

1 **Tracing the origin of the panda's thumb.**

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24

25 **Abstract**

26 We investigate the relative development of the carnivoran radial sesamoids to untangle
27 the evolution of this iconic structure. In the pandas (both giant and red), this “false
28 thumb” is known to perform a grasping role during bamboo feeding in both the red and
29 giant pandas. An original locomotor role has been inferred for ailurids, but this remains
30 to be ascertained for ursids. A large sample of radial sesamoids of *Indarctos arctoides*
31 from the Miocene of Batallones-3 (Spain) indicates that this early ailuropodine bear
32 displayed a relatively hypertrophied radial sesamoid, with a configuration more similar
33 to that of the red panda and other carnivorans than to that of giant pandas. This false
34 thumb is the first evidence of this feature in the Ursidae, which can be linked to a more
35 herbivorous diet. Moreover, in the two extant pandas, the false thumb should not be
36 interpreted as an anatomical convergence, but as an exaptive convergence regarding its
37 use during the bamboo feeding, which changes the evolutionary view of this singular
38 structure.

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41 Introduction

42 Locality and age.

43 Batallones 3 (BAT-3) is one of the nine fossil vertebrate localities from the fossiliferous
44 area of Cerro de los Batallones (Morales, J. et al. 2008) (Madrid Basin, Spain; Fig. 1).
45 All 9 Batallones fossil sites have been dated based on their faunal composition as
46 belonging to the late Vallesian (MN10); approximately 9 Ma (Morales, J. et al. 2008;
47 López-Antoñanzas et al. 2010). The exceptionally rich record of carnivorans in
48 Batallones-3 has been attributed to [the](#) fact that this pseudokarstic locality acted as a
49 natural trap for all kinds of carnivorous vertebrates (Morales, J. et al. 2008; Calvo et al.
50 2013; Domingo et al. 2013), including not only mammalian carnivorans (Abella 2011;
51 Salesa et al. 2012; Abella et al. 2013a, b; Monescillo et al. 2014; Siliceo et al. 2014;
52 Valenciano et al. in press), but also scavenging birds (Morales, J. et al. 2008) as well as
53 monitor lizards (Delfino et al. 2013). *Indarctos arctoides* is among the most abundant
54 carnivorans from Batallones-3, being represented by as many as 1984 identifiable
55 remains (updated relative to Abella et al. 2013b). The sample of radial sesamoids of *I.*
56 *arctoides* described here consists of 13 fossils remains, which correspond to a minimum
57 number of ~~16~~[8](#) individuals, ~~which~~ which represent by far the most complete collection of this
58 species and probably of the genus as a whole (Abella et al. 2013a, b).

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

61 The radial sesamoid (also called 'sesamoid bone of the muscle *abductor digiti I*
62 *longus*' or 'os radiale externum') is present in many carnivorans and other mammals
63 (marsupials, multituberculates, rodents, insectivorans, chiropterans, scandentians, and
64 primates), being related to the tendon of the m. *abductor digiti I longus* at the level of
65 the joint between the scapholunar and the trapezium (Krause and Jenkins 1983; Szalay

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66 1994; Le Minor 1994). By definition a sesamoid is a small and more or less rounded
67 masses embedded in certain tendons and usually related to joint surfaces. Their
68 functions probably are to modify pressure, to diminish friction, and occasionally to alter
69 the direction of a muscle pull. (Gray 1977; Barone 2000). However, the radial sesamoid
70 can be considered a special kind of sesamoid, with a completely different role and
71 therefore, subjected to different anatomical ~~rules~~strictures. In most instances, this bone
72 is of similar size ~~as to~~ other sesamoids, or even vestigial, but in some mammals, such as
73 talpids (Krause and Jenkins 1983; Sánchez-Villagra and Menke 2005), many tenrecids
74 (Salton and Sargis 2008) and elephants (Hutchinson et al. 2011), it constitutes a digit-
75 like element that is variously called ‘os falciforme’, ‘prepollex’ or ‘predigit’.
76 Furthermore, a truly hypertrophied radial sesamoid, ~~so as to constitute~~constituting a
77 functional ‘false thumb’, ~~was is~~ considered to be present in the giant panda, *Ailuropoda*
78 *melanoleuca* (Lankester and Lydekker 1901; Wood-Jones 1939 a, b; Davis 1964; Gould
79 1978; Chorn and Hoffmann 1978; Endo et al. 1996, 1999a, b, 2001a; Antón, et al. 2006;
80 Salesa et al. 2006a, b) and, to a lesser extent, in the red panda, *Ailurus fulgens* (Roberts
81 and Gittleman 1984; Endo et al. 2001b, 2007; Antón et al. 2006; Salesa et al. 2006b).
82 The functional role of the radial sesamoid as a grasping structure essentially depends on
83 its size and degree of movement relative to the metapodials and other wrist bones, thus
84 being only possible when the radial sesamoid is relatively long compared to other bones
85 of the manus (Abella et al. 2013a). In the two pandas, the large radial sesamoid
86 performs a manipulatory role during bamboo feeding (Wood-Jones 1939a, b; Davis
87 1964; Chorn and Hoffmann 1978; Roberts and Gittleman 1984; Salesa et al. 2006a, b),
88 by providing some degree of opposability and thereby functioning as a ‘false thumb’ or
89 ‘pseudo-thumb’.

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90 Ever since Gould’s seminal essay on the ‘panda’s thumb’ (Gould 1980; Gould
91 and Vrba 1982), this structure has become one of the most famous examples to illustrate
92 the contingent nature of evolution, as opposed to optimality of design. The panda’s false
93 thumb illustrates one of the Darwinian principles of historical inference; namely, that
94 based on finding discordances (imperfections or oddities) between the anatomy of an
95 organism and its current circumstances, which make no sense outside the evolutionary
96 paradigm (Gould 2002). More recently, with the recognition that lesser pandas are only
97 distantly related to giant pandas but also display an enlarged radial sesamoid involved in
98 bamboo feeding activities, the false thumb of both pandas has acquired further
99 significance as one of the most remarkable examples of convergent evolution (Antón et
100 al. 2006; Salesa et al. 2006b). Given their similar grasping function during bamboo
101 feeding and based on extant taxa alone, it might seem warranted to infer that the giant
102 and lesser pandas’ hypertrophied radial sesamoids constitute a remarkable case of
103 convergent adaptation. However, the radial sesamoid is not employed as a truly
104 opposable and freely movable thumb in either the giant or lesser panda (contra Davis
105 1964). In the former, the ‘false thumb’ constitutes a part of a double pincer-like,
106 manipulative functional apparatus in which the hand flexes around the scapholunar and
107 the unciform, so as to grasp objects between the true digits and both the radial sesamoid
108 and the pisiform (Endo et al. 1999a, b, 2001a; Antón et al. 2006). In contrast, the less
109 marked hypertrophy of the radial sesamoid of the lesser panda, coupled with associated
110 musculoskeletal differences, indicate the possession of a different grasping mechanism
111 (Endo et al. 2001b, 2007; Antón et al. 2006; Salesa et al. 2006b; Abella et al. 2013a),
112 more similar to that displayed by other small to medium-sized carnivorans. In the latter
113 taxa, these grasping abilities are employed not only in food manipulation, but also in

114 arboreal climbing behaviours along thin branches (Antón et al. 2006), given the lack in
115 these taxa of the true thumb opposability characteristic of primates.

116 The simultaneous locomotor and manipulatory role of the radial sesamoid in
117 ailurids casts some doubts on the adaptive origin of this structure. In fact, locomotion
118 has been favoured as the original primary role of this structure, based on the information
119 provided by the fossil record (Antón et al. 2006; Salesa et al. 2006b). The remains of the
120 extinct ailurid *Simocyon batalleri* from Spain traced the possession of a hypertrophied
121 radial sesamoid in this group back to the Late Miocene, clearly prior to the acquisition
122 of the extreme herbivorous adaptations of the extant *Ai. fulgens* (Salesa et al. 2006b,
123 2008). This is confirmed by the common occurrence ~~in~~of this feature in younger
124 members of the same lineage, even if not as well developed as in the Ailuridae (Wallace
125 2011). This fact indicates that, in ailurids, the large radial sesamoid originally
126 ~~performed~~had a primary locomotor role, probably related to climbing on thin branches
127 (Antón et al. 2006; Salesa et al. 2006b), having been subsequently co-opted to perform a
128 manipulatory function and thus constituting an exaptation rather than adaptation to
129 bamboo feeding (Antón et al. 2006).

130 In the giant panda lineage, the evolutionary origin of the false thumb is less well
131 understood, an thus ~~being it is~~ uncertain whether it should be considered an exaptation
132 regarding its current role in bamboo feeding (Hutchinson et al. 2011), as in lesser
133 pandas (Antón et al. 2006; Salesa et al. 2006a, b), or rather as an adaptation to food
134 manipulation, as customarily ~~considered~~thought (Wood-Jones 1939a, b; Davis 1964;
135 Endo et al. 1999b; Antón et al. 2006; Salesa et al. 2006b). The interpretation of the giant
136 panda's false thumb as an adaptation to manipulation is supported by the small (ursine-
137 like) radial sesamoid previously reported for the Late Miocene ailuropodine genus
138 *Indarctos* (Roussiakis 2001). However, this interpretation is contradicted by the

139 presence of a somewhat hypertrophied radial sesamoid in the spectacled bear
140 (*Tremarctos ornatus*), thus contrasting with the much smaller, round and more compact
141 radial sesamoid of the remaining extant ursids (Lankester and Lydekker 1901; Davis
142 1964; Endo et al. 1999c; Salesa et al. 2006b). Based on the presence of a relatively large
143 sesamoid in *T. ornatus*, it has been suggested that some degree of radial sesamoid
144 hypertrophy might be symplesiomorphic for ursids as a whole, having been
145 subsequently reduced in ursines (Salesa et al. 2006a), which would support an exaptive
146 explanation for the hypertrophied sesamoid of *A. melanoleuca*. ~~Discerning~~
147 ~~Discriminating~~ between these two ~~competing~~-hypotheses (adaptation vs. exaptation) in
148 the case of the giant panda's false thumb is impossible without recourse~~ing~~ to the
149 information provided by the fossil record (Salesa et al. 2006b). Here we test these
150 hypotheses based on the radial sesamoid of *Indarctos*, which according to recent
151 cladistic analyses would be an early member of the (~~Ailuropodinae~~), more specifically
152 belonging to the sister-taxon (~~Indarctini~~) of the giant panda lineage in a strict sense
153 (~~Ailuropodini~~) (Abella et al. ~~2011~~; 2012; 2014). In particular, we rely on a large sample
154 of fossil radial sesamoids of *I. arctoides* Déperet, 1895 from the late Vallesian (MN10)
155 of Batallones, which is about 3 million years older than the single radial sesamoid
156 previously reported for this genus, ~~corresponding~~-~~belonging~~ to *I. punjabiensis* (formerly
157 attributed to *I. atticus* ~~atticus~~) from the Turolian (MN12) of Pikermi (Roussiakis 2001).

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159 **Materials and methods**

160 **Studied material.** Based on size and morphology, a total of 13 (eight right and
161 five left) radial sesamoids from Batallones-3 can be attributed to *I. arctoides*; eight are
162 thought to be male and five are thought to be female, belonging to a minimum number
163 of eight individuals (four males and four females). They are the following: BAT-

164 3'06.220 (female, left); BAT-3'06.827 (male, left); BAT-3'08.366 (male, right); BAT-
165 3'09.109 (female, left); BAT-3'09.128 (male, left); BAT-3'09.399 (male, left); BAT-
166 3'09.529 (male, right); BAT-3'09.717 (female, left); BAT-3'09.875 (male, right); BAT-
167 3'09.1341 (male, right); BAT-3'11.1714 (male, left); BAT-3'12.2568 (female, left); and
168 BAT-3'13.666 (female, right). The comparative sample, which includes skeletons of
169 extant and extinct carnivorans, is ~~reported on~~recorded in the Supporting Information
170 Table 1 (SIT 1). Because the radial sesamoid is rarely preserved on the
171 museum/collection specimens and the extant specimens have been gathered from many
172 collections worldwide, these measurements could be considered as the largest collection
173 of radial sesamoids ever compiled.

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

187 **Measurements.** Measurements (in mm) taken ~~in~~on the sample of carnivorans
188 (including *I. arctoides*): maximum length of the first metacarpal (MCL); maximum

189 length of the radial sesamoid (RSL); and maximum length of the radial sesamoid facet
190 for the scapholunar (SLFL). Notice that the latter two lengths are measured in the dorso-
191 palmar axis. To evaluate the relative development of the radial sesamoid in these taxa,
192 we relied on two ratios. RSL/MCL reflects the length of the radial sesamoid relative to
193 that of the rest of the manus, and hence it is intended as a proxy for the potential
194 grasping efficiency of the resulting pincer-like mechanism. In turn, SLFL/RSL
195 measures the relative development of the articular facet for the scapholunar, thereby
196 reflecting both the radial sesamoid portion that protrudes from the scapholunar, as well
197 as the potential degree of movement at the scapholunar-radial sesamoid joint.

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199 **Results**

200 **Description.**

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

211 To identify the insertion areas on the radial sesamoid, we built a simplified
212 muscle, tendon and ligament insertion map (Fig. 3), similar to those previously
213 available ~~from~~ in the literature (Salesa et al. 2006a, b; Fisher et al. 2009), although

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2 214 correcting several inaccuracies in some of these publications (Salesa et al. 2006a, b)
3 215 regarding anatomical topography.

4 216 We identified up to five different attachment areas on the radial sesamoid of *I.*
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6 217 *arctoides*, two for muscles or muscle tendons and three for ligaments (Figs. 4 and 5).
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8 218 On the lateral face, about mid-length, the attachment for the m. *opponens digiti I* and
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10 219 *abductor digiti I brevis* can be clearly discerned, constituting a longitudinal ridge-like
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12 220 insertion that extends onto the palmar side of the bone (Figs. 4 and 5). The development
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14 221 of this insertion is variable to some degree, and in the larger specimens the original
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16 222 flattened morphology of the sesamoid has been modified into a more cylindrical one.
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18 223 Insertion for the tendon of the ventral head of the m. *abductor digiti I longus* is situated
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20 224 close to the articular facet for the scapholunar, extending over most of the dorsal and
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22 225 proximal aspects of the radial sesamoid. One of these insertion areas coincides with the
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24 226 place where the McI and the radial sesamoid articulate in the giant panda; in the case of
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26 227 *I. arctoides* it is a rounded and slightly rough surface, and does not show any
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28 228 articulation surface. On the distolateral edge of the latter, there is a rough structure,
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30 229 sometimes present as a distal protrusion and in other instances consisting in a round pit,
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32 230 which we interpret as the insertion area for the transvers~~ea~~l carposesamoid ligament.
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34 231 There are two other ligament attachments, one dorsodistal and another proximodorsal,
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36 232 corresponding for the volar and the lateral carposesamoid ligaments respectively.
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39 233 The radial sesamoid ~~displays~~has a lateral articular facet for the scapholunar and
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41 234 a concave rough area on the palmar side of the palmar apex (presumably indicating the
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43 235 original presence of a cartilaginous tip). Both the size and the shape of the palmar
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45 236 cartilaginous tip of the radial sesamoid are unknown because this cartilage has not
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47 237 fossilized. However, based on similarities with the radial sesamoid of the lesser panda,
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49 238 it might have been similar to that of this extant species, i.e., somewhat L-shaped
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239 following the curve of the insertion for the muscles *abductor digiti I brevis* and
240 *opponens digiti I* (Endo et al. 2001b). In all the preserved specimens, the dorso-palmar
241 (long) axis of the bone is slightly curved towards the lateropalmar side. However, in
242 some specimens the marked development of the lateral muscle attachments for the
243 *abductor digiti I brevis* and *opponens digiti I* has blurred such a morphology, resulting
244 in a more cylindrical (less curved) shape. On the proximal end, the articular facet for the
245 scapholunar displays an oval contour, and is slightly convex to flat on its dorsolateral
246 portion. The size of this facet is ~~somehow~~ variable among the specimens, and in the
247 larger ones it may reach the distal face of the radial sesamoid.

248

249 **Metrical comparisons.**

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

257 There are several clear outliers regarding the proportions (Fig. 6). First, the giant
258 panda differs from all the remaining taxa ~~by displayingin having~~ an extremely
259 hypertrophied radial sesamoid, ~~being which is~~ almost as long as the first metacarpal
260 (Table 1). The reported ratio, in fact, represents only a minimum estimate, since the
261 length of the cartilaginous tip, which does not fossilize but may constitute almost a third
262 of the total length of this structure in some extant species (Antón et al. 2006), is not
263 included in the computation. Second, there are several taxa (ursines, *Meles*, *Lontra*,

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264 *Lynx*, and procyonids) that display just the opposite proportions, with relatively small
265 radial sesamoids, whose length is almost completely occupied by the facet for the
266 scapholunar. Both myologic features and digit mobility could explain such reduced
267 morphology of the radial sesamoid of procyonids, in spite of their relatively developed
268 grasping abilities (McLearn 1992; Fisher et al. 2009). Ursine bears, in contrast, ~~display~~
269 have a relatively small radial sesamoid (Endo et al. 1999c), most likely due to an
270 evolutionary trend towards increased body size and a more terrestrial lifestyle. ~~Both the~~
271 ~~mustelidae~~The mustelid genera *Meles* and *Lontra* have adaptations towards fossorial
272 and aquatic life-~~form~~styles respectively, ~~not and needing~~don't need the extra pad for
273 their locomotion or feeding habits. Felids similarly ~~display~~have a very small, flat and
274 rounded radial sesamoid (Salesa et al. 2006b), which is completely useless as a false
275 thumb, but with a relatively high RSL/MCL index due to their very short first
276 metacarpal. With regard to the SLFL/RSL index, which quantifies the relative
277 development of the radial sesamoid facet for the scapholunar (Table 2), there is a
278 gradient among the studied carnivorans. ~~Independently of the RSL/MCL index, in some~~
279 ~~species (ursine bears, felines and procyonids for example) the radial sesamoid is almost~~
280 ~~completely occupied by the facet for the scapholunar, so there is no protruding portion~~
281 ~~of the sesamoid left to act as a support during locomotion (and even less to function as a~~
282 ~~false thumb in manipulative behaviours).~~ In the mephitidae the only measured index
283 was the RSL/MCL since the specimens were preserved as dried tissues, however these
284 ~~were found to presenshowed~~t a relatively small radial sesamoid, very much related to
285 their ~~eursorial~~terrestrial-fossorial adaptations.

286 *Indarctos arctoides* approaches the proportions of species such as the red panda,
287 in which the radial sesamoid is used as a false thumb, but also those of quite arboreal
288 large mustelids (such as the ~~terrestrial~~ wolverine and the ~~seansorial~~ fisher), in which this

289 bone is not described ~~to as~~ having a manipulative function. The proportions of the
290 radial sesamoid of *I. arctoides* therefore significantly depart from those of the only
291 previously known specimen of this genus, specifically *I. punjabiensis* from the Turolian
292 locality of Pikermi (Roussiakis 2001). The radial sesamoid of the latter taxon is
293 relatively smaller, resembling the condition of *T. ornatus* and displaying a lesser
294 development compared to the extant giant panda (Salesa et al. 2006a).

295

296 Discussion

297 To evaluate the use of the radial sesamoid within the Carnivora, one must gather
298 as much information as possible for the whole familyOrder. There is not much
299 anatomical research done on this bone (~~rather than~~ aside from the ~~typical~~-giant pandas
300 Vs.vs. red pandas papers ~~and texts~~). However, we did find some papers on other
301 carnivorans; for example it has been previously suggested that, among nandiinids and
302 viverrids, the radial sesamoid is better developed among arboreal species (Taylor 1974),
303 particularly in small-bodied and climbing taxa (such as *Nandinia* or *Genetta*),
304 associated with the possession of a large and laterally-oriented pisiform (Taylor 1974;
305 Antón et al. 2006). Although the plot in figure 6 seems to be somewhat uninformative
306 due to some outliers with derived anatomical adaptations, such as the felidae, which
307 have reduced a McI, there is still a tendency towards a larger radial sesamoid, with
308 relatively smaller facet for the scapholunar in arboreal carnivorans versus the more
309 cursorial members of the group. Our results for the comparative sample support such an
310 interpretation not only for viverrids, but also, to a lesser extent, for arboreal mustelids
311 (Ewer 1998; Mangas et al. 2007; Jennings and Veron 2009; Larivière and Jennings
312 2009), which display have a radial sesamoid that is almost as hypertrophied as that of *I.*
313 *arctoides*. The radial sesamoid of the latter is clearly larger than that of ursines, and

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314 most similar to those of *Ai. fulgens* as well as large terrestrial and scansorial mustelids
315 (*Gulo* and *Pekania*). The development of the radial sesamoid in *I. arctoides* is
316 somewhat intermediate between those of *Tremarctos* and *Ailuropoda*. Accordingly, the
317 condition of *I. arctoides* represents the oldest evidence of a somewhat hypertrophied
318 radial sesamoid in the giant panda lineage (Fig. 7). In this figure we can see that most of
319 the families of Arctoidea have lineages of medium sized to enlarged radial sesamoids,
320 which together with the supposed arboreal locomotion of the primitive forms could give
321 us an idea of the degree of development of this structure. Terrestrial and aquatic forms
322 would have reduced the radial sesamoid to its minimal form.

323 The relatively large radial sesamoid of spectacled bears, coupled with their
324 frequent climbing behaviours (Ríos-Uzeda et al. 2006), led previous authors to conclude
325 that this bone would play ~~a~~ mainly a locomotor role ~~for~~ in this taxon (Salesa et al.
326 2006a). However, this hypothesis is at odds with the large body size of *T. ornatus* (with
327 males reaching as much as 175 kg (Nowak 1999)), which precludes climbing on small
328 arboreal supports in the way that lesser pandas do. In fact, among extant ursids, the
329 radial sesamoid is not functionally involved at all in climbing behaviours, which are
330 performed instead by relying on forelimb claws and the propulsive force generated by
331 the hind limbs (Sasaki et al. 2005). In contrast, spectacled bears ~~display~~ show
332 ~~elaborate~~ ed feeding activities, ~~in relation~~ related to a very herbivorous diet that mostly
333 relies on ripe fruits, bromeliad hearts, berries and palm hearts (Peyton 1980; Mondolfi
334 1989; Nowak 1999; Ríos-Uzeda et al. 2006). For example, spectacled bears are known
335 to tear off the leaves of large bromeliads to eat their bases, as well as to forage on the
336 hearts of smaller ones by ripping them off from the substrate (Nowak 1999). Based on
337 these considerations, although the use of the radial sesamoid in such feeding activities
338 requires further confirmation (Salesa et al. 2006a), we favour the view that the well-

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339 developed radial sesamoid of *T. ornatus* is likely related to the more elaborate ~~d~~-feeding
340 activities of this taxon compared to ursines.

341 In *I. arctoides*, with an average estimated body mass even ~~larger~~-~~greater~~ than
342 that of *T. ornatus* (ca. 200 kg Abella 2011; Abella et al., 2013b), the radial sesamoid
343 similarly could not have performed a locomotor role during climbing on thin branches.
344 Both skull morphology and dental characteristics (Abella 2011; Monesillo et al. 2014)
345 suggest that this taxon, like the extant *T. ornatus*, would have consumed a large amount
346 of plant material (Abella 2011; Abella et al. 2013a), even displaying some incipient
347 durophagous adaptation ([Abella 2011](#)) (although less clearly expressed than in later
348 ailuropodines). All this evidence strongly suggests that, in early members of the giant
349 panda lineage, the radial sesamoid might have already performed a role in feeding-
350 related manipulative behaviours. This is further supported by the high and low values
351 displayed by the RSL/MCL and SLFL/RSL ratios (~~respectively~~) in *I. arctoides*,
352 suggesting that its radial sesamoid was already being used as a pseudo-opposable
353 grasping structure. If correct, this interpretation would imply that *I. arctoides* provides
354 the oldest evidence of a feeding-related radial sesamoid. In this regard, the original role
355 of this bone ~~in~~-~~at~~ the base of the giant panda lineage might differ from that in ailurids,
356 given that a feeding-related manipulative role for the latter is not supported by the
357 dental morphology of the extinct *Simocyon*, which together with its much smaller body
358 mass ~~instead~~ suggest ~~instead~~-a grasping role during arboreal locomotion (Salesa et al.
359 2006b).

360 On the other hand, the possession of similarly enlarged radial sesamoids in both
361 the early ailuropodine *Indarctos* and extant tremarctine bears suggests that a moderately
362 well-developed radial sesamoid is likely to represent the plesiomorphic condition for
363 crown ursids as a whole, with the more hypertrophied condition of extant ailuropodines

364 (*A. melanoleuca*) and the reduced radial sesamoid of ursines representing more derived,
365 diverging morphologies evolved after the split of these groups (Fig. 7). In fact, from
366 both an evolutionary and morphofunctional viewpoint, it is ~~very~~ remarkable that,
367 besides its less hypertrophied size, the radial sesamoid of *I. arctoides* has ~~closer~~ greater
368 morphological ~~similarities~~ similarity to those of the lesser panda and other carnivorans
369 with a relatively well-developed radial sesamoid, rather than to the specialized
370 condition of giant pandas (Fig. 8 and Supporting information Video 1: SIV1). In
371 particular, *Ai. fulgens* ~~displays~~ has an almost cylindrical radial sesamoid, with a cup-
372 shaped rough structure on its palmar tip and no contact with the first metacarpal (Endo
373 et al. 2001b; Antón et al. 2006; Fisher et al. 2009). In contrast, *A. melanoleuca*
374 ~~possesses~~ has a flattened radial sesamoid, with a curved ossified tip and a clear contact
375 between the radial sesamoid and the first metacarpal (Davis 1964; Endo et al. 1996,
376 1999c, 2008; Salesa et al. 2006a, b). The configuration of the giant panda provides a
377 more efficient grasp, not only due to the larger size of the radial sesamoid, but also
378 because of its different orientation (more medial instead of palmar), the ossification of
379 the cartilaginous tip (giving the m. *abductor digiti I brevis* a more complete bony
380 attachment, instead of inserting partly on a cartilage), and its articulation with the first
381 metacarpal (thus resulting in a greater efficiency of to the pincer-like mechanism of the
382 pseudo-thumb).

383 This lack of articulation between the radial sesamoid and the first metacarpal in
384 *Ai. fulgens* has led some authors to conclude that, in the red panda lineage, the
385 hypertrophy of this bone ~~would have~~ evolved completely independently from that of the
386 giant panda (Endo et al. 2007, 2008). However, such an inference is not supported by
387 the morphology of the relatively large radial sesamoid of the extinct ailuropodine *I.*
388 *arctoides*. The latter, although having an ursid-like overall morphology, is functionally

389 more comparable to that of the lesser panda. Specifically, the radial sesamoid of *I.*
390 *arctoides* is only flattened in young individuals, would have possessed a non-ossified
391 (cartilaginous) tip and shows no indication of articulation with the first metacarpal. This
392 suggests that the somewhat hypertrophied configuration of the Late Miocene ursid *I.*
393 *arctoides* and the other carnivorans with well-developed radial sesamoids ~~is best~~ could
394 be interpreted as the symplesiomorphic condition for the Arctoidea. In fact, since a
395 relatively large radial sesamoid is retained by certain extant Nandiinidae and Viverridae,
396 the possibility cannot be discounted that this morphology is a synapomorphie
397 synapomorphy for all crown Carnivora (i.e., having originated before the split between
398 the Caniformia and Feliformia), in which it would have displayed an original role
399 related to arboreal locomotion. This interpretation is reinforced by the presence of
400 various arboreal adaptations in the postcranial skeleton of stem carnivorans, such as
401 *Amphicyonodon* from the Early Oligocene of Europe, miacids or other extinct mammals
402 such as multituberculates (Krause and Jenkins 1983; Cirot 1992; Heinrich and Houde
403 2006; Salesa et al. 2006b; Spaulding and Flynn 2009).

404 ~~This~~The presence of developed radial sesamoids in ~~primitive forms related to~~
405 ~~eanidae basal Caniformia~~(~~which extant species possess a small and lenticular sesamoid~~),
406 enhances the idea ~~of the presence of that~~ this feature could have been widespread in the
407 basal carnivorans (Fig. 7).

408 A moderately well-developed radial sesamoid involved in locomotion might
409 therefore be the primitive condition for both ailurids and ursids. The latter is supported
410 by the relatively small (ca. 15-30 kg) body mass of basal ursids such as *Ballusia* and
411 *Ursavus*, in which a relatively large radial sesamoid might have favoured agile climbing
412 behaviours and even above-branch quadrupedalism. This hypothesis cannot be yet
413 tested based on fossil remains, but it is potentially falsifiable if radial sesamoids of more

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414 primitive extinct ursids were found in the future. Unlike in small-bodied carnivorans
415 such as viverrids and mustelids, with the subsequent increase in body mass during ursid
416 evolution, the original locomotor role of the radial sesamoid would have been lost. This
417 would have enabled the reduction of this bone in ursines, whereas in both ailuropodines
418 and tremarctines this would have been precluded by increased selection pressures posed
419 by more elaborate, feeding-related manipulatory behaviours. The smaller radial
420 sesamoid of *I. punjabensis*, recorded several million years later from the Turolian
421 locality of Pikermi, ~~may~~suggests a secondary reduction of this bone during the
422 evolution of the *Indarctos* lineage (thus paralleling that occurred in ursines), possibly
423 due to the significant increase in body size and gradual change of feeding habits
424 towards a more carnivorous diet (Abella 2011). This interpretation fits well with the
425 forearm morphology of *I. punjabensis*, which displays proportions ~~to that~~like those of
426 extant brown bears (Roussiakis 2001), thus suggesting a much more cursorial
427 locomotion than in *I. arctoides* (Abella et al. 2011). In contrast, at some point in the
428 giant panda lineage, the radial sesamoid would have been co-opted to perform even
429 more elaborate manipulative behaviours related to a more complex plant matter feeding,
430 leading to further adaptive specialisations that would have provided the false thumb
431 with even more refined grasping abilities.

432

433 **Conclusions**

434 The fossil remains of the extinct ailuropodine *Indarctos arctoides* enables to
435 trace back the possession of a large radial sesamoid, most likely involved in elaborated
436 herbivorous feeding activities, to the Late Miocene. ~~CThe~~ comparison with other
437 carnivorans suggests that the possession of a relatively large radial sesamoid probably
438 represents the primitive condition for most members of this group, originally displaying

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439 a grasping role during arboreal locomotor behaviours in small-bodied taxa. Given the
440 subsequent body size increase and ~~the~~ concomitant loss of its original locomotor
441 function during ursid evolution, the radial sesamoid would have been reduced in ursines
442 (mainly in relation to a more cursorial locomotion, but also to a more omnivorous diet),
443 but retained in both ailuropodines and tremarctines due to the [performance-acquisition](#)
444 of a new manipulatory role in grasping activities related to herbivorous feeding. From
445 this condition, the radial sesamoid would have been subsequently hypertrophied in later
446 members of the giant panda lineage, by acquiring more specific adaptations to bamboo
447 feeding.

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

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668 **Author contribution statement**

669 Conceived and designed the experiments: JA PM JM.

670 Performed the experiments: JA APR AV.

671 Analyzed the data: JA MDE AV.

672 Contributed reagents/materials/analysis tools: JA AV APR DH.

673 Wrote the paper: JA DMA JM.

674

675 **Figure legends**

676

677 Figure 1

678 Schematic map of Cerro de los Batallones (Torrejón de Velasco, Comunidad de Madrid,

679 Spain), showing the location of the nine sites. The site of Batallones-3 is denoted with a

680 star. Oscar Sanisidro helped us with this figure using Adobe Illustrator and Adobe

681 Photoshop CS4.

682

683 Figure 2

684 In situ photograph showing the fossil remains of an almost articulated forepaw of

685 *Indarctos arctoides* from Batallones-3 (BAT-3'09.870-882 and BAT-3'09.884-900) in

686 anatomical connection. Scale bars equal 5 cm.

687

688 Figure 3

689 Schematic drawing showing the insertion areas for the main tendons, muscles and

690 muscle ligaments of the left radial sesamoid of *Indarctos arctoides*, for both the young

691 adult morphology (a: lateral view; b: medial view) and the senile adult one (c: lateral

692 view; d: medial view). CT: hypothetical cartilaginous tip insertion; AB+OP: Insertion

693 area for the muscles *abductor digiti I brevis* and *opponens digiti I*; LCV: insertion area
694 for the volar carposesamoid ligament; Fc: facet for the scapholunar; LCT: insertion area
695 for transverse carposesamoid ligament; ADIL: insertion area for the tendon of the
696 muscle *abductor digiti I longus*; LCL: insertion area for lateral carposesamoid ligament.

697

698 Figure 4

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

703

704 Figure 5

705 Schematic drawing of the right forepaw of *Indarctos arctoides*, showing the main
706 ligaments involved in the fixation of the radial sesamoid to the scapholunar, and the
707 main muscle tendons involved in the grasping action. . a: disto-palmar view; b: medial
708 view; c: dorso-distal view. LCV: volar carposesamoid ligament; Fc: facet for the
709 scapholunar; LCT: transverse carposesamoid ligament; ADIL: tendon of the muscle
710 *abductor digiti I longus*; LCL: lateral carposesamoid ligament; M: magnum; TR:
711 trapezoid; TZ: trapezium; Sc: scapholunar; RS: radial sesamoid.

712

713 Figure 6

714 Bivariate plot of the SLFL/RSL index versus the RSL/MCL index in carnivorans. These
715 results show the combination of the two indexes that are used in this paper, which give
716 an idea of the development of the radial sesamoid complex relative to the rest of the
717 forepaw. [Family codes: 1 and purple stand for Ursidae; 2 and black stand for](#)

1 718 [Mustelidae; 3 and Red stand for Ailuridae; 4 and orange stand for Procyonidae; 5 and](#)
2 719 [yellow stand for Felidae; 6 and blue stand for Viverridae.](#) “F” marks the fossil
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4 specimens.
5 720
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9 722 Figure 7
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11 723 Schematic tree showing the position and degree of development of the radial sesamoids,
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13 724 phylogenetic relationships, and temporal ranges of the members of the Carnivora
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15 725 referred to in this work. Three levels are considered, extracted from Figure 6, relative to
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17 726 the indices used in this work. Only the Ursidae and the Ailuridae are shown in more
18
19 727 detail. In the rest of the families two or more states of the character may be shown due
20
21 728 to the presence of different lineages inside the group (usually the arboreal ones show the
22
23 729 more-developed radial sesamoid). Outlines of some radial sesamoids are shown besides
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25 730 the families which present large radial sesamoids. Numbers are 1: *Indarctos arctoides*, 2:
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27 731 *Ailuropoda melanoleuca*, 3: *Martes foina*, 4: *Gulo gulo*, 5: *Simocyon batalleri*, 6:
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29 732 *Pristinailurus bristoli*, 7: *Ailurus fulgens* and 8: *Paradoxurus hermafroditus*. The
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31 733 development of some of the radial sesamoids of some lineages are unknown due to the
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33 734 lack of extant specimens. Modified from Salesa et al. 2006b, Sato et al. 2009 and Sato
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35 735 et al. 2012.
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37 736
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39 737 Figure 8
40
41 738 Comparative schematic drawing showing the grasping complex of the right forepaw in
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43 739 *Ailuropoda melanoleuca* (a), *Ailurus fulgens* (b) and *Indarctos arctoides* (c). Partly
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45 740 modified from refs. 31 and 37, based on the 3D images derived by us from the scanned
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47 741 fossil remains.
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744 Supporting information Video 1 (SIV1).

745 Video showing the grasping action of the right forepaw, based on the fossil remains of

746 *Indarctos arctoides* from Batallones 3. This video only shows the last phase of the

747 movement, since supination of the forepaw and flexion of carpals and metacarpals occur

748 prior to the digit flexion shown here.

749

750 Supporting Information Table 1 (SIT 1).

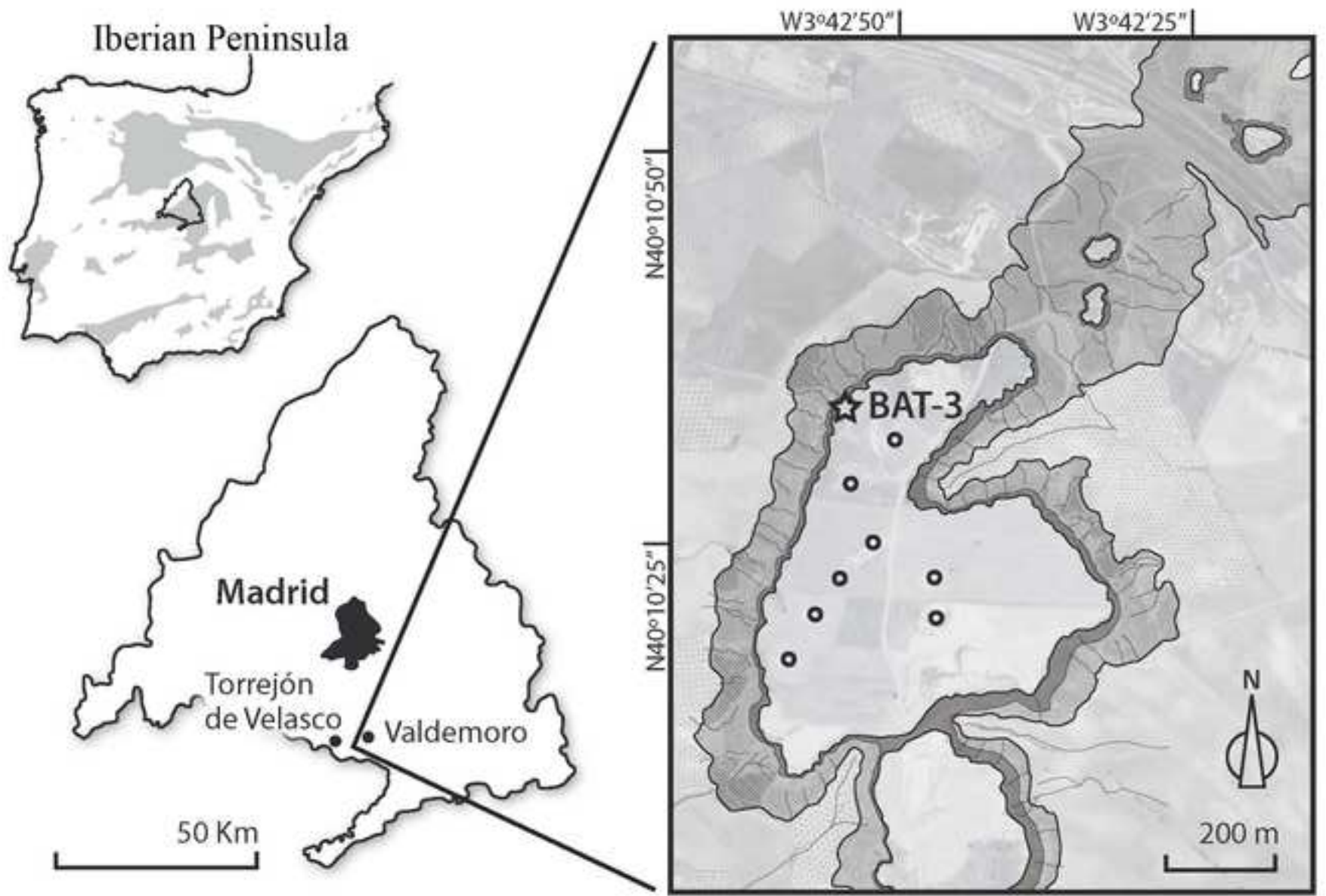
751 List of taxa included in the comparative sample, which includes skeletons of extant and

752 extinct carnivorans, showing sample size (N), species name, housing institution and

753 catalogue number.

Figure

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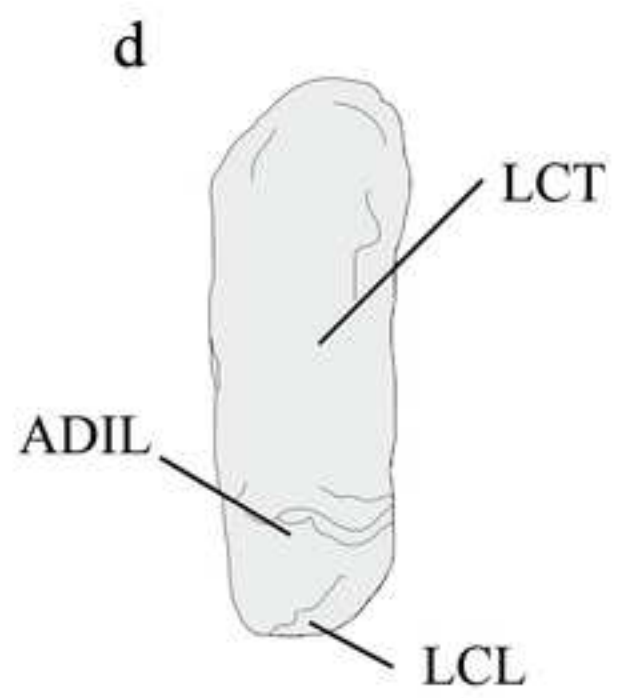
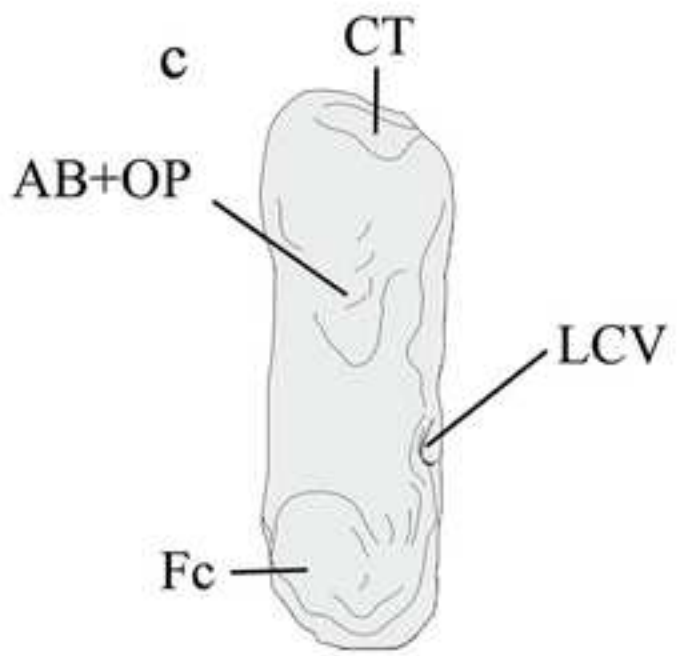
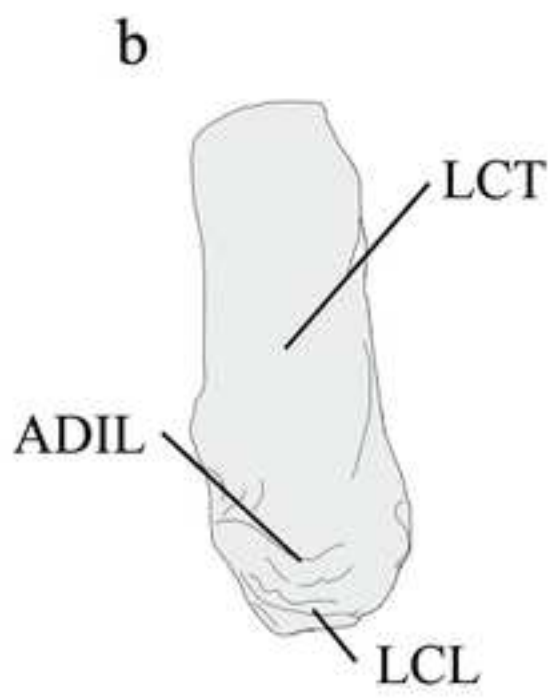
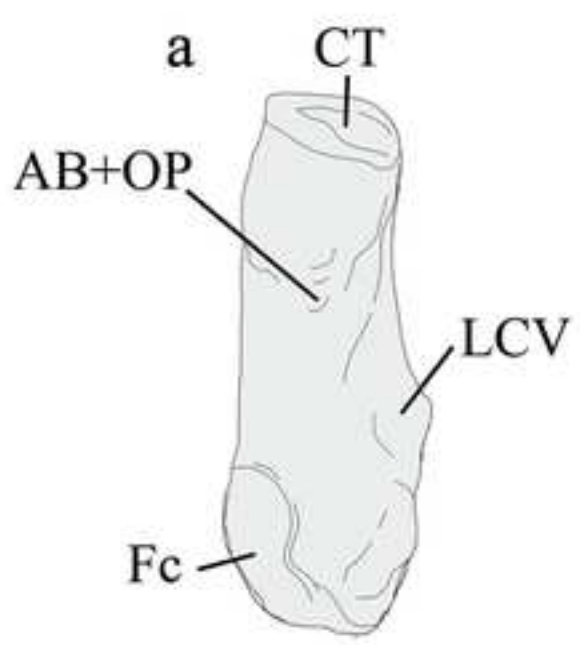


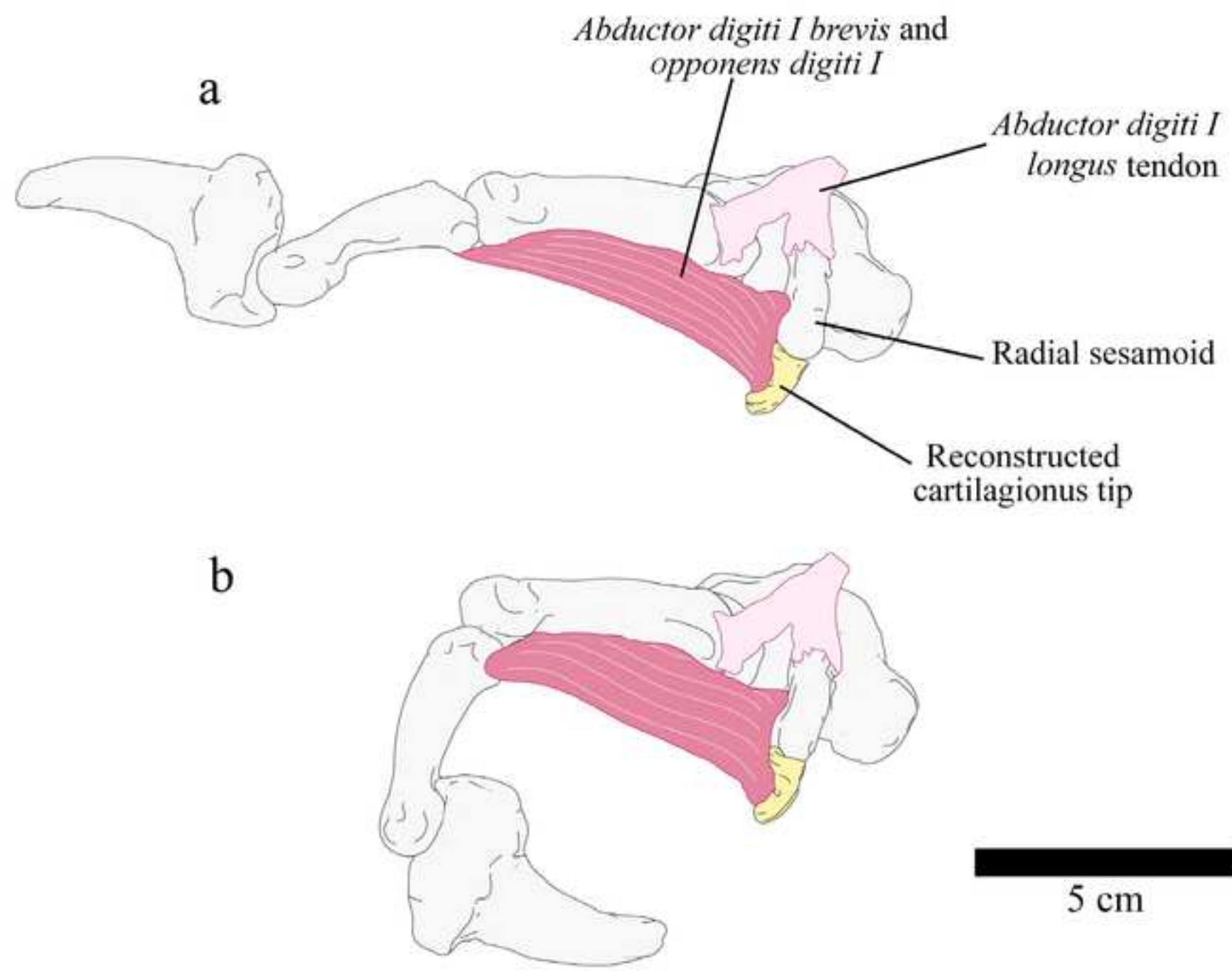
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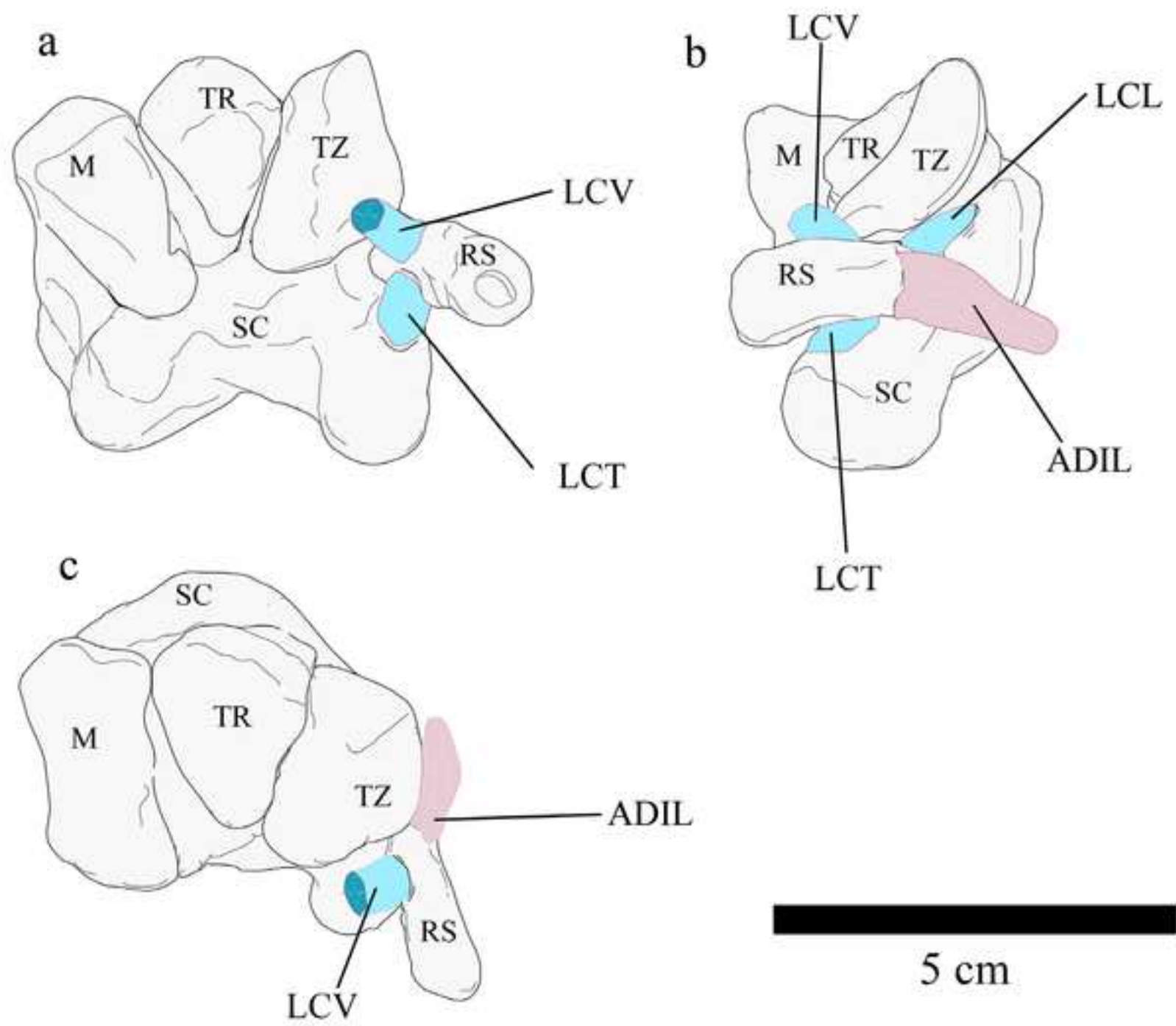
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Radial sesamoid

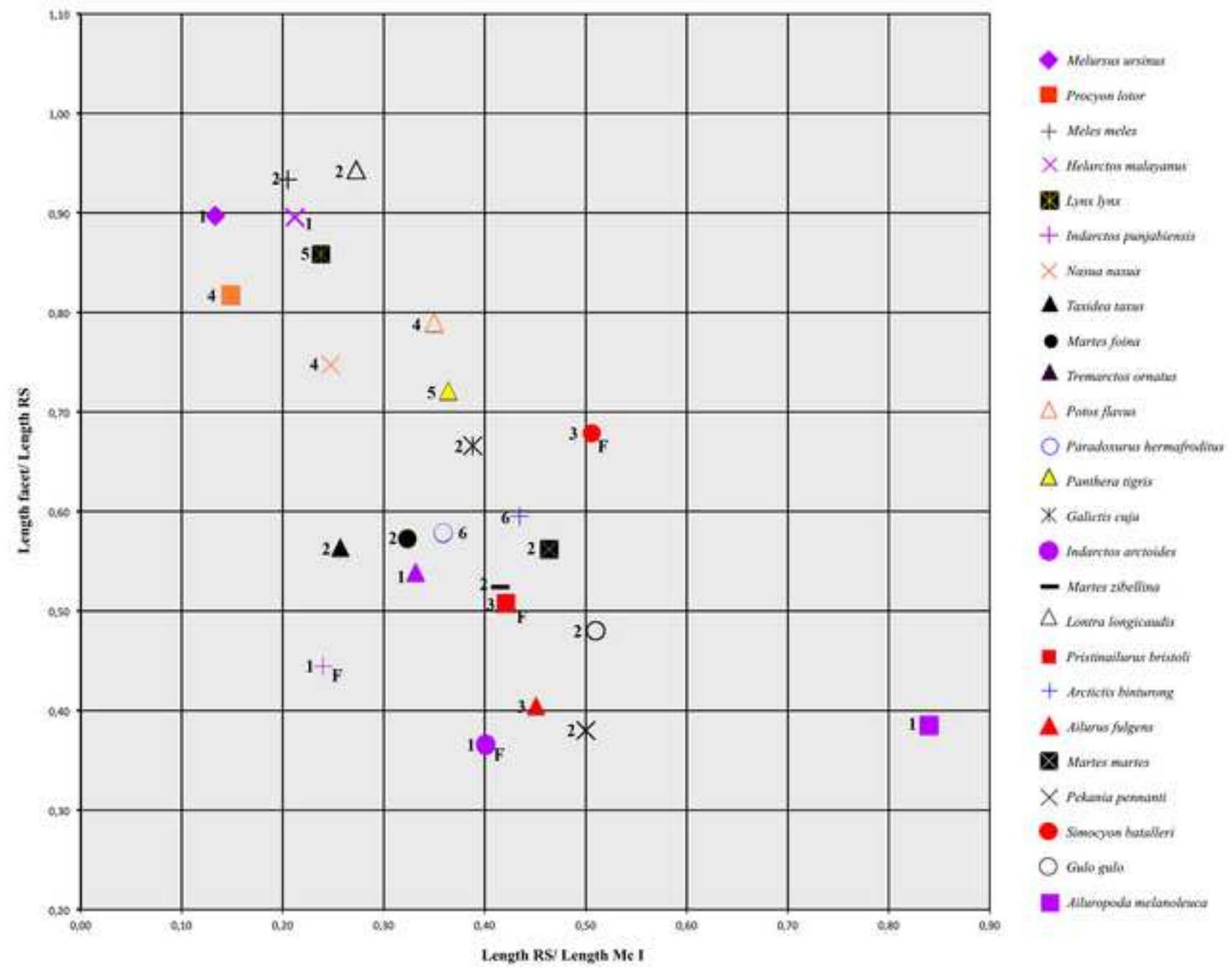






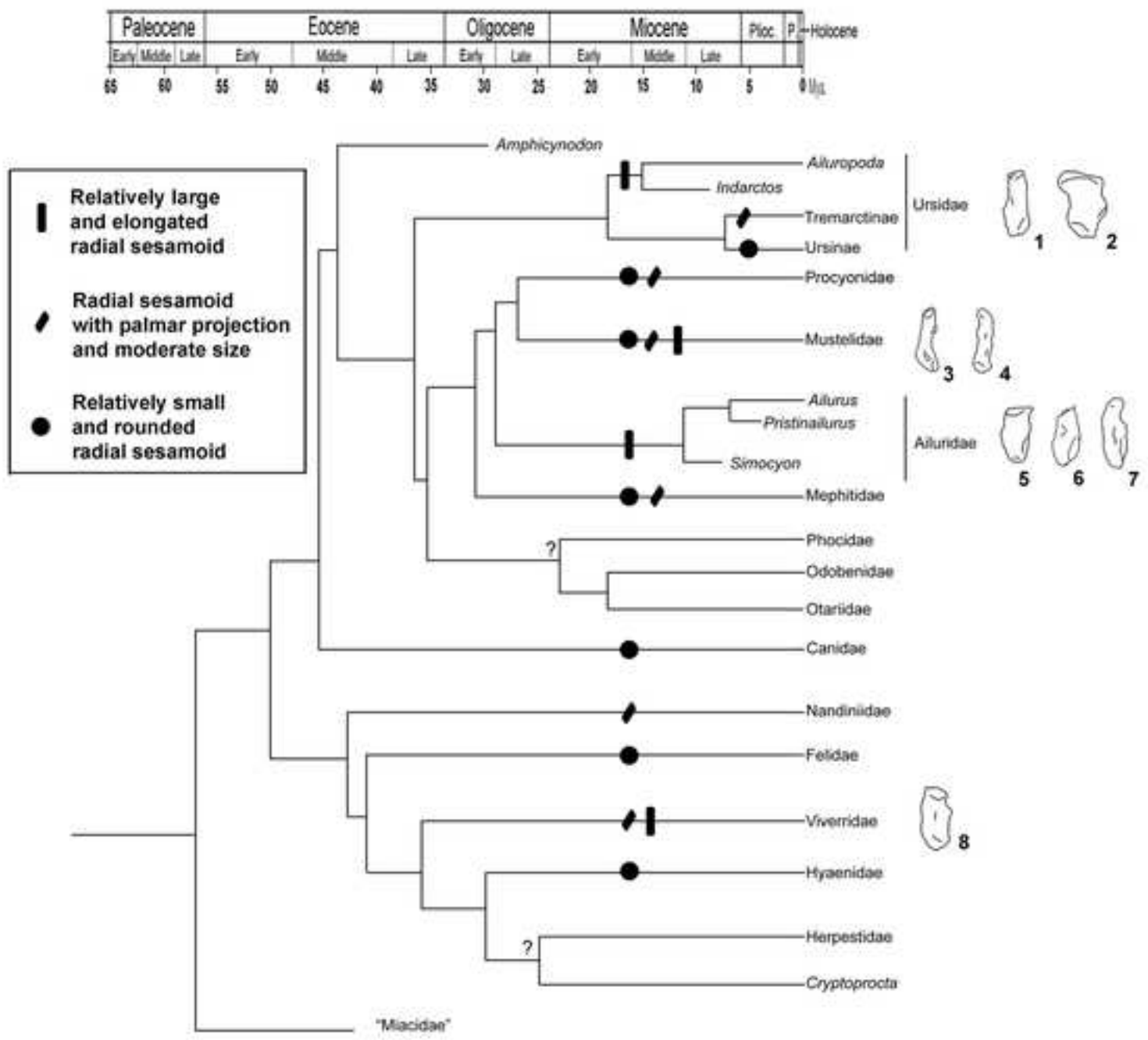
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Figure

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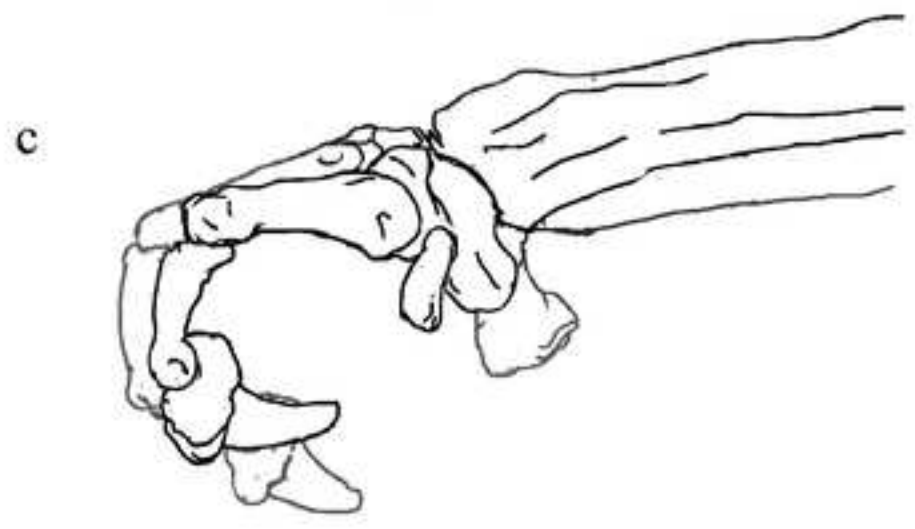
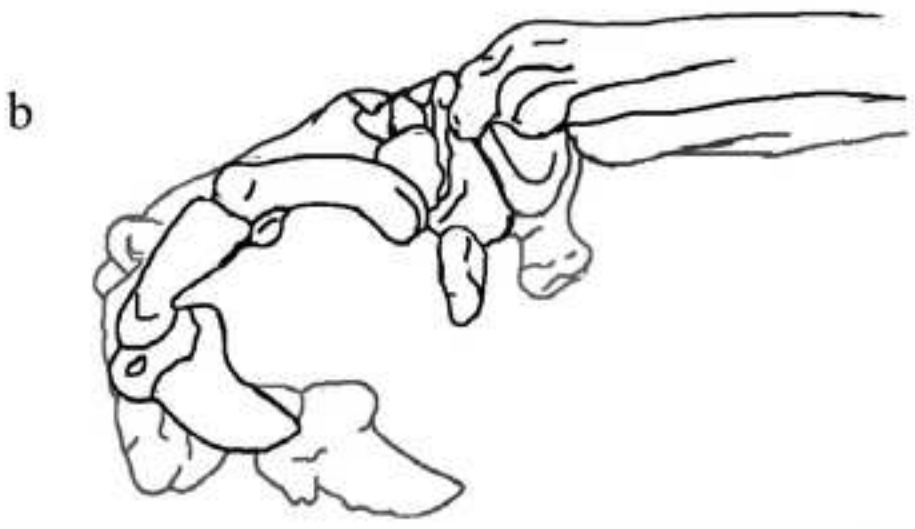
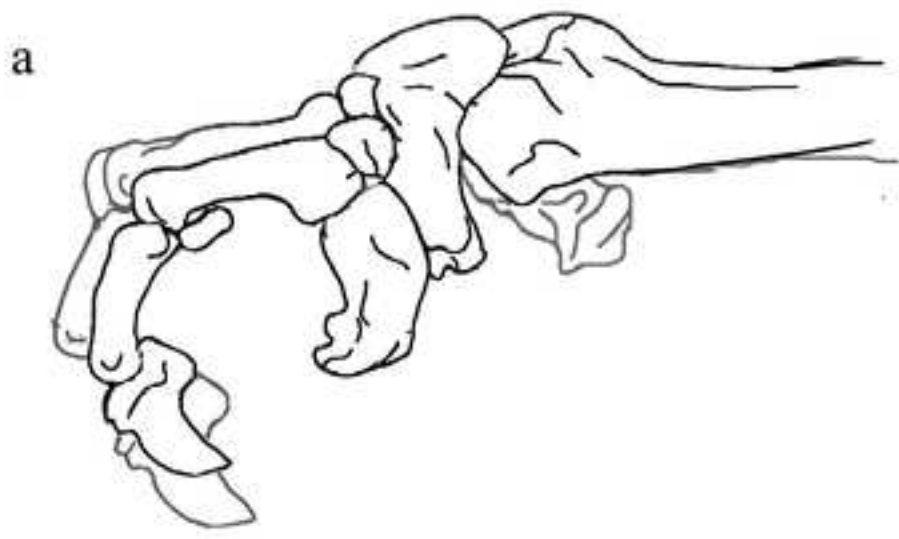


Table 1. Index of relative length of the radial sesamoid (RSL / MCL) in *Indarctos arctoides* (only adults) compared to other carnivorans.

N	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
1	<i>Lynx lynx</i>	0.238	Felidae	Terrestrial

Abbreviations: N, sample size; RSL, maximum length of the radial sesamoid; MCL, maximum length of the first metacarpal.

1 **Table 2.** Index of relative size of the radial sesamoid facet for the scapholunar (SLFL /
 2 RSL) in *Indarctos arctoides* compared to other carnivorans.
 3

N	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

4

5 Abbreviations: N, sample size; RSL, maximum length of the radial sesamoid; SLFL,

6 maximum dimension of the radial sesamoid facet for the scapholunar.

7

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