

Tracing the origin of the panda's thumb

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Received: 14 April 2015 / Revised: 19 May 2015 / Accepted: 21 May 2015 / Published online: 3 June 2015
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Abstract We investigate the relative development of the carnivoran radial sesamoids to untangle the evolution of this iconic structure. In the pandas (both giant and red), this ‘false thumb’ is known to perform a grasping role during bamboo feeding in both the red and giant pandas. An original locomotor role has been inferred for ailurids, but this remains to be ascertained for ursids. A large sample of radial sesamoids of *Indarctos arctoides* from the Miocene of Batallones-3 (Spain) indicates that this early ailuropodine bear displayed a relatively hypertrophied radial sesamoid, with a configuration more similar to that of the red panda and other carnivorans than to that of giant pandas. This false thumb is the first evidence of this feature in the Ursidae, which can be linked to a more herbivorous diet. Moreover, in the two extant pandas, the false thumb should not be interpreted as an anatomical convergence, but as an exaptive convergence regarding its use during the bamboo feeding, which changes the evolutionary view of this singular structure.

Keywords Cerro de los Batallones · Late Miocene · Radial sesamoid · Carnivora · Ursidae

Introduction

Locality and age

Batallones-3 (BAT-3) is one of the nine fossil vertebrate localities from the fossiliferous area of Cerro de los Batallones (Morales et al. 2008) (Madrid Basin, Spain; Fig. 1). All nine Batallones fossil sites have been dated based on their faunal composition as belonging to the late Vallesian (MN10), approximately 9 Ma (Morales et al. 2008; López-Antoñanzas et al. 2010). The exceptionally rich record of carnivorans in Batallones-3 has been attributed to the fact that this pseudokarstic locality acted as a natural trap for all kinds of carnivorous vertebrates (Morales et al. 2008; Calvo et al. 2013; Domingo et al. 2013), including

Communicated by: Sven Thatje

Electronic supplementary material The online version of this article (doi:10.1007/s00114-015-1286-3) contains supplementary material, which is available to authorized users.

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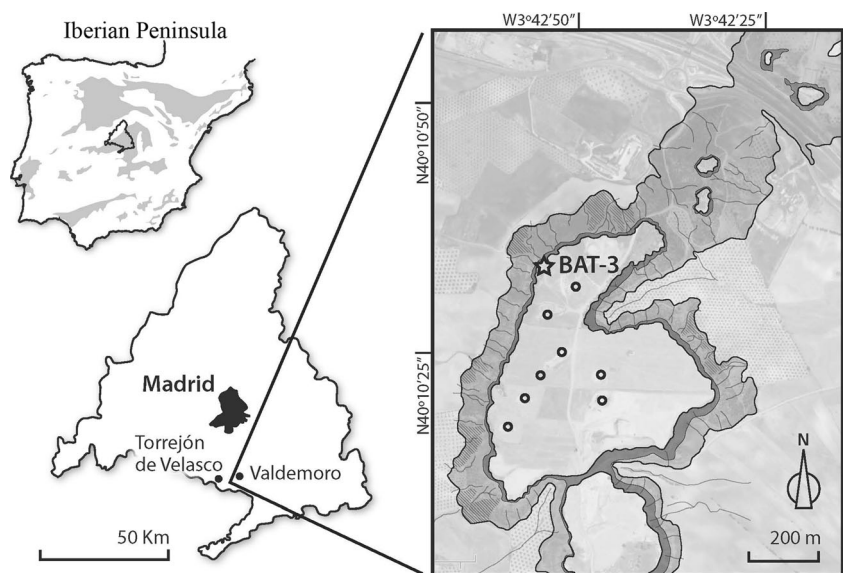
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Fig. 1 Schematic map of Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid, Spain), showing the location of the nine sites. The site of Batallones-3 is denoted with a star



not only mammalian carnivorans (Abella 2011; Salesa et al. 2012; Abella et al. 2013a, b; Monescillo et al. 2014; Siliceo et al. 2014; Valenciano et al. 2015), but also scavenging birds (Morales et al. 2008) as well as monitor lizards (Delfino et al. 2013). *Indarctos arctoides* is among the most abundant carnivorans from Batallones-3, being represented by as many as 1984 identifiable remains (updated relative to Abella et al. 2013b). The sample of radial sesamoids of *I. arctoides* described here consists of 13 fossil remains, which correspond to a minimum number of eight individuals, which represent by far the most complete collection of this species and probably of the genus as a whole (Abella et al. 2013a, b).

Radial sesamoids and the evolutionary significance of the panda's false thumb

The radial sesamoid (also called 'sesamoid bone of the muscle *abductor digiti I longus*' or 'os radiale externum') is present in many carnivorans and other mammals (marsupials, multituberculates, rodents, insectivorans, chiropterans, scandentians and primates), being related to the tendon of the m. *abductor digiti I longus* at the level of the joint between the scapholunar and the trapezium (Krause and Jenkins 1983; Szalay 1994; Le Minor 1994). By definition, a sesamoid is a small and more or less rounded mass embedded in certain tendons and usually related to joint surfaces. Their functions probably are to modify pressure, to diminish friction, and occasionally to alter the direction of a muscle pull (Gray 1977; Barone 2000). However, the radial sesamoid can be considered a special kind of sesamoid, with a completely different role and therefore subjected to different anatomical strictures. In most instances, this bone is of similar size to other sesamoids, or even vestigial, but in some mammals, such as talpids (Krause and Jenkins 1983; Sánchez-Villagra and

Menke 2005), many tenrecids (Salton and Sargis 2008) and elephants (Hutchinson et al. 2011), it constitutes a digit-like element that is variously called 'os falciforme', 'prepollex' or 'predigit'. Furthermore, a truly hypertrophied radial sesamoid, constituting a functional 'false thumb', is considered to be present in the giant panda, *Ailuropoda melanoleuca* (Lankester and Lydekker 1901; Wood-Jones 1939a, b; Davis 1964; Gould 1978; Chorn and Hoffmann 1978; Endo et al. 1996, 1999a, b, 2001a; Antón, et al. 2006; Salesa et al. 2006a, b) and, to a lesser extent, in the red panda, *Ailurus fulgens* (Roberts and Gittleman 1984; Endo et al. 2001b, 2007; Antón et al. 2006; Salesa et al. 2006b). The functional role of the radial sesamoid as a grasping structure essentially depends on its size and degree of movement relative to the metapodials and other wrist bones, thus being only possible when the radial sesamoid is relatively long compared to other bones of the manus (Abella et al. 2013a). In the two pandas, the large radial sesamoid performs a manipulatory role during bamboo feeding (Wood-Jones 1939a, b; Davis 1964; Chorn and Hoffmann 1978; Roberts and Gittleman 1984; Salesa et al. 2006a, b) by providing some degree of opposability and thereby functioning as a 'false thumb' or 'pseudo-thumb'.

Ever since Gould's seminal essay on the 'panda's thumb' (Gould 1980; Gould and Vrba 1982), this structure has become one of the most famous examples to illustrate the contingent nature of evolution, as opposed to optimality of design. The panda's false thumb illustrates one of the Darwinian principles of historical inference, namely, that based on finding discordances (imperfections or oddities) between the anatomy of an organism and its current circumstances, which make no sense outside the evolutionary paradigm (Gould 2002). More recently, with the recognition that lesser pandas are only distantly related to giant pandas but also display an enlarged radial sesamoid involved in bamboo feeding activities, the

false thumb of both pandas has acquired further significance as one of the most remarkable examples of convergent evolution (Antón et al. 2006; Salesa et al. 2006b). Given their similar grasping function during bamboo feeding and based on extant taxa alone, it might seem warranted to infer that the giant and lesser pandas' hypertrophied radial sesamoids constitute a remarkable case of convergent adaptation. However, the radial sesamoid is not employed as a truly opposable and freely movable thumb in either the giant or lesser panda (contra Davis 1964). In the former, the 'false thumb' constitutes a part of a double pincer-like, manipulative functional apparatus in which the hand flexes around the scapholunar and the uniform, so as to grasp objects between the true digits and both the radial sesamoid and the pisiform (Endo et al. 1999a, b, 2001a; Antón et al. 2006). In contrast, the less marked hypertrophy of the radial sesamoid of the lesser panda, coupled with associated musculoskeletal differences, indicate the possession of a different grasping mechanism (Endo et al. 2001b, 2007; Antón et al. 2006; Salesa et al. 2006b; Abella et al. 2013a), more similar to that displayed by other small- to medium-sized carnivorans. In the latter taxa, these grasping abilities are employed not only in food manipulation but also in arboreal climbing behaviours along thin branches (Antón et al. 2006), given the lack in these taxa of the true thumb opposability characteristic of primates.

The simultaneous locomotor and manipulatory role of the radial sesamoid in ailurids casts some doubts on the adaptive origin of this structure. In fact, locomotion has been favoured as the original primary role of this structure, based on the information provided by the fossil record (Antón et al. 2006; Salesa et al. 2006b). The remains of the extinct ailurid *Simocyon batalleri* from Spain traced the possession of a hypertrophied radial sesamoid in this group back to the Late Miocene, clearly prior to the acquisition of the extreme herbivorous adaptations of the extant *Ai. fulgens* (Salesa et al. 2006b, 2008). This is confirmed by the common occurrence of this feature in younger members of the same lineage, even if not as well developed as in the Ailuridae (Wallace 2011). This fact indicates that, in ailurids, the large radial sesamoid originally had a primary locomotor role, probably related to climbing on thin branches (Antón et al. 2006; Salesa et al. 2006b), having been subsequently co-opted to perform a manipulatory function and thus constituting an exaptation rather than adaptation to bamboo feeding (Antón et al. 2006).

In the giant panda lineage, the evolutionary origin of the false thumb is less well understood, and thus it is uncertain whether it should be considered an exaptation regarding its current role in bamboo feeding (Hutchinson et al. 2011), as in lesser pandas (Antón et al. 2006; Salesa et al. 2006a, b), or rather as an adaptation to food manipulation, as customarily thought (Wood-Jones 1939a, b; Davis 1964; Endo et al. 1999b; Antón et al. 2006; Salesa et al. 2006b). The interpretation of the giant panda's false thumb as an adaptation to

manipulation is supported by the small (ursine-like) radial sesamoid previously reported for the Late Miocene ailuropodine genus *Indarctos* (Roussiakis 2001). However, this interpretation is contradicted by the presence of a somewhat hypertrophied radial sesamoid in the spectacled bear (*Tremarctos ornatus*), thus contrasting with the much smaller, round and more compact radial sesamoid of the remaining extant ursids (Lankester and Lydekker 1901; Davis 1964; Endo et al. 1999c; Salesa et al. 2006b). Based on the presence of a relatively large sesamoid in *T. ornatus*, it has been suggested that some degree of radial sesamoid hypertrophy might be symplesiomorphic for ursids as a whole, having been subsequently reduced in ursines (Salesa et al. 2006a), which would support an exaptive explanation for the hypertrophied sesamoid of *A. melanoleuca*. Discriminating between these two hypotheses (adaptation vs. exaptation) in the case of the giant panda's false thumb is impossible without recourse to the information provided by the fossil record (Salesa et al. 2006b). Here, we test these hypotheses based on the radial sesamoid of *Indarctos*, which according to recent cladistic analyses would be an early member of the Ailuropodinae, more specifically belonging to the sister-taxon Indarctini of the giant panda lineage in a strict sense Ailuropodini (Abella et al. 2012, 2014). In particular, we rely on a large sample of fossil radial sesamoids of *I. arctoides* Déperet, 1895 from the late Vallesian (MN10) of Batallones, which is about 3 million years older than the single radial sesamoid previously reported for this genus, belonging to *Indarctos punjabiensis* (formerly attributed to *Indarctos atticus atticus*) from the Turolian (MN12) of Pikermi (Roussiakis 2001).

Materials and methods

Studied material Based on size and morphology, a total of 13 (eight right and five left) radial sesamoids from Batallones-3 can be attributed to *I. arctoides*; eight are thought to be male and five are thought to be female, belonging to a minimum number of eight individuals (four males and four females). They are the following: BAT-3'06.220 (female, left); BAT-3'06.827 (male, left); BAT-3'08.366 (male, right); BAT-3'09.109 (female, left); BAT-3'09.128 (male, left); BAT-3'09.399 (male, left); BAT-3'09.529 (male, right); BAT-3'09.717 (female, left); BAT-3'09.875 (male, right); BAT-3'09.1341 (male, right); BAT-3'11.1714 (male, left); BAT-3'12.2568 (female, left) and BAT-3'13.666 (female, right). The comparative sample, which includes skeletons of extant and extinct carnivorans, is recorded in the Supporting Information Table 1 (SIT 1). Because the radial sesamoid is rarely preserved on the museum/collection specimens and the extant specimens have been gathered from many collections worldwide, these measurements could be considered as the largest collection of radial sesamoids ever compiled.

Methods Virtual models of the studied bones were derived by means of a 3D NextEngine HD and Artec 3D laser surface scanners. Once the scanning process was completed, the layers from the captured images were fused with the software Rhinoceros v.5, where further cleaning and review of the 3D parts took place. The next step was to export the 29 skeletal parts to an animation program, in this case the free software Blender. Subsequently, all parts were mounted together in the correct anatomical positions, both flexed and relaxed, and virtual vectors were inserted into the bone elements, simulating the tendons and muscles, representing the hand movements. Such placement ensures a realistic movement (of the last moments of the flexion movement, not including the pronation of the manus nor the flexion of the carpals and metacarpals) to this set of virtual representations of the fossil manus of *Indarctos* (Supporting information Video 1: SIV1).

Measurements Measurements (in mm) taken on the sample of carnivorans (including *I. arctoides*): maximum length of the first metacarpal (MCL), maximum length of the radial sesamoid (RSL) and maximum length of the radial sesamoid facet for the scapholunar (SLFL). Notice that the latter two lengths are measured in the dorso-palmar axis. To evaluate the relative development of the radial sesamoid in these taxa, we relied on two ratios. RSL/MCL reflects the length of the radial sesamoid relative to that of the rest of the manus, and hence it is intended as a proxy for the potential grasping efficiency of the resulting pincer-like mechanism. In turn, SLFL/RSL measures the relative development of the articular facet for the scapholunar, thereby reflecting both the radial sesamoid portion that protrudes from the scapholunar, as well as the potential degree of movement at the scapholunar-radial sesamoid joint.

Results

Description

All the studied radial sesamoids of *I. arctoides* from Batallones-3 (Fig. 2) are dorsopalmarly elongated and somewhat mediolaterally compressed. They show considerable variation in size, which is at least partly attributable to sexual dimorphism (this is obvious from other postcranial elements; Abella et al. 2013b), with the smaller specimens being attributable to females and the larger ones to males. To some extent, variation in size and especially robusticity of this bone may be attributable to ontogenetic differences, with adult (especially older) individuals presumably displaying larger and stouter bones than young adults or immature individuals, especially regarding overall bone length and the development of the muscle and tendon attachments (Fig. 3).

To identify the insertion areas on the radial sesamoid, we built a simplified muscle, tendon and ligament insertion map (Fig. 3), similar to those previously available in the literature (Salesa et al. 2006a, b; Fisher et al. 2009), although correcting several inaccuracies in some of these publications (Salesa et al. 2006a, b) regarding anatomical topography.

We identified up to five different attachment areas on the radial sesamoid of *I. arctoides*, two for muscles or muscle tendons and three for ligaments (Figs. 4 and 5). On the lateral face, about mid-length, the attachment for the *m. opponens digiti I* and *abductor digiti I brevis* can be clearly discerned, constituting a longitudinal ridge-like insertion that extends onto the palmar side of the bone (Figs. 4 and 5). The development of this insertion is variable to some degree, and in the larger specimens, the original flattened morphology of the sesamoid has been modified into a more cylindrical one. Insertion for the tendon of the ventral head of the *m. abductor digiti I*

Fig. 2 In situ photograph showing the fossil remains of an almost articulated forepaw of *Indarctos arctoides* from Batallones-3 (BAT-3'09.870-882 and BAT-3'09.884-900) in anatomical connection. Scale bars equal 5 cm



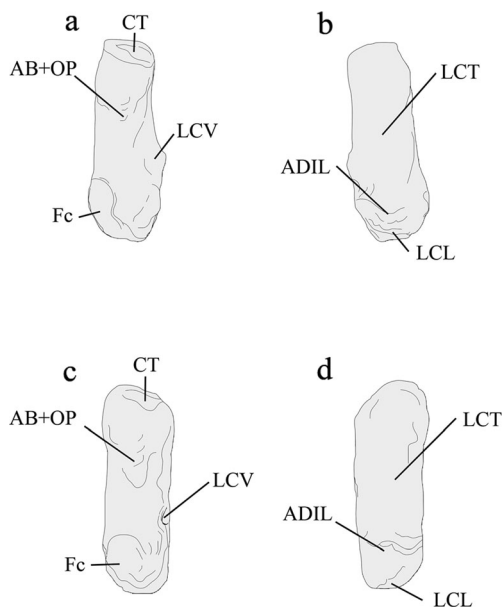


Fig. 3 Schematic drawing showing the insertion areas for the main tendons, muscles and muscle ligaments of the left radial sesamoid of *Indarctos arctoides*, for both the young adult morphology (**a** lateral view, **b** medial view) and the senile adult one (**c** lateral view, **d** medial view). *CT* hypothetical cartilaginous tip insertion, *AB+OP* insertion area for the muscles *abductor digiti I brevis* and *opponens digiti I*, *LCV* insertion area for the volar carposesamoid ligament, *Fc* facet for the scapholunar, *LCT* insertion area for transverse carposesamoid ligament, *ADIL* insertion area for the tendon of the muscle *abductor digiti I longus*; *LCL* insertion area for lateral carposesamoid ligament

longus is situated close to the articular facet for the scapholunar, extending over most of the dorsal and proximal aspects of the radial sesamoid. One of these insertion areas coincides with the place where the first metacarpal

(McI) and the radial sesamoid articulate in the giant panda; in the case of *I. arctoides*, it is a rounded and slightly rough surface and does not show any articulation surface. On the distolateral edge of the latter, there is a rough structure, sometimes present as a distal protrusion and in other instances consisting in a round pit, which we interpret as the insertion area for the transverse carposesamoid ligament. There are two other ligament attachments, one dorsodistal and another proximodorsal, corresponding for the volar and the lateral carposesamoid ligaments respectively.

The radial sesamoid has a lateral articular facet for the scapholunar and a concave rough area on the palmar side of the palmar apex (presumably indicating the original presence of a cartilaginous tip). Both the size and the shape of the palmar cartilaginous tip of the radial sesamoid are unknown because this cartilage has not fossilized. However, based on similarities with the radial sesamoid of the lesser panda, it might have been similar to that of this extant species, i.e. somewhat L-shaped following the curve of the insertion for the muscles *abductor digiti I brevis* and *opponens digiti I* (Endo et al. 2001b). In all the preserved specimens, the dorso-palmar (long) axis of the bone is slightly curved towards the latero-palmar side. However, in some specimens, the marked development of the lateral muscle attachments for the *abductor digiti I brevis* and *opponens digiti I* has blurred such a morphology, resulting in a more cylindrical (less curved) shape. On the proximal end, the articular facet for the scapholunar displays an oval contour and is slightly convex to flat on its dorsolateral portion. The size of this facet is variable among the specimens, and in the larger ones it may reach the distal face of the radial sesamoid.

Fig. 4 Schematic drawing of the grasping action of the right forepaw of *Indarctos arctoides*, based on the fossil remains of Batallones-3, showing the main muscles involved. Only the last phase of the movement is shown, since supination of the forepaw occurs prior to the digit flexion shown here. **a** extended phalanges, **b** flexed phalanges

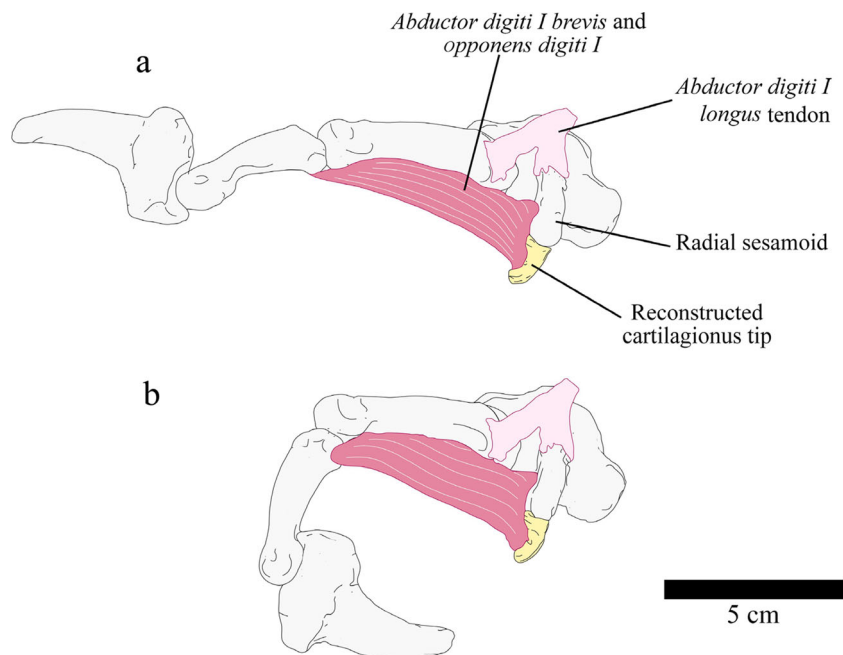
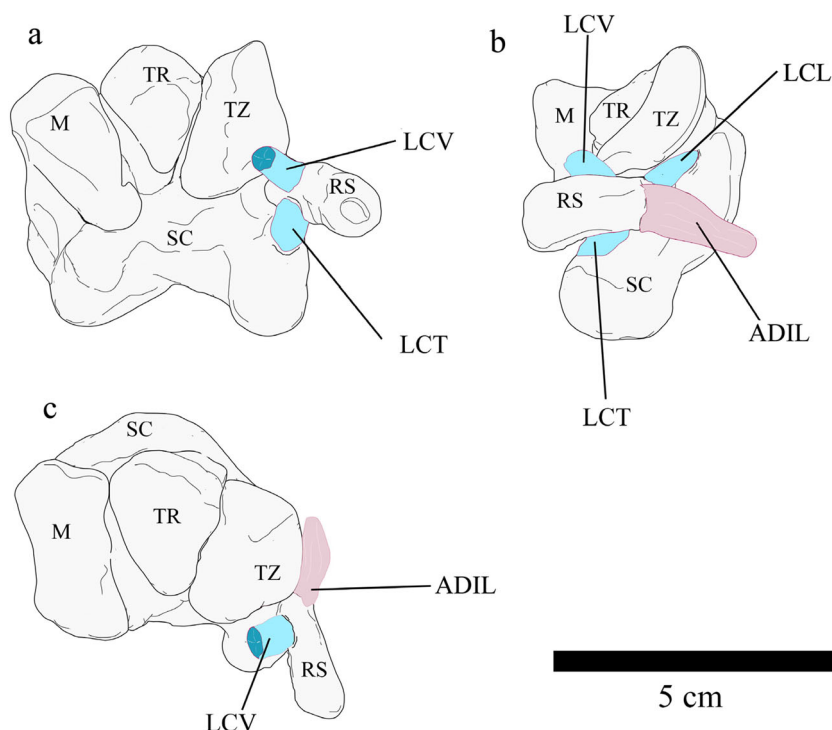


Fig. 5 Schematic drawing of the right forepaw of *Indarctos arctoides*, showing the main ligaments involved in the fixation of the radial sesamoid to the scapholunar and the main muscle tendons involved in the grasping action. **a** disto-palmar vie, **b** medial view, **c** dorso-distal view. *LCV* volar carposesamoid ligament, *LCT* transverse carposesamoid ligament, *ADIL* tendon of the muscle *abductor digiti I longus*, *LCL* lateral carposesamoid ligament, *M* magnum, *TR* trapezoid, *TZ* trapezium, *SC* scapholunar, *RS* radial sesamoid



Metric comparisons

We measured the development of the radial sesamoid relative to the first metacarpal (RSL/MCL; Table 1) and that of the facet for the scapholunar related to the length of the radial sesamoid (SLFL/RSL; Table 2) in *I. arctoides* compared to other selected carnivorans. These two indexes were plotted together to visualize species affinities based on their grasping capabilities (Fig. 6), although this was possible only when both the indices were available (in some specimens, the facet of the radial sesamoid could not be measured because it was prepared preserving some dried tissues).

There are several clear outliers regarding the proportions (Fig. 6). First, the giant panda differs from all the remaining taxa in having an extremely hypertrophied radial sesamoid, which is almost as long as the first metacarpal (Table 1). The reported ratio, in fact, represents only a minimum estimate, since the length of the cartilaginous tip, which does not fossilize but may constitute almost a third of the total length of this structure in some extant species (Antón et al. 2006), is not included in the computation. Second, there are several taxa (ursines, *Meles*, *Lontra*, *Lynx* and procyonids) that display just the opposite proportions, with relatively small radial sesamoids, whose length is almost completely occupied by the facet for the scapholunar. Both myologic features and digit mobility could explain such reduced morphology of the radial sesamoid of procyonids, in spite of their relatively developed grasping abilities (McLearn 1992; Fisher et al. 2009). Ursine bears, in contrast, have a relatively small radial

sesamoid (Endo et al. 1999c) most likely due to an evolutionary trend towards increased body size and a more terrestrial lifestyle. The mustelid genera *Meles* and *Lontra* have adaptations towards fossorial and aquatic lifestyles, respectively, and do not need the extra pad for their locomotion or feeding habits. Felids similarly have a very small, flat and rounded radial sesamoid (Salesa et al. 2006b), which is completely useless as a false thumb, but with a relatively high RSL/MCL index due to their very short first metacarpal. With regard to the SLFL/RSL index, which quantifies the relative development of the radial sesamoid facet for the scapholunar (Table 2), there is a gradient among the studied carnivorans. In the Mephitidae, the only measured index was the RSL/MCL since the specimens were preserved as dried tissues; however, these showed a relatively small radial sesamoid, very much related to their terrestrial-fossorial adaptations.

I. arctoides approaches the proportions of species such as the red panda, in which the radial sesamoid is used as a false thumb, but also those of quite arboreal large mustelids (such as the wolverine and the fisher), in which this bone is not described as having a manipulative function. The proportions of the radial sesamoid of *I. arctoides*, therefore, significantly depart from those of the only previously known specimen of this genus, specifically *I. punjabiensis* from the Turolian locality of Pikermi (Roussiakis 2001). The radial sesamoid of the latter taxon is relatively smaller, resembling the condition of *T. ornatus* and displaying a lesser development compared to the extant giant panda (Salesa et al. 2006a).

Table 1 Index of relative length of the radial sesamoid (RSL/MCL) in *Indarctos arctoides* (only adults) compared to other carnivorans

Sample size	Species	Index	Family	Locomotor type
4	<i>Ailuropoda melanoleuca</i>	0.840	Ursidae	Terrestrial
2	<i>Gulo gulo</i>	0.510	Mustelidae	Semi-arboreal
1	<i>Simocyon batalleri</i>	0.506	Ailuridae	Semi-arboreal
2	<i>Pekania pennanti</i>	0.504	Mustelidae	Arboreal
1	<i>Martes martes</i>	0.464	Mustelidae	Semi-arboreal
2	<i>Ailurus fulgens</i>	0.451	Ailuridae	Arboreal
2	<i>Arctictis binturong</i>	0.435	Viverridae	Arboreal
2	<i>Pristinailurus bristoli</i>	0.421	Ailuridae	Semi-arboreal
3	<i>Martes zibellina</i>	0.415	Mustelidae	Semi-arboreal
7	<i>Indarctos arctoides</i>	0.401	Ursidae	Terrestrial
4	<i>Galictis cuja</i>	0.388	Mustelidae	Terrestrial
1	<i>Panthera tigris</i>	0.364	Felidae	Terrestrial
2	<i>Paradoxurus hermafroditus</i>	0.359	Mustelidae	Arboreal
1	<i>Potos flavus</i>	0.350	Procyonidae	Arboreal
1	<i>Tremarctos ornatus</i>	0.332	Ursidae	Terrestrial
3	<i>Martes foina</i>	0.324	Mustelidae	Semi-arboreal
1	<i>Lyncodon patagonicus</i>	0.282	Mustelidae	Terrestrial
1	<i>Leopardus geoffroyi</i>	0.277	Felidae	Terrestrial
3	<i>Lontra longicaudis</i>	0.273	Mustelidae	Terrestrial-freshwater
1	<i>Eira barbara</i>	0.262	Mustelidae	Semi-arboreal
2	<i>Taxidea taxus</i>	0.257	Mustelidae	Terrestrial
4	<i>Nasua nasua</i>	0.248	Procyonidae	Semi-arboreal
1	<i>Indarctos punjabiensis</i>	0.240	Ursidae	Terrestrial
1	<i>Lynx lynx</i>	0.238	Felidae	Terrestrial
1	<i>Helarctos malayanus</i>	0.212	Ursidae	Terrestrial
2	<i>Meles meles</i>	0.205	Mustelidae	Terrestrial
2	<i>Spilogale gracilis</i>	0.152	Mephitidae	Terrestrial
4	<i>Conepatus chinga</i>	0.150	Mephitidae	Terrestrial
2	<i>Procyon lotor</i>	0.149	Procyonidae	Semi-arboreal
1	<i>Procyon cancrivorus</i>	0.136	Procyonidae	Terrestrial
1	<i>Melursus ursinus</i>	0.133	Ursidae	Terrestrial

RSL maximum length of the radial sesamoid, MCL maximum length of the first metacarpal

Discussion

To evaluate the use of the radial sesamoid within the Carnivora, one must gather as much information as possible for the whole order. There is not much anatomical research done on this bone (aside from the giant pandas vs. red pandas papers). However, we did find some papers on other carnivorans; for example, it has been previously suggested that, among nandiinids and viverrids, the radial sesamoid is better developed among arboreal species (Taylor 1974), particularly in small-bodied and climbing taxa (such as *Nandinia* or *Genetta*), associated with the possession of a large and laterally oriented pisiform (Taylor 1974; Antón et al. 2006). Although the plot in Fig. 6 seems to be somewhat uninformative due to some outliers with derived anatomical adaptations, such as the Felidae, which have a reduced MCL, there is still

a tendency towards a larger radial sesamoid, with relatively smaller facet for the scapholunar in arboreal carnivorans versus the more cursorial members of the group. Our results for the comparative sample support such an interpretation not only for viverrids but also, to a lesser extent, for arboreal mustelids (Ewer 1998; Mangas et al. 2007; Jennings and Veron 2009; Larivière and Jennings 2009), which have a radial sesamoid that is almost as hypertrophied as that of *I. arctoides*. The radial sesamoid of the latter is clearly larger than that of ursines, and most similar to those of *Ai. fulgens* as well as large terrestrial and scansorial mustelids (*Gulo* and *Pekania*). The development of the radial sesamoid in *I. arctoides* is somewhat intermediate between those of *Tremarctos* and *Ailuropoda*. Accordingly, the condition of *I. arctoides* represents the oldest evidence of a somewhat hypertrophied radial sesamoid in the giant panda lineage

Table 2 Index of relative size of the radial sesamoid facet for the scapholunar (SLFL/RSL) in *Indarctos arctoides* compared to other carnivorans

Sample size	Species	Index	Family	Locomotor type
7	<i>Indarctos arctoides</i>	0.366	Ursidae	Terrestrial
3	<i>Pekania pennanti</i>	0.381	Mustelidae	Arboreal
4	<i>Ailuropoda melanoleuca</i>	0.385	Ursidae	Terrestrial
2	<i>Ailurus fulgens</i>	0.405	Ailuridae	Arboreal
1	<i>Indarctos punjabiensis</i>	0.444	Ursidae	Terrestrial
2	<i>Gulo gulo</i>	0.480	Mustelidae	Semi-arboreal
2	<i>Pristinailurus bristoli</i>	0.508	Ailuridae	Semi-arboreal
3	<i>Martes zibellina</i>	0.524	Mustelidae	Semi-arboreal
1	<i>Tremarctos ornatus</i>	0.539	Ursidae	Terrestrial
1	<i>Martes martes</i>	0.562	Mustelidae	Semi-arboreal
2	<i>Taxidea taxus</i>	0.564	Mustelidae	Terrestrial
3	<i>Martes foina</i>	0.573	Mustelidae	Semi-arboreal
2	<i>Paradoxurus hermafroditus</i>	0.579	Viverridae	Arboreal
1	<i>Arctitis binturong</i>	0.595	Viverridae	Arboreal
4	<i>Galictis cuja</i>	0.666	Mustelidae	Arboreal
1	<i>Simocyon batalleri</i>	0.678	Ailuridae	Semi-arboreal
1	<i>Panthera tigris</i>	0.721	Felidae	Terrestrial
1	<i>Nasua nasua</i>	0.747	Procyonidae	Semi-arboreal
1	<i>Potos flavus</i>	0.790	Procyonidae	Arboreal
1	<i>Procyon lotor</i>	0.818	Procyonidae	Semi-arboreal
1	<i>Lynx lynx</i>	0.859	Felidae	Terrestrial
1	<i>Helarctos malayanus</i>	0.895	Ursidae	Terrestrial
1	<i>Melursus ursinus</i>	0.897	Ursidae	Terrestrial
1	<i>Meles meles</i>	0.934	Mustelidae	Semi-fossorial
1	<i>Lontra longicaudis</i>	0.943	Mustelidae	Terrestrial-freshwater

RSL maximum length of the radial sesamoid, SLFL maximum dimension of the radial sesamoid facet for the scapholunar

(Fig. 7). In this figure, we can see that most of the families of Arctoidea have lineages of medium-sized to enlarged radial sesamoids, which together with the supposed arboreal locomotion of the primitive forms could give us an idea of the degree of development of this structure. Terrestrial and aquatic forms would have reduced the radial sesamoid to its minimal form.

The relatively large radial sesamoid of spectacled bears, coupled with their frequent climbing behaviours (Ríos-Uzeda et al. 2006), led previous authors to conclude that this bone would play mainly a locomotor role in this taxon (Salesa et al. 2006a). However, this hypothesis is at odds with the large body size of *T. ornatus* (with males reaching as much as 175 kg; Nowak 1999), which precludes climbing on small arboreal supports in the way that lesser pandas do. In fact, among extant ursids, the radial sesamoid is not functionally involved at all in climbing behaviours, which are performed instead by relying on forelimb claws and the propulsive force generated by the hind limbs (Sasaki et al. 2005). In contrast, spectacled bears show elaborate feeding activities, related to a very herbivorous diet that mostly relies on ripe fruits, bromeliad hearts, berries and palm hearts (Peyton 1980; Mondolfi

1989; Nowak 1999; Ríos-Uzeda et al. 2006). For example, spectacled bears are known to tear off the leaves of large bromeliads to eat their bases, as well as to forage on the hearts of smaller ones by ripping them off from the substrate (Nowak 1999). Based on these considerations, although the use of the radial sesamoid in such feeding activities requires further confirmation (Salesa et al. 2006a), we favour the view that the well-developed radial sesamoid of *T. ornatus* is likely related to the more elaborate feeding activities of this taxon compared to ursines.

In *I. arctoides*, with an average estimated body mass even greater than that of *T. ornatus* (ca. 200 kg; Abella 2011; Abella et al., 2013b), the radial sesamoid similarly could not have performed a locomotor role during climbing on thin branches. Both skull morphology and dental characteristics (Abella 2011; Monescillo et al. 2014) suggest that this taxon, like the extant *T. ornatus*, would have consumed a large amount of plant material (Abella 2011; Abella et al. 2013a), even displaying some incipient durophagous adaptation (Abella 2011), although less clearly expressed than in later ailuropodines. All this evidence strongly suggests that, in early members of the giant panda lineage, the radial sesamoid

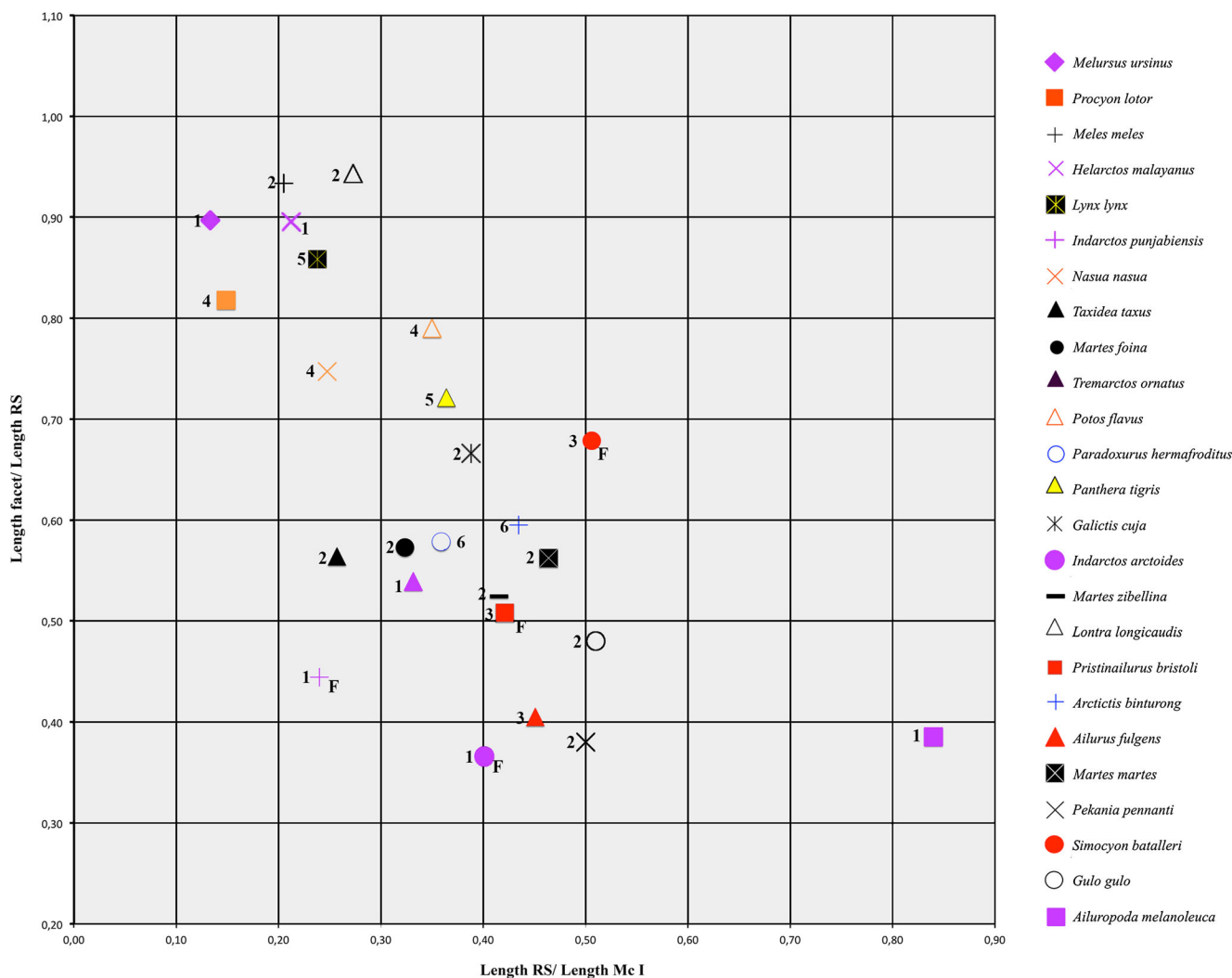


Fig. 6 Bivariate plot of the SLFL/RSL index versus the RSL/MCL index in carnivorans. These results show the combination of the two indexes that are used in this paper, which give an idea of the development of the radial sesamoid complex relative to the rest of the forepaw. Family codes:

1 and purple stand for Ursidae, 2 and black stand for Mustelidae, 3 and red stand for Ailuridae, 4 and orange stand for Procyonidae, 5 and yellow stand for Felidae and 6 and blue stand for Viverridae. F marks the fossil specimens

might have already performed a role in feeding-related manipulative behaviours. This is further supported by the high and low values displayed by the RSL/MCL and SLFL/RSL ratios, respectively, in *I. arctoides*, suggesting that its radial sesamoid was already being used as a pseudo-opposable grasping structure. If correct, this interpretation would imply that *I. arctoides* provides the oldest evidence of a feeding-related radial sesamoid. In this regard, the original role of this bone at the base of the giant panda lineage might differ from that in ailurids, given that a feeding-related manipulative role for the latter is not supported by the dental morphology of the extinct *Simocyon*, which together with its much smaller body mass instead suggest a grasping role during arboreal locomotion (Salesa et al. 2006b).

On the other hand, the possession of similarly enlarged radial sesamoids in both the early ailuropodine *Indarctos* and extant tremarctine bears suggests that a moderately well-

developed radial sesamoid is likely to represent the plesiomorphic condition for crown ursids as a whole, with the more hypertrophied condition of extant ailuropodines (*A. melanoleuca*) and the reduced radial sesamoid of ursines representing more derived, diverging morphologies evolved after the split of these groups (Fig. 7). In fact, from both an evolutionary and morphofunctional viewpoint, it is remarkable that, besides its less hypertrophied size, the radial sesamoid of *I. arctoides* has greater morphological similarity to those of the lesser panda and other carnivorans with a relatively well-developed radial sesamoid, rather than to the specialized condition of giant pandas (Fig. 8 and supporting information video 1: SIV1). In particular, *Ai. fulgens* has an almost cylindrical radial sesamoid, with a cup-shaped rough structure on its palmar tip and no contact with the first metacarpal (Endo et al. 2001b; Antón et al. 2006; Fisher et al. 2009). In contrast, *A. melanoleuca* has a flattened radial sesamoid, with a curved

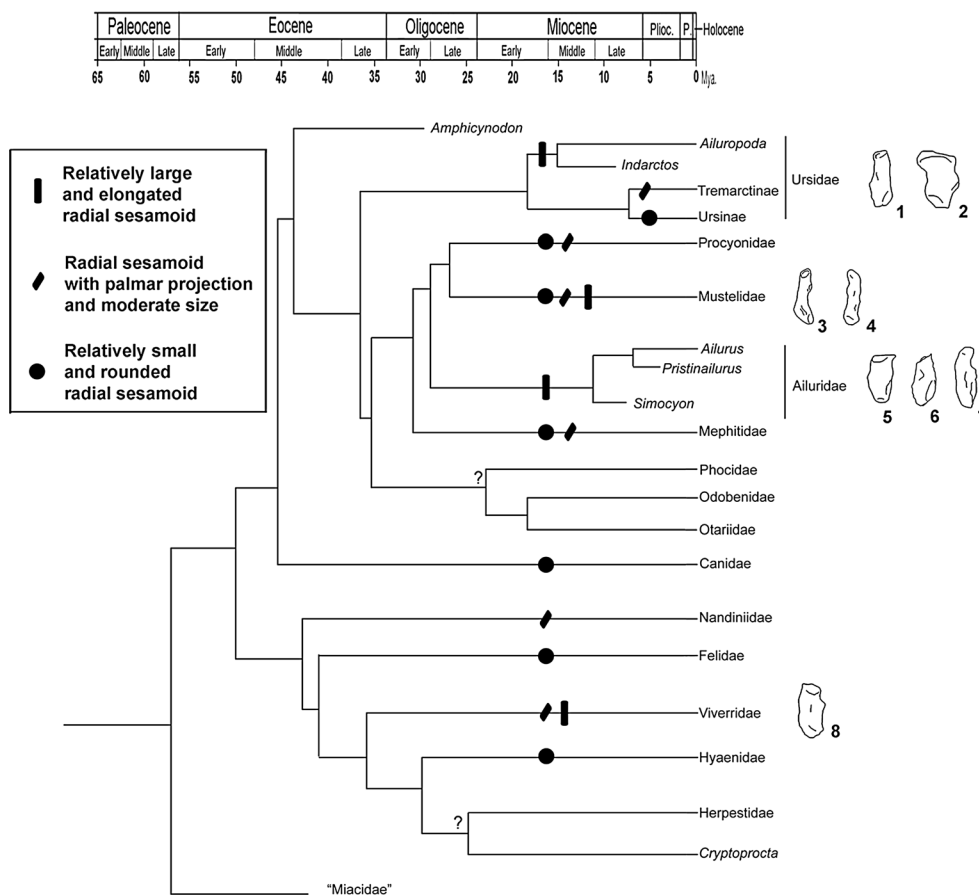


Fig. 7 Schematic tree showing the position and degree of development of the radial sesamoids, phylogenetic relationships and temporal ranges of the members of the Carnivora referred to in this work. Three levels are considered, extracted from Fig. 6, relative to the indices used in this work. Only the Ursidae and the Ailuridae are shown in more detail. In the rest of the families, two or more states of the character may be shown due to the presence of different lineages inside the group (usually the arboreal ones show the more-developed radial sesamoid). Outlines of some radial

sesamoids are shown besides the families which present large radial sesamoids. Numbers are 1, *Indarctos arctoides*; 2, *Ailuropoda melanoleuca*; 3, *Martes foina*; 4, *Gulo gulo*; 5, *Simocyon batalleri*; 6, *Pristinailurus bristoli*; 7, *Ailurus fulgens* and 8, *Paradoxurus hermafroditus*. The development of some of the radial sesamoids of some lineages is unknown due to the lack of extant specimens. Modified from Salesa et al. (2006b), Sato et al. (2009) and Sato et al. (2012)

ossified tip and a clear contact between the radial sesamoid and the first metacarpal (Davis 1964; Endo et al. 1996, 1999c, 2008; Salesa et al. 2006a, b). The configuration of the giant panda provides a more efficient grasp, not only due to the larger size of the radial sesamoid but also because of its different orientation (more medial instead of palmar), the ossification of the cartilaginous tip (giving the *m. abductor digiti I brevis* a more complete bony attachment, instead of inserting partly on a cartilage), and its articulation with the first metacarpal (thus resulting in a greater efficiency of to the pincer-like mechanism of the pseudo-thumb).

This lack of articulation between the radial sesamoid and the first metacarpal in *Ai. fulgens* has led some authors to conclude that, in the red panda lineage, the hypertrophy of this bone evolved completely independently from that of the giant panda (Endo et al. 2007, 2008). However, such an inference is not supported by the morphology of the relatively large

radial sesamoid of the extinct ailuropodine *I. arctoides*. The latter, although having an ursid-like overall morphology, is functionally more comparable to that of the lesser panda. Specifically, the radial sesamoid of *I. arctoides* is only flattened in young individuals, would have possessed a non-ossified (cartilaginous) tip and shows no indication of articulation with the first metacarpal. This suggests that the somewhat hypertrophied configuration of the Late Miocene ursid *I. arctoides* and the other carnivorans with well-developed radial sesamoids could be interpreted as the symplesiomorphic condition for the Arctoidea. In fact, since a relatively large radial sesamoid is retained by certain extant Nandiniidae and Viverridae, the possibility cannot be discounted that this morphology is a synapomorphy for all crown Carnivora (i.e. having originated before the split between the Caniformia and Feliformia), in which it would have displayed an original role related to arboreal locomotion. This

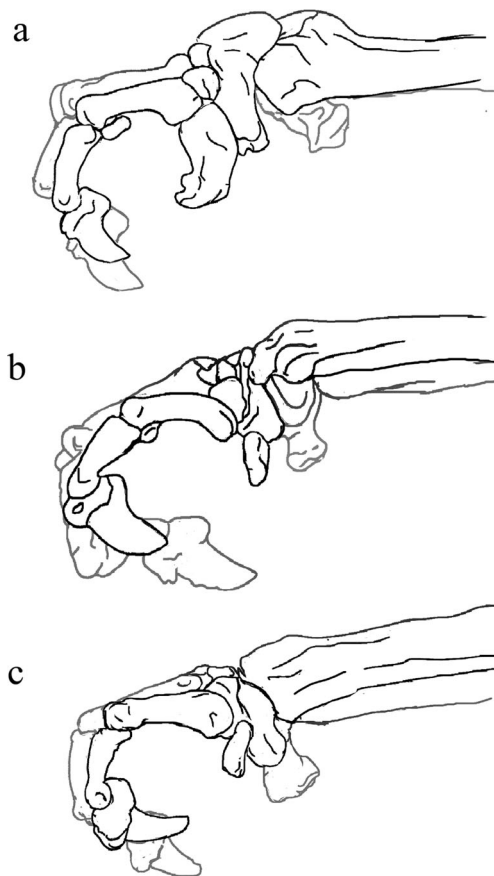


Fig. 8 Comparative schematic drawing showing the grasping complex of the right forepaw in **a** *Ailuropoda melanoleuca*, **b** *Ailurus fulgens* and **c** *Indarctos arctoides*. Partly modified from refs. 31 and 37, based on the 3D images derived by us from the scanned fossil remains

interpretation is reinforced by the presence of various arboreal adaptations in the postcranial skeleton of stem carnivorans, such as *Amphicyonodon* from the Early Oligocene of Europe, miacids or other extinct mammals such as multituberculates (Krause and Jenkins 1983; Cirot 1992; Heinrich and Houde 2006; Salesa et al. 2006b; Spaulding and Flynn 2009). The presence of developed radial sesamoids in basal Caniformia enhances the idea that this feature could have been widespread in the basal carnivorans (Fig. 7).

A moderately well-developed radial sesamoid involved in locomotion might therefore be the primitive condition for both ailurids and ursids. The latter is supported by the relatively small (ca. 15–30 kg) body mass of basal ursids such as *Ballusia* and *Ursavus*, in which a relatively large radial sesamoid might have favoured agile climbing behaviours and even above-branch quadrupedalism. This hypothesis cannot be yet tested based on fossil remains, but it is potentially falsifiable if radial sesamoids of more primitive extinct ursids were found in the future. Unlike in small-bodied carnivorans such as viverrids and mustelids, with the subsequent increase in body mass during ursid evolution, the original locomotor role of the radial sesamoid would have been lost. This would

have enabled the reduction of this bone in ursines, whereas in both ailuropodines and tremarctines, this would have been precluded by increased selection pressures posed by more elaborate, feeding-related manipulatory behaviours. The smaller radial sesamoid of *I. punjabiensis*, recorded several million years later from the Turolian locality of Pikermi, suggests a secondary reduction of this bone during the evolution of the *Indarctos* lineage (thus paralleling that occurred in ursines), possibly due to the significant increase in body size and gradual change of feeding habits towards a more carnivorous diet (Abella 2011). This interpretation fits well with the forearm morphology of *I. punjabiensis*, which displays proportions like those of extant brown bears (Roussiakis 2001), thus suggesting a much more cursorial locomotion than in *I. arctoides* (Abella et al. 2011). In contrast, at some point in the giant panda lineage, the radial sesamoid would have been co-opted to perform even more elaborate manipulative behaviours related to a more complex plant matter feeding, leading to further adaptive specializations that would have provided the false thumb with even more refined grasping abilities.

Conclusions

The fossil remains of the extinct ailuropodine *I. arctoides* enables to trace back the possession of a large radial sesamoid, most likely involved in elaborate herbivorous feeding activities, to the Late Miocene. Comparison with other carnivorans suggests that the possession of a relatively large radial sesamoid probably represents the primitive condition for most members of this group, originally displaying a grasping role during arboreal locomotor behaviours in small-bodied taxa. Given the subsequent body size increase and concomitant loss of its original locomotor function during ursid evolution, the radial sesamoid would have been reduced in ursines (mainly in relation to a more cursorial locomotion, but also to a more omnivorous diet), but retained in both ailuropodines and tremarctines due to the acquisition of a new manipulatory role in grasping activities related to herbivorous feeding. From this condition, the radial sesamoid would have been subsequently hypertrophied in later members of the giant panda lineage by acquiring more specific adaptations to bamboo feeding.

Although additional data on the radial sesamoid morphology of extinct ursids and other carnivorans (not available at the moment due to the scarce fossil radial sesamoid record) are required to fully test this scenario, the currently available evidence from the fossil record strongly suggests that the false thumb of lesser and giant pandas is best interpreted as a case of exaptive convergence, supporting the view that this process (Poe et al. 2007; Legreneur et al. 2011; Hutchinson et al. 2011) might be more widespread than previously recognized.

Acknowledgments This study was supported by the Spanish Ministerio de Economía y Competitividad (CGL2011-25754, CGL2011-28681 and RYC-2009-04533 to D.M.A.), the Universidad Complutense de Madrid (BSCH-UCM910607) and the Generalitat de Catalunya (2009 SGR 754 GRC and 2014 SGR 416 GRC). J.A. thanks the ‘Proyecto Prometeo’ of the ‘Secretaría de Educación Superior, Ciencia Tecnología e Innovación’, Republic of Ecuador. A.V. is a researcher in formation in the CSIC program JAE-PRE_CP2011 (CSIC program ‘Junta para la ampliación de estudios’), co-funded by the European Social Fund and has received funding from the European Union’s Seventh Framework Programme (FP7/2007–2013) under grant agreement no. 226506 (SYNTHESESYS; SE-TAF-3637), the USC School of Medicine (Columbia, South Carolina, USA) and the AMNH (Collection Study Grant Programme 2014). M.D.E. thanks the MACN for a PhD student grant. We are indebted to S. Roussiakis for photographs of the radial sesamoid of *I. punjabiensis* from Pikermi; to S. Wallace, M.A. Nieto Cambra, R. Portela Miguez, E. Westwig, D. Lunde, E. López Errasquin, D. Kalthoff, P. Moreno, F. Pastor, D. Flores and S. Lucero and D. Verzi and I. Olivares for the access to comparative material under their care; to M. Bastir (Paleoanthropology Group, MNCN, Spain) for the scans of the radius and ulna of *I. arctoides*; to Louis de Bonis for his recommendations on the manuscript; to Ó. Sanisidro for Fig. 1; and to the editors and the many reviewers who helped us to improve this manuscript.

Authors’ contribution J.A., P.M. and J.M. conceived and designed the experiments. J.A., A.P.R. and A.V. performed the experiments. J.A., M.D.E. and A.V. analysed the data. J.A., A.V., A.P.R. and D.H. contributed reagents/materials/analysis tools. J.A., D.M.A. and J.M. wrote the paper.

References

- Abella J (2011) *Indarctos arctoides* Depéret, 1895 (Carnivora, Mammalia) del yacimiento vallesiano de Batallones 3 (cuena de Madrid). PhD. dissertation, Universidad Autónoma de Madrid / Museo Nacional de Ciencias Naturales
- Abella J, Montoya P, Morales J (2011) New species of *Agriarctos* (Ailuropodinae, Ursidae, Carnivora) in the locality of Nombrevilla 2 (Zaragoza, Spain). *Estud Geol* 67:187–191
- Abella J, Alba DV, Robles JM, Valenciano A, Rotgers C, Carmona R, Montoya P, Morales J (2012) *Kretzoiarctos* gen. nov., the oldest member of the giant panda clade. *PLoS One* 7:e48985
- Abella J, Valenciano A, Pérez-Ramos A, Montoya P, Morales J (2013a) The radial sesamoid of *Indarctos arctoides*, the first evidence of a feeding related false thumb [abstract]. *Anat Rec* 296:271–272, **Special Feature – 1**
- Abella J, Valenciano A, Pérez-Ramos A, Montoya P, Morales J (2013b) On the socio-sexual behaviour of the extinct ursid *Indarctos arctoides*: an approach based on its baculum size and morphology. *PLoS One* 8:e77711
- Abella J, Montoya P, Morales J (2014) Paleodiversity of the superfamily Ursoidea (Carnivora, Mammalia) in the Spanish Neogene, related to environmental changes. *J Iberian Geol* 40:11–18
- Antón M, Salesa MJ, Pastor JF, Peigné S, Morales J (2006) Implications of the functional anatomy of the hand and forearm of *Ailurus fulgens* (Carnivora, Ailuridae) for the evolution of the ‘false-thumb’ in pandas. *J Anat* 209:757–764
- Barone R (2000) Anatomie Comparée des mammifères domestiques. Tome 1 and 2. Paris: Éditions Vigot
- 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
- Chom J, Hoffmann RS (1978) *Ailuropoda melanoleuca*. *Mamm Species* 110:1–6
- Cirot E (1992) Étude phylogénétique de quelques genres d’Arctoidea de l’Oligocène eurasiatique. Comparaison des données morphologiques et moléculaires. Dissertation, University of Poitiers
- Davis DD (1964) The giant panda. A morphological study of evolutionary mechanisms. *Fieldiana: Zool Me* 3:1–339
- Delfino M, Abella J, Sánchez IM, Alba D (2013) A nearly complete *Varanus* specimen from the Late Miocene of Cerro de los Batallones (Madrid Basin). Volume: 11th EAVP Meeting, Villers-sur-Mer, France, p 33
- Domingo MS, Alberdi MT, Azanza B, Silva PG, Morales J (2013) Origin of an assemblage massively dominated by carnivores from the Miocene of Spain. *PLoS One* 8:e63046
- Endo H, Sasaki N, Yamagiwa D, Uetake Y, Kurohmaru M, Hayashi Y (1996) Functional anatomy of the radial sesamoid bone in the giant panda (*Ailuropoda melanoleuca*). *J Anat* 189:587–592
- Endo H, Yamagiwa D, Hayashi Y, Koie H, Yamaya Y, Kimura J (1999a) Role of the giant panda’s ‘pseudo-thumb’. *Nature* 397:309–310
- Endo H, Hayashi Y, Yamagiwa D, Kurohmaru M, Koie H, Yamaya Y, Kimura J (1999b) CT examination of the manipulation system in the giant panda (*Ailuropoda melanoleuca*). *J Anat* 195:295–300
- Endo H, Makita T, Sasaki M, Arishima K, Yamamoto M, Hayashi Y (1999c) Comparative anatomy of the radial sesamoid bone in the polar bear (*Ursus maritimus*), the brown bear (*Ursus arctos*) and the giant panda (*Ailuropoda melanoleuca*). *J Vet Med Sci* 61:903–907
- Endo H, Sasaki M, Hayashi Y, Koie H, Yamaya Y, Kimura J (2001a) Carpal bone movements in gripping action of the giant panda (*Ailuropoda melanoleuca*). *J Anat* 198:243–246
- Endo H, Sasaki M, Kogiku H, Yamamoto M, Arishima K (2001b) Radial sesamoid bone as a part of the manipulation system in the lesser panda (*Ailurus fulgens*). *Ann Anat* 183:181–184
- Endo H, Hama N, Niizawa N, Kimura J, Itou T, Koie H, Sakai T (2007) Three-dimensional reconstruction of the manipulation system in the lesser panda. *Mamm Study* 32:99–103
- Endo H, Hama N, Niizawa N, Kimura J, Itou T, Koie H, Sakai T (2008) Three-dimensional imaging of the manipulating apparatus in the lesser panda and the giant panda. In: Endo H, Frey R (eds) Anatomical imaging: towards a new morphology (eds H.). Springer, Japan, pp 61–66
- Ewer RF (1998) The carnivores. Cornell University Press, Ithaca, New York
- 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
- Gould SJ (1978) The panda’s peculiar thumb. *Nat Hist* 87:20–30
- Gould SJ (1980) The panda’s thumb: more reflections in natural history. Norton, New York
- Gould SJ (2002) The Structure of evolutionary theory. The Belknap Press of Harvard University Press
- Gould SJ, Vrba ES (1982) Exaptation—a missing term in the science of form. *Paleobiology* 8:4–15
- Gray H (1977) Anatomy, descriptive and surgical. Bounty Books, New York
- Heinrich RE, Houde P (2006) Postcranial anatomy of *Viverravus* (Mammalia, Carnivora) and implications for substrate use in basal Carnivora. *J Vert Paleontol* 26:422–435
- Hutchinson JR, Delmer C, Miller CE, Hildebrandt T, Pitsillides A, Boyde A (2011) From flat foot to fat foot: structure, ontogeny, function, and evolution of elephant “sixth toes”. *Science* 334:1699–1703
- Jennings AP, Veron G (2009) Family Viverridae (civets, genets and oiyans). In: Wilson DE, Mittermeier RA (eds) Handbook of mammals of the world. 1. Carnivores. Lynx Editions, Barcelona, pp 174–233
- Krause WD, Jenkins FA (1983) The postcranial skeleton of North American multituberculates. *Bull Mus Comp Zool* 150:199–246

- Lankester ER, Lydekker R (1901) On the affinities of *Aeluropus melanoleucus*, A. Milne-Edwards. *Trans. Linn Soc Lon Zool* 8: 163–172
- Larivière S, Jennings AP (2009) Family Mustelidae (weasels and relatives). In: Wilson DE, Mittermeier RA (eds) *Handbook of mammals of the world. 1. Carnivores*. Lynx Editions, Barcelona, pp 564–656
- Le Minor JM (1994) The sesamoid bone of musculus abductor pollicis longus (os radiale externum or prepollex) in primates. *Acta Anat* 150:227–231
- Legreneur P, Laurin M, Monteil KM, Bels V (2011) Convergent exaptation of leap up for escape in distantly related arboreal amniotes. *Adapt Behav* 20:61–77
- López-Antoñanzas R, Peláez-Campomanes P, Álvarez-Sierra MA, García-Paredes I (2010) New species of *Hispanomys* (Rodentia, Cricetodontinae) from the Upper Miocene of Batallones (Madrid, Spain). *Zool J Linn Soc* 160:725–747
- Mangas JG, Carroblés M, Alcázar LH, Bellón D, Virgós E (2007) Aproximación al estudio de la ecología espacial de especies simpátricas: la garduña (*Martes foina*) y la gineta (*Genetta genetta*). *Galemys*, 19 (Número especial):61–71
- McLearn D (1992) Locomotion, posture, and feeding behavior of kinkajous, coatis and raccons. *J Mammal* 73:245–261
- Mondolfi E (1989) Notes on the distribution, habitat, food habits, status and conservation of the spectacled bear (*Tremarctos ornatus*) in Venezuela. *Mammalia* 53:525–544
- Monescillo MFG, Salesa MJ, Antón M, Siliceo G, Morales J (2014) *Machairodus aphanistus* (Felidae, Machairodontinae, Homotherini) from the Late Miocene (Vallesian, MN10) site of Batallones-3 (Torrejón de Velasco, Madrid, Spain). *J Vert Paleontol* 34:699–709
- Morales J et al (2008) El sistema de yacimientos de mamíferos miocenos del Cerro de los Batallones, Cuenca de Madrid: Estado actual y perspectivas Paleontologica Nova SEPAZ 8:41–117
- Nowak RM (1999) *Walker's mammals of the world*, vol I, 6th edn. The Johns Hopkins University Press, Baltimore Maryland
- Peyton B (1980) Ecology, distribution, and food habits of spectacled bears, *Tremarctos ornatus*, in Peru. *J Mammal* 61:639–652
- Poe S, Goheen JR, Hulebak EP (2007) Convergent exaptation and adaptation in solitary island lizards. *Proc R Soc B* 274:2231–2237
- Ríos-Uzeda B, Gómez H, Wallace RB (2006) Habitat preference of the Andean bear (*Tremarctos ornatus*) in the Bolivian Andes. *J Zool* 268:271–278
- Roberts MS, Gittleman JL (1984) *Ailurus fulgens*. *Mamm Species* 222:1–8
- Roussiakis SJ (2001) Postcranial remains of *Indarctos* (Ursidae, Mammalia) from the classical locality of Pikermi (Attica, Greece), with a description of the front limb. *Senckenb Lethaea* 81:347–358
- Salesa MJ, Siliceo G, Antón M, Abella J, Montoya P, Morales J (2006a) Anatomy of the “false thumb” of *Tremarctos ornatus* (Carnivora, Ursidae, Tremarctinae): phylogenetic and functional implications. *Estud Geol* 62:389–394
- Salesa MJ, Antón M, Peigné S, Morales J (2006b) Evidence of a false thumb in a fossil carnivore clarifies the evolution of pandas. *Proc Natl Acad Sci U S A* 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, Morales J, Peigné S (2012) 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
- Salton JA, Sargis EJ (2008) Evolutionary morphology of the Tenrecoidea (Mammalia) carpal complex. *Biol J Linn Soc* 93:267–288
- Sánchez-Villagra MR, Menke PR (2005) The mole's thumb—evolution of the hand skeleton in talpids (Mammalia). *Zool* 108:3–12
- Sasaki M, Endo H, Wiig O, Derocher AE, Tsubota T, Taru H, Yamamoto M, Arishima K, Hayashi Y, Kitamura N, Yamada J (2005) Adaptation of the hindlimbs for climbing in bears. *Ann Anat* 187: 153–160
- Sato JJ, Wolsan M, Minami S, Hosoda T, Sinaga MH, Hiyama K, Yamaguchi Y, Suzuki H (2009) Deciphering and dating the red panda's ancestry and early adaptive radiation of Musteloidea. *Mol Phylogenet Evol* 53:907–922
- Sato JJ, Wolsan M, Minami S, Prevosti FJ, D'Elia G, Begg C, Begg K, Hosoda T, Campbell KL, Suzuki H (2012) Evolutionary and biogeographic history of weasel-like carnivorans (Musteloidea). *Mol Phylogenet Evol* 63:745–757
- Siliceo G, Salesa MJ, Antón M, Monescillo MFG, Morales J (2014) *Promegantereon ogygia* (Felidae, Machairodontinae, Smilodontini) from the Vallesian (Late Miocene, MN10) of Spain: morphological and functional differences in two noncontemporary populations. *J Vert Paleontol* 34:407–418
- Spaulding M, Flynn JF (2009) Anatomy of the postcranial skeleton of “*Miacis*” *uintensis* (Mammalia: Carnivoramorpha). *J Vert Paleontol* 29:1212–1223
- Szalay FS (1994) *Evolutionary history of the marsupials and an analysis of osteological characters*. Cambridge University Press, London
- Taylor ME (1974) The functional anatomy of the forelimb of some African Viverridae (Carnivora). *J Morphol* 143:307–336
- Valenciano A, Abella J, Sanisidro O, Hartstone-Roses A, Álvarez-Sierra MA, Morales J (2015) Complete description of the skull and mandible of the giant mustelid *Eomellivora piveteaui* Ozansoy, 1965 (Mammalia, Carnivora, Mustelidae) from Batallones (MN10), Late Miocene (Madrid, Spain). *J Vert Paleontol*. doi:10.1080/02724634.2014.934570
- Wallace SC (2011) Advanced members of the Ailuridae (lesser or red pandas—subfamily Ailurinae). In: Glatston AR (ed) *Red panda. Biology and conservation of the first panda*. Academic, San Diego, pp 43–60
- Wood-Jones F (1939a) The ‘thumb’ of the giant panda. *Nature* 143:157
- Wood-Jones F (1939b) The forearm and manus of the giant panda, *Ailuropoda melanoleuca*, M.-Edw. With an account of the mechanism of its grasp. *Proc Zool Soc B* 109:113–129