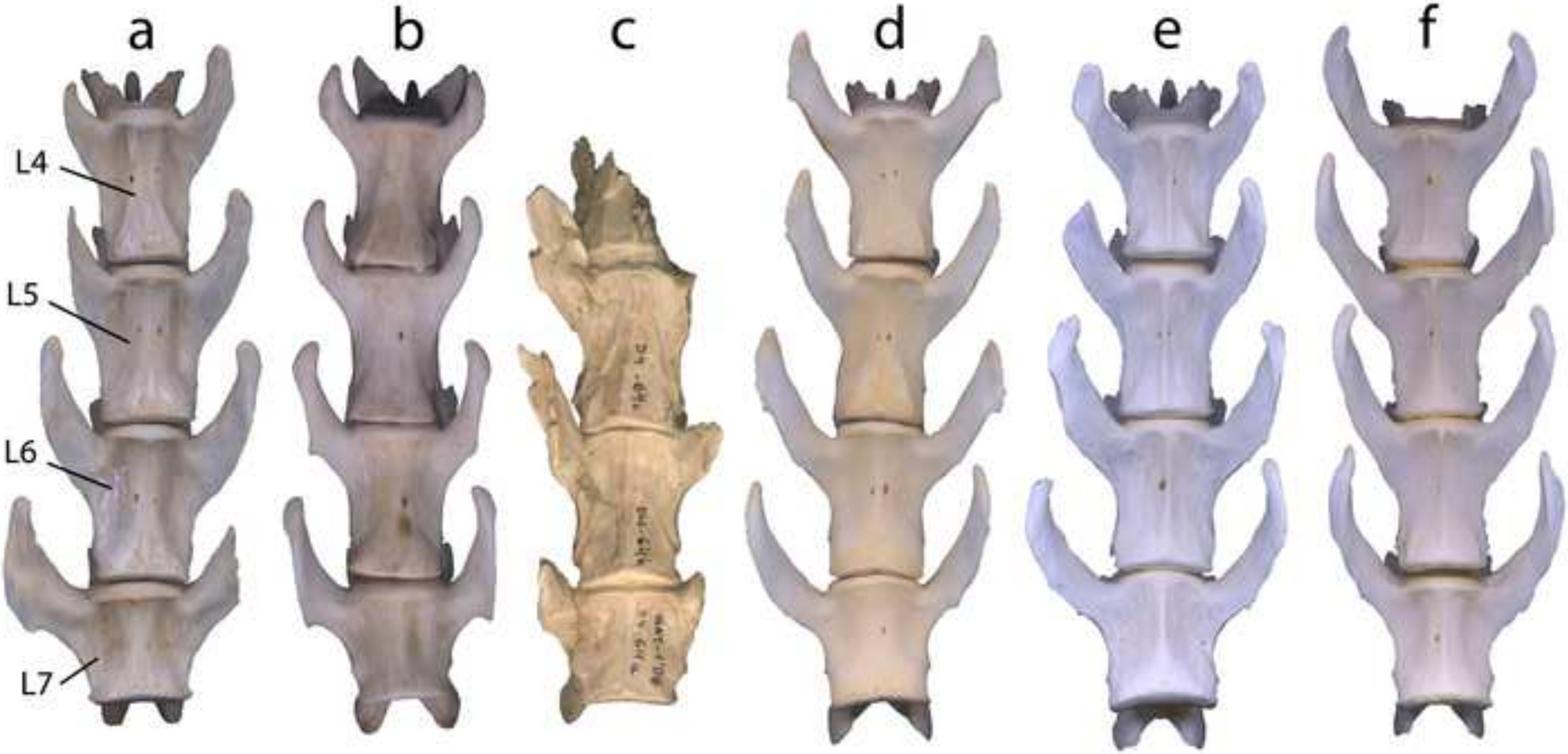


Figure 9



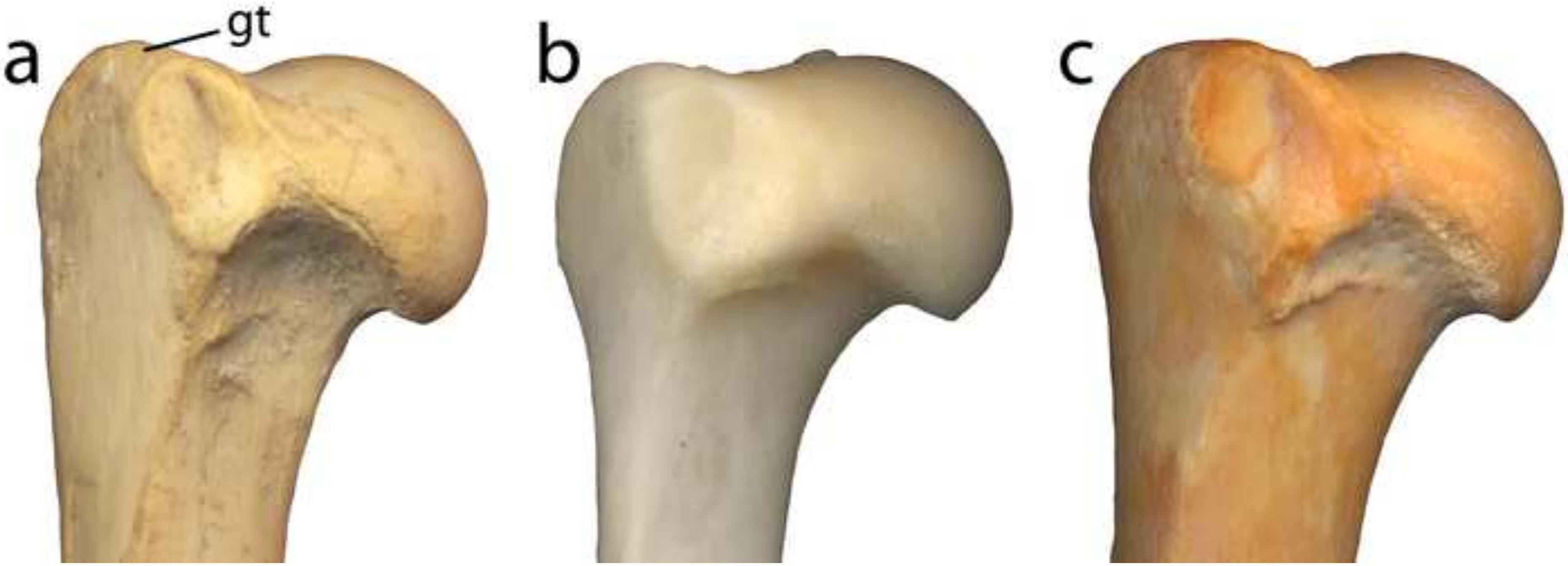

a
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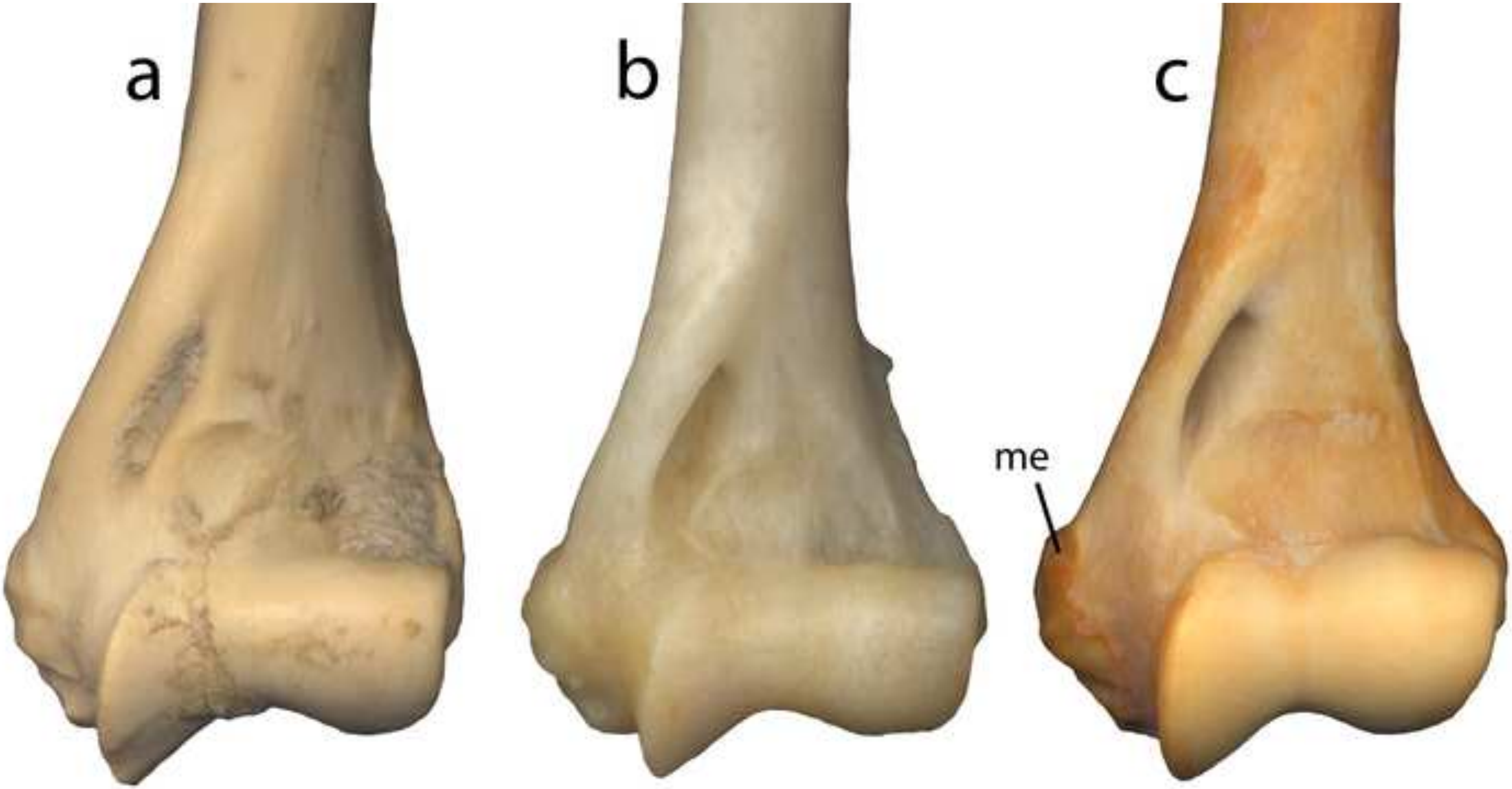
Figure 11



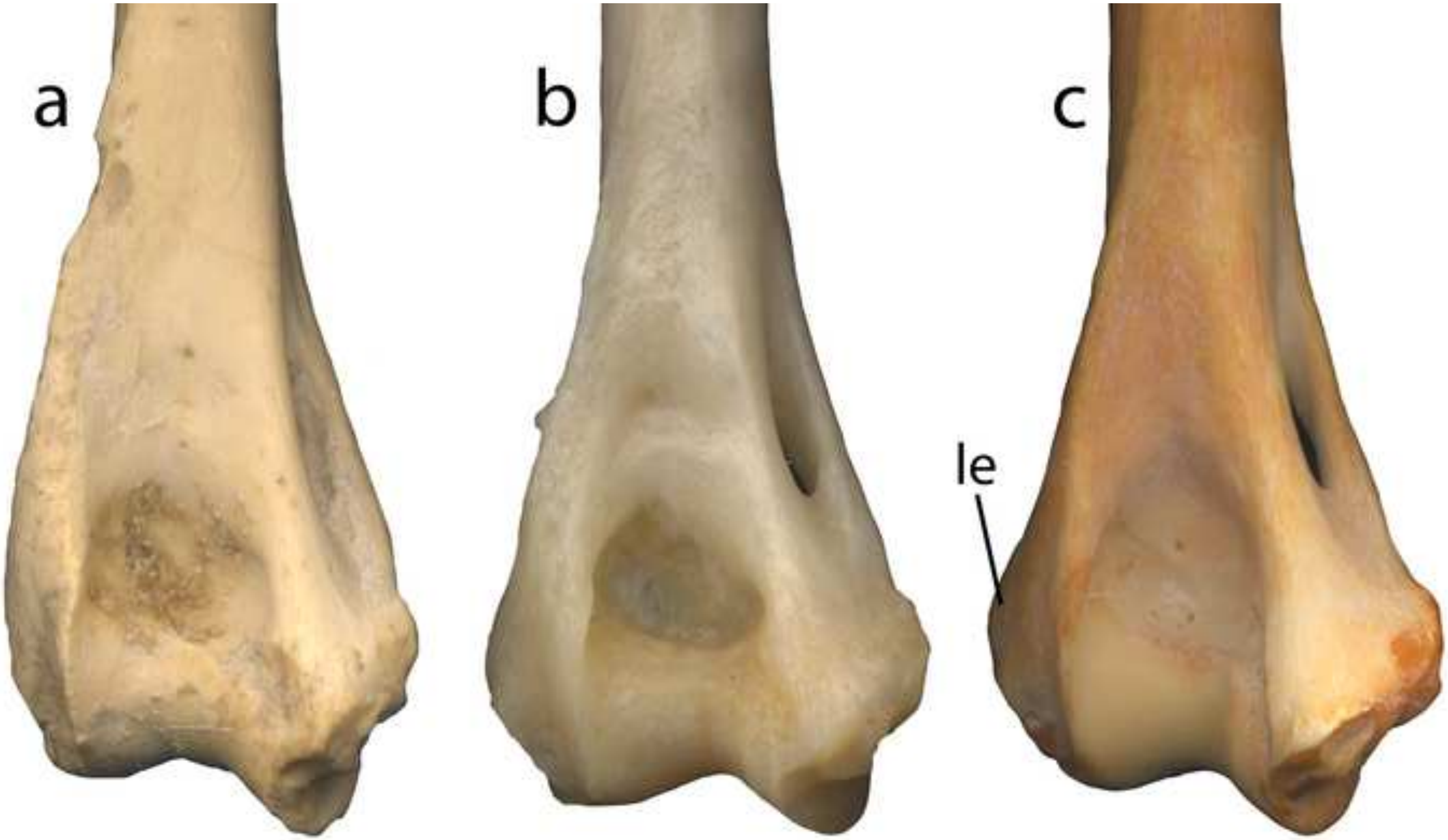

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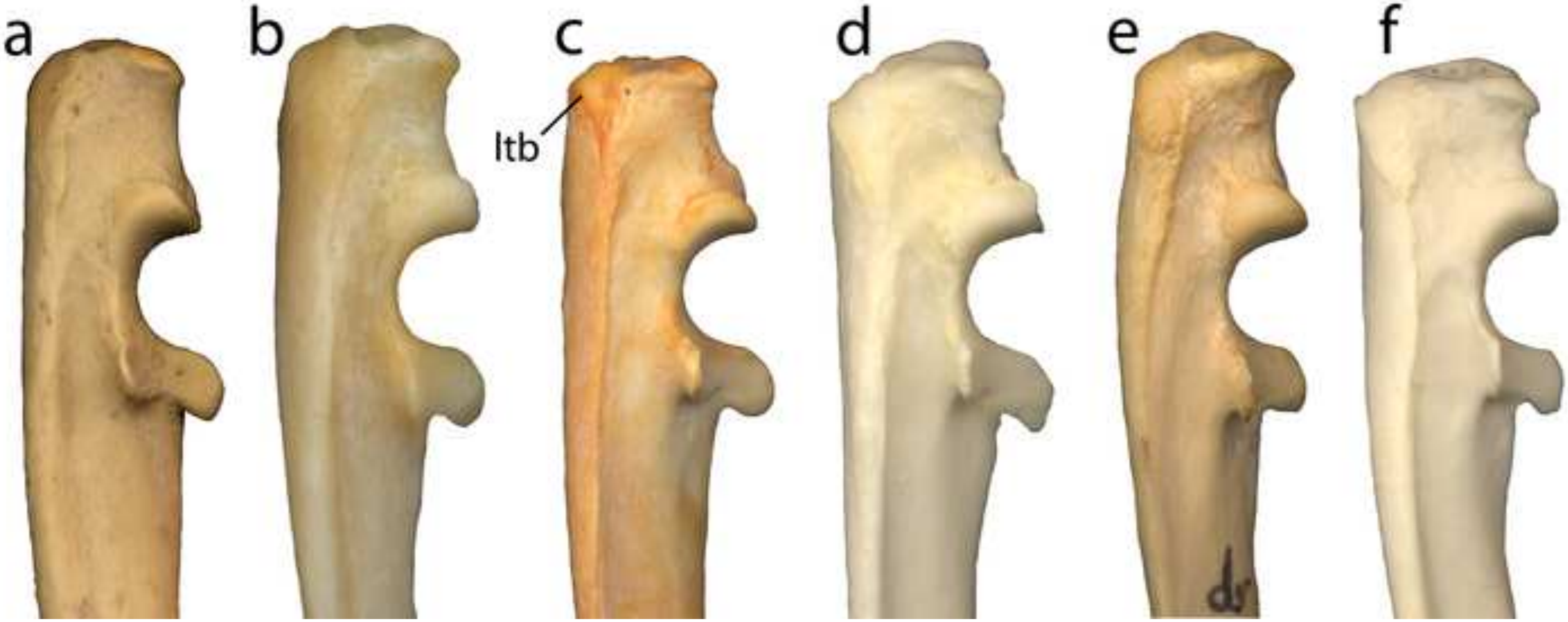
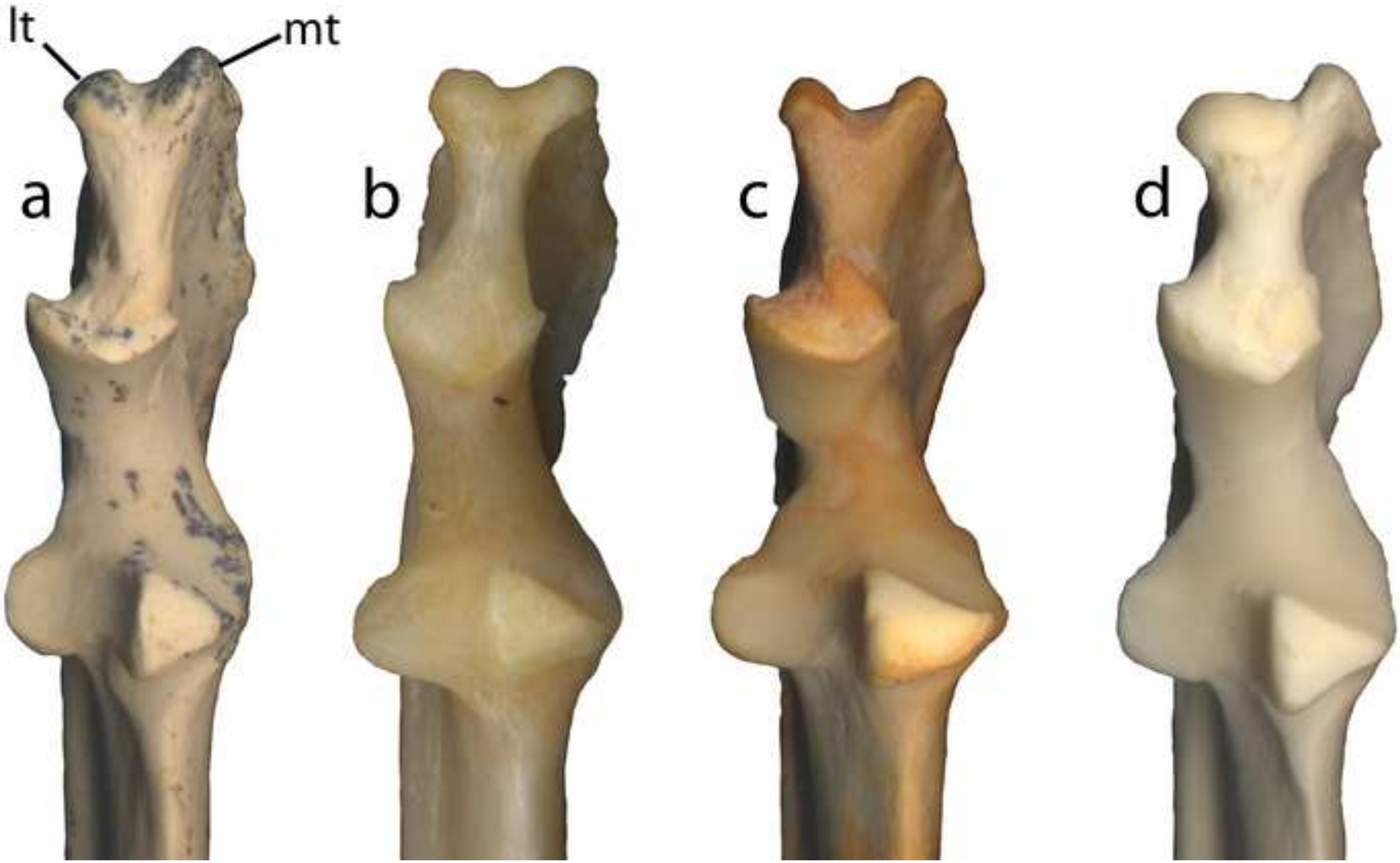
Figure 13

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d

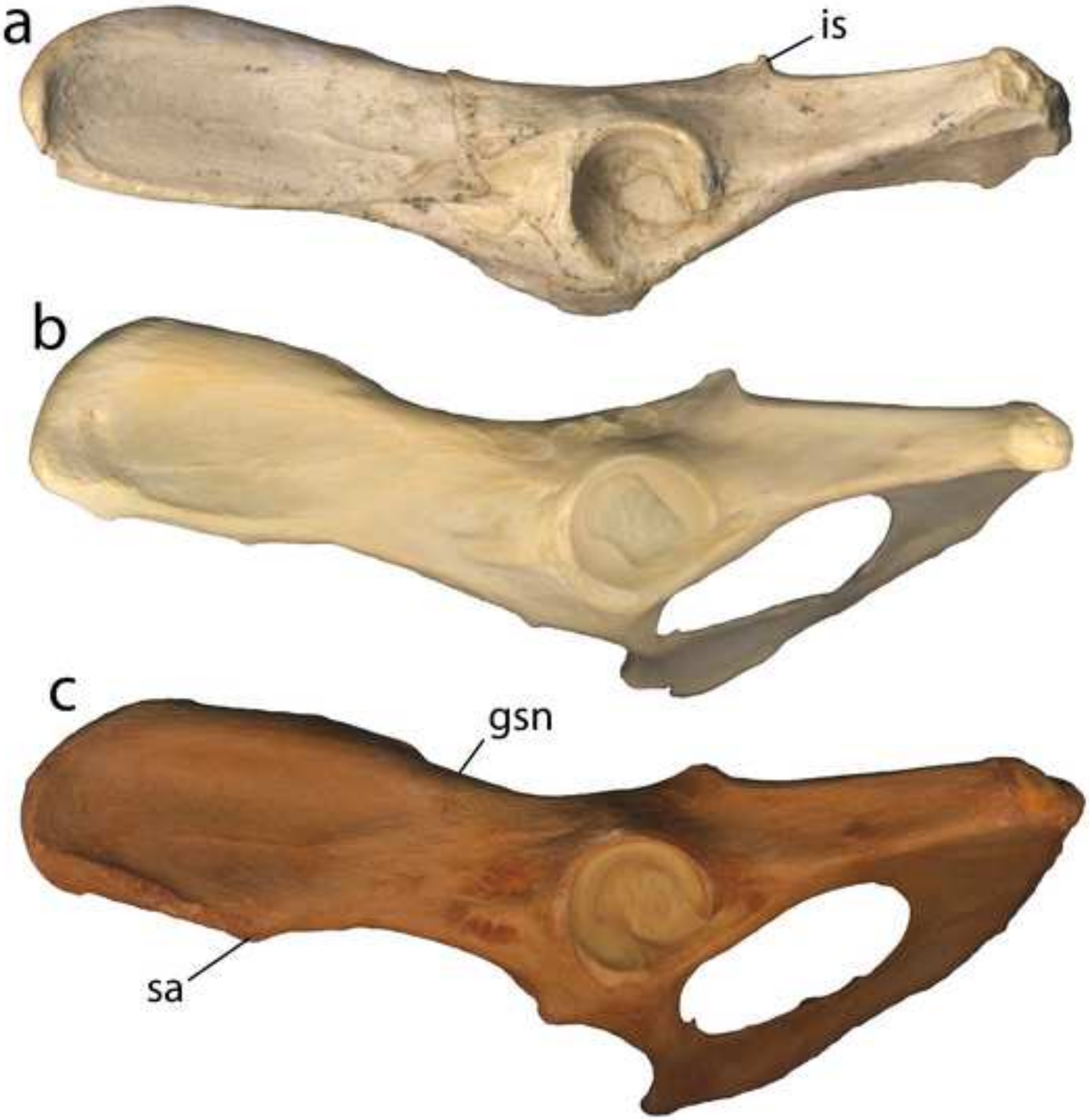
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Figure 16

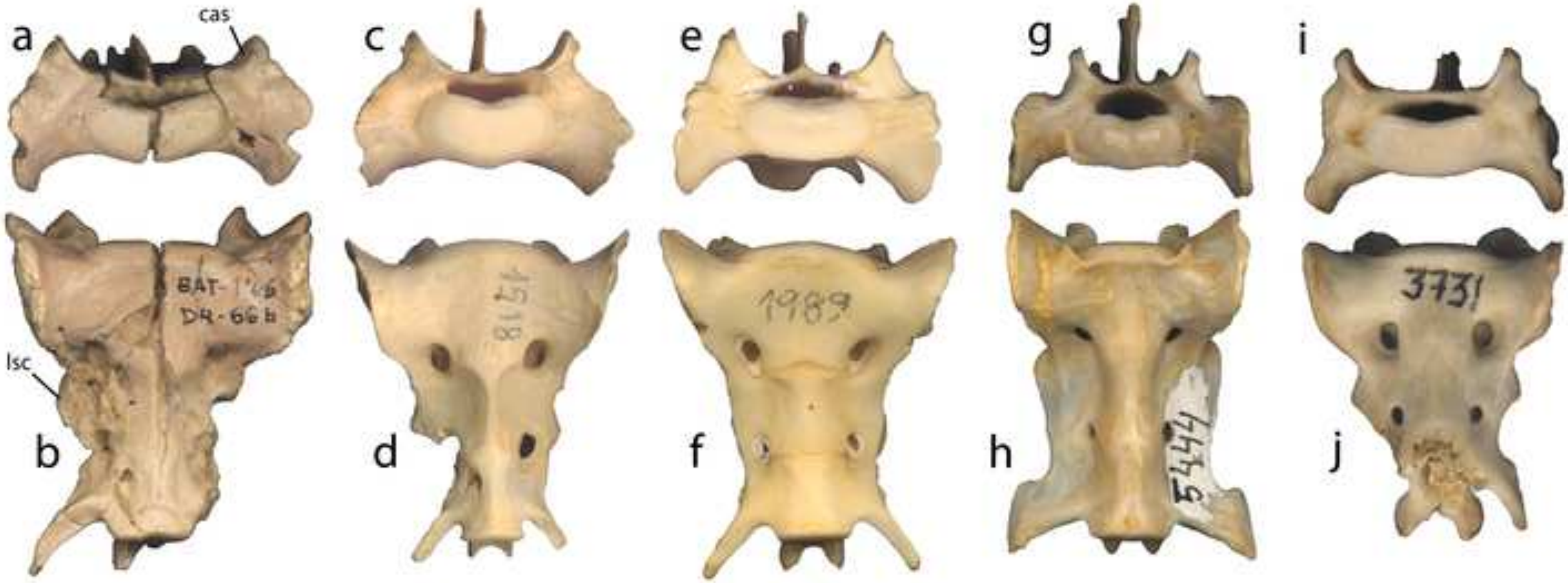
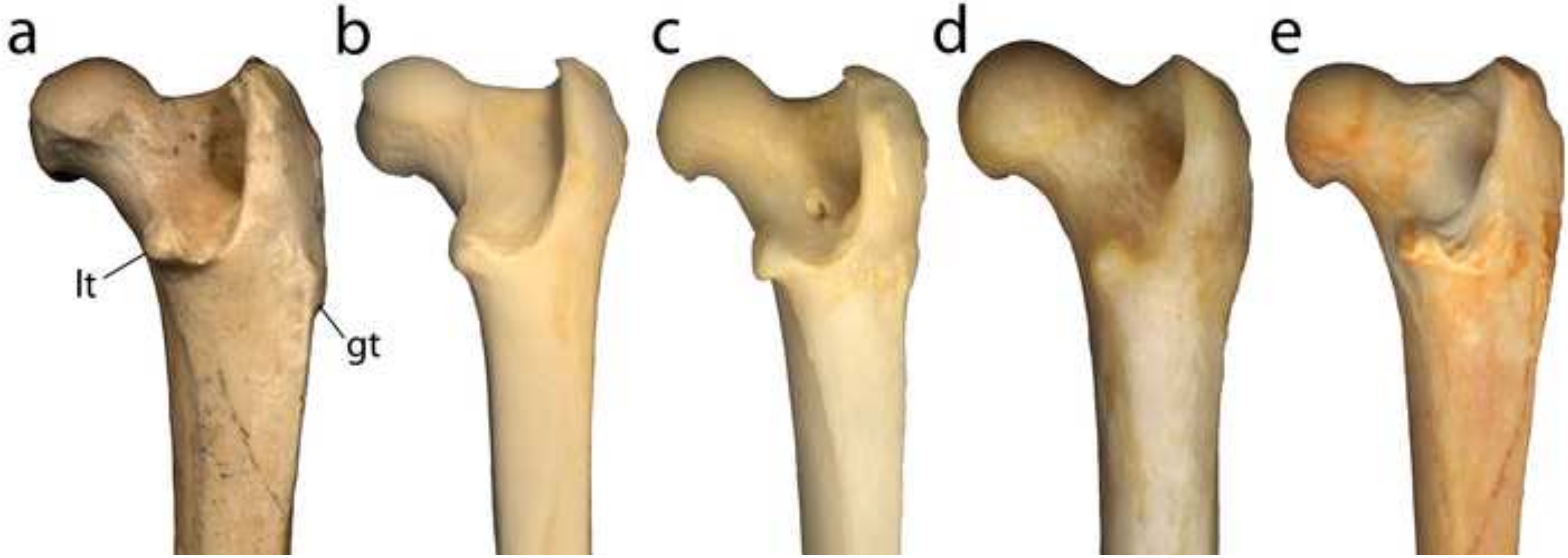
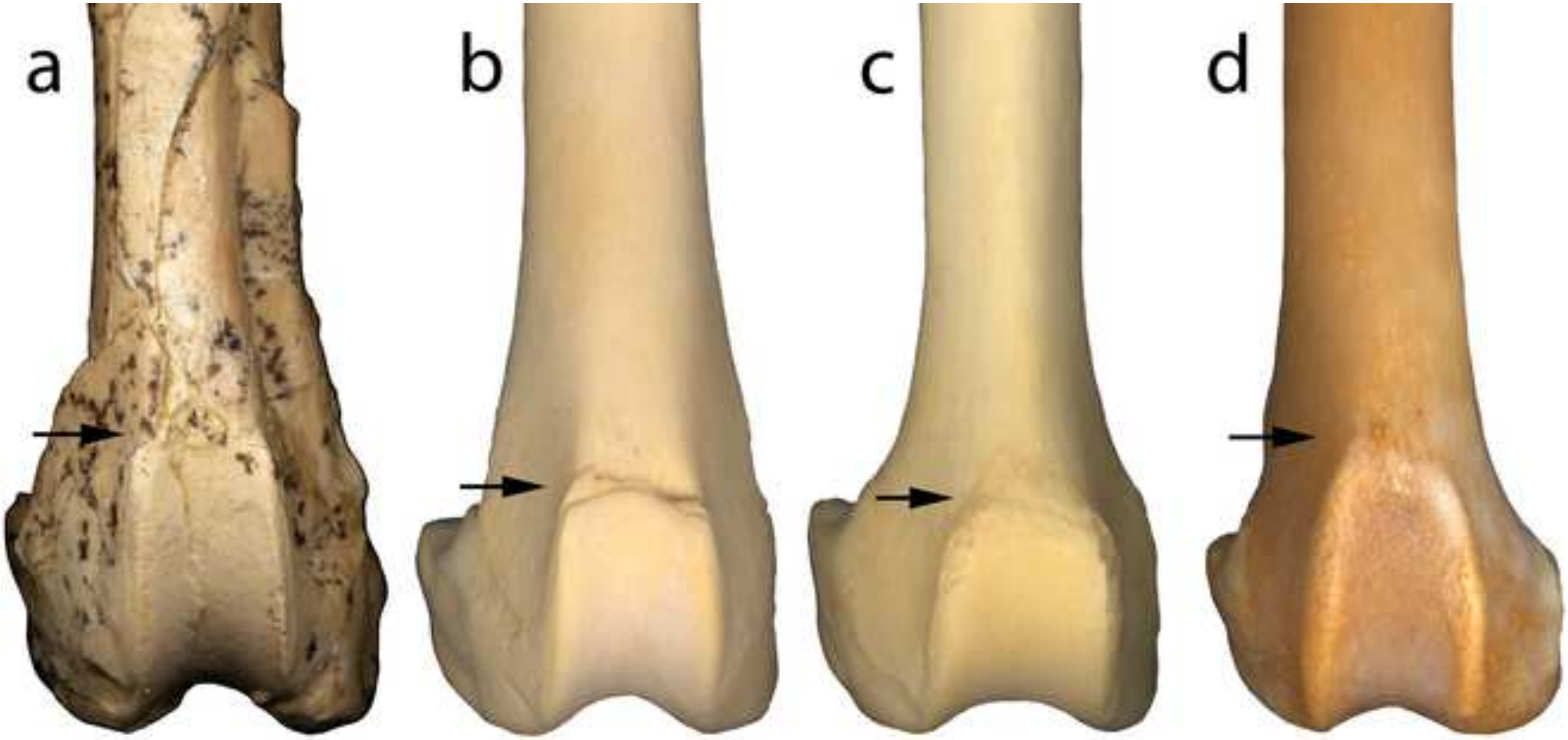


Figure 17




a
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d

Figure 19

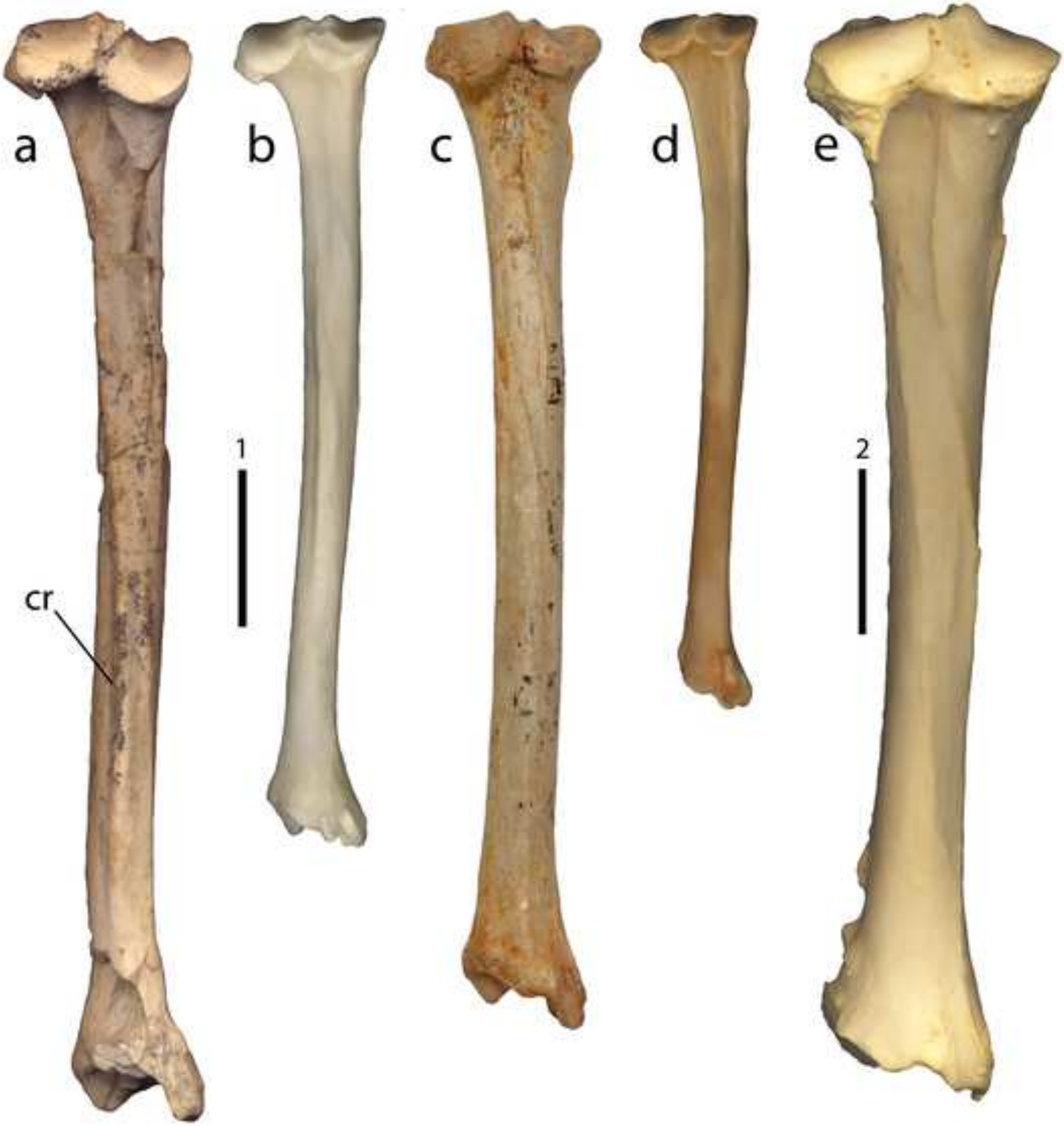

Figure 20

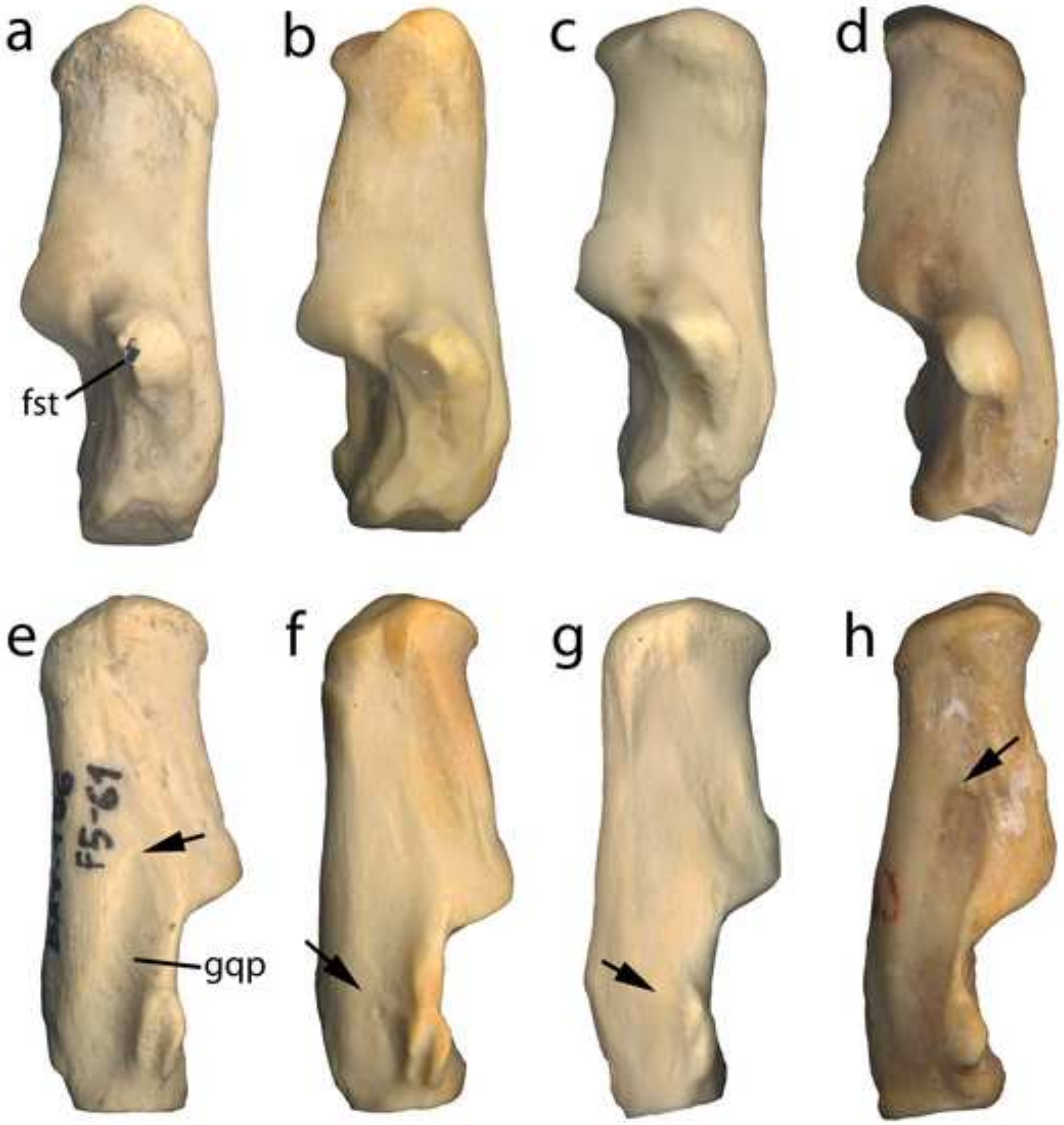

Figure 21

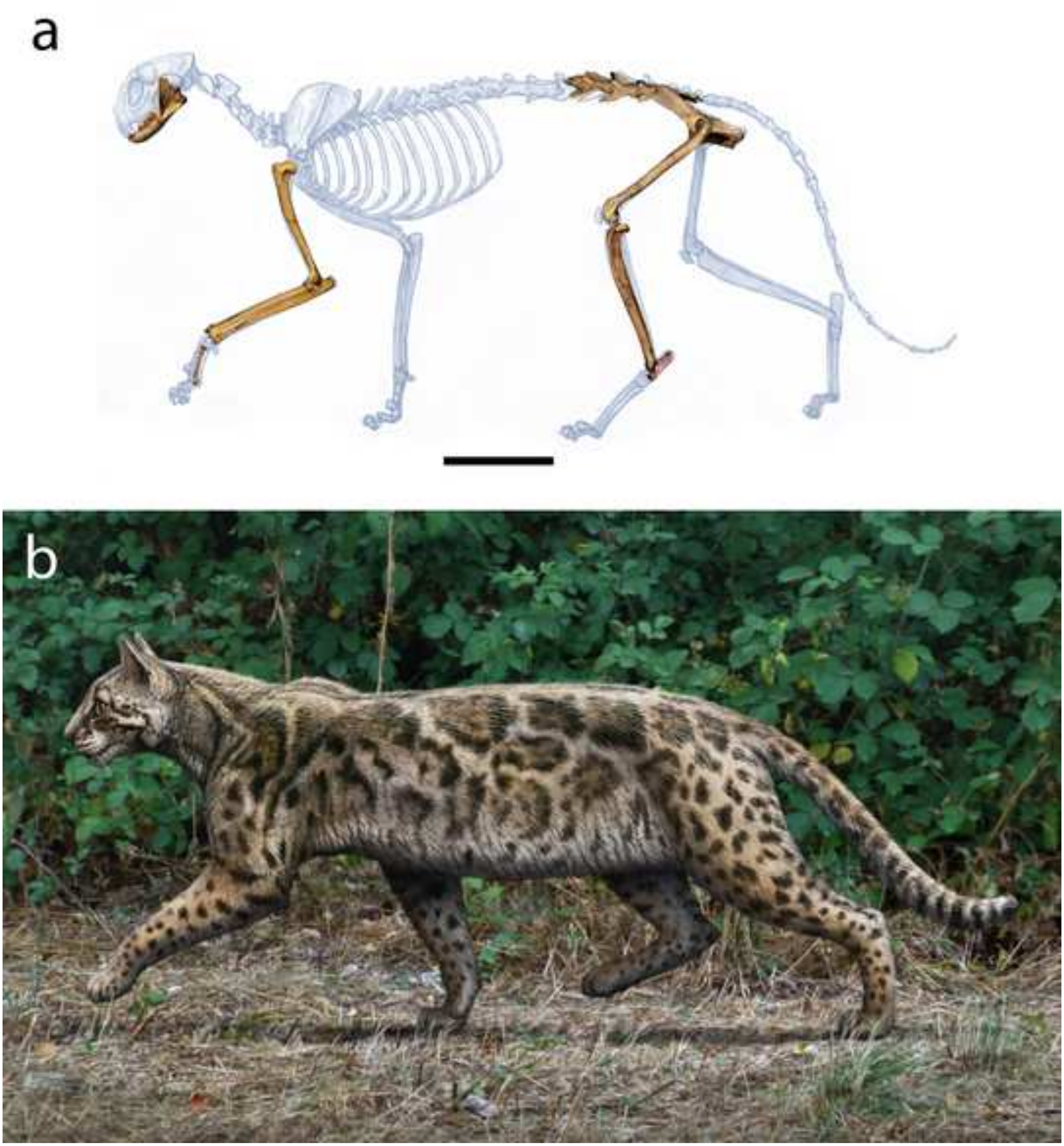

Table 1. Measurements of the postcranial bones of *L. vallesiensis* from Batallones-1.

Element	**Number**	**tl**	**pw**	**dw**	**pl**
Right femur	BAT-1’06 D4-67a	142.13	26.80	24.73	
Left femur	BAT-1’06 D4-67b	141.04	24.88	23.33	
Right tibia	BAT-1’06 D4-103	147.28*	25.25	18.21	25.10
Left tibia	BAT-1’06 D4-110	144.86	25.30	18.32	22.84*
Left radius	B/S-575	111.84	9.62	13.60	
Right radius	B-2074s	108.32	9.72	13.56	
Left humerus	BAT-1’02 D6-58	122.69	17.30	19.72	24.12
Right humerus	B-4968	123.44*	18.00	19.46	23.84
Left coxal	BAT-1’06 D4-66a	99.36	-	-	
Right Mc I	BAT-1’03 D4-239	13.58	5.14	4.00	
Right Mc II	BAT-1’03 D5-162	32.31	4.85	5.57	
Right Mc III	BAT-1’04 D4-184	37.71	6.35	5.82	
Right Mc IV	BAT-1’03 E4-164	36.37	5.18	5.41	
Right Mc V	BAT-1’04 E5-129	29.24	5.18	5.58	
Left Mc V	BAT-1’04 E5-212	29.01	5.17	5.63	

Table 2. Measurements of the postcranial bones of *L. vallesiensis* from Batallones-1.

Element	**Number**	**tl**	**oh**	**ah**	**aw**
Right ulna	BAT-1’08 C8-24	131.06	15.02	16.67	-
Right ulna	BAT-1’06 E5-50	123.73	13.06	14.80	-
Right ulna	B-2074(6)	128.12	13.44*	14.84	-
Sacrum	BAT-1’06 D4-66b	33.94	-	-	-
Left talus	BAT-1’03 D6-300	19.42	-	12.46	13.11
Right calcaneus	BAT-1’06 F5-61	33.19	-	16.36	14.18
Left calcaneus	BAT-1’04 D6-62	31.34	-	15.68	14.93
Left calcaneus	BAT-1’03 D6-301	34.40	-	16.10	14.39

Table 3. Brachial, Crural and Intermembral indexes of *L. vallesiensis* and several species of Felidae and Viverridae. Data taken from Salesa (2002).

Species	**BIn**	**CIn**	**IIn**
Felis lybica	98.75	95.35	85.08
Caracal caracal	91.34	95.45	80.73
Leopardus pardalis	88.39	95.50	85.14
Puma yaguarondi	81.86	95.58	77.33
Profelis aurata	86.11	95.97	80.31
Prionailurus viverrinus	89.79	96.97	82.92
Lynx pardinus	96.31	99.72	82.11
Leopardus wiedii	85.48	100.55	81.05
Leopardus tigrinus	84.50	100.49	81.07
Leopardus geoffroyi	89.34	100.09	84.73
Prionailurus planiceps	88.87	101.69	81.97
Pardofelis marmorata	83.19	102.69	80.65
Prionailurus bengalensis	86.90	102.77	83.49
Lynx lynx	97.89	103.30	82.75
Felis silvestris	94.59	104.81	86.01
Leptailurus serval	95.78	101.87	87.38
Felis chaus	97.66	111.72	93.36
Catopuma temminckii	87.40	118.42	73.95
Neofelis nebulosa	81.92	99.21	82.47
Puma concolor	83.90	93.72	82.70
Uncia uncia	91.41	103.12	84.93
Panthera pardus	82.24	92.63	84.95
Panthera onca	80.80	86.61	87.71
Acinonyx jubatus	103.30	105.00	90.10
Panthera leo	95.35	88.77	91.91
Genetta genetta	85.77	106.05	80.55
Civettictis civetta	88.64	96.44	81.88
Leptofelis vallesiensis	89.16–91.13	103.01–104.04	80.23–80.93