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Postcranial remains of *Indarctos atticus* (Ursidae, Mammalia) from the classical locality of Pikermi (Attica, Greece), with a description of the front limb

With 9 Tables and 3 Plates

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Abstract

The front limb of *Indarctos atticus* has many characters in common with *Ursus arctos* both in proportions and morphology. The brachial index and the length proportions between the metacarpals and the radius or the humerus are similar with those of *U. arctos*. Only the first metacarpal of *I. atticus* seems slightly shortened and the distal part of the humerus less developed compared with those of *U. arctos*. The bones of *I. atticus* show great morphological similarities with those of *U. arctos*, while it seems that there is no close resemblance with *Ailuropoda* except for the presence of an entepicondylar foramen. Compared to specimens of *I. atticus* from Concud, present findings show interesting differences that are discussed.

Key words: Carnivora, Ursidae, *Indarctos*, Late Miocene, Pikermi, Greece.

Kurzfassung

[Postcraniale Reste von *Indarctos atticus* (Ursidae, Mammalia) von der klassischen Lokalität Pikermi (Attica, Griechenland), mit einer Beschreibung des Vorderbeins.] — Die Vorderextremität von *Indarctos atticus* hat mit *Ursus arctos* viele gemeinsame Merkmale, sowohl in den Proportionen als auch in der Morphologie. Der Brachial-Index und die Proportionen der Länge zwischen den Metacarpalia und dem Radius oder dem Humerus sind ähnlich mit denjenigen von *U. arctos*. Nur das erste Metacarpale von *I. atticus* sieht ein bißchen kleiner aus verglichen mit denjenigen von *U. arctos*. Der distale Teil des Humerus ist auch weniger breit. Die Knochen von *I. atticus* zeigen große morphologische Ähnlichkeiten mit denen von *U. arctos*, hingegen scheint es, daß es keine besonderen Ähnlichkeiten mit *Ailuropoda* außer der Anwesenheit von einem Foramen entepicondyloideum gibt. Im Vergleich mit *I. atticus* aus Concud weisen unsere Funde interessante Unterschiede aus, die besprochen werden.

Introduction

Indarctos atticus (WEITHOFER 1888 *ex* DAMES MS) first became known from Pikermi and is one of the rarest and least well known carnivores of the Pikermi fauna. The first remain of this species was a mandibular fragment described (but not figured) by DAMES (1883) as *Hyaenarctos* sp. That specimen contained M_1, M_2 and the alveolus of M_3, and it was restudied and figured by WEITHOFER (1888: pl. 12 figs 1-2) as *Hyaenarctos atticus*. According to the comments of WEITHOFER (1888: 233), DAMES had told him that this specimen was a new species. That specimen was labelled as *Hyaenarctos atticus*, which led WEITHOFER to apply that name to it, and it is now considered a species of *Indarctos*. HELBING (1932) was the first to mention the occurrence of *Indarctos* in Samos. HELBING thought the Pikermi specimen was too fragmentary and did not identify it, but named the Samos specimen *Indarctos* sp. In the meantime PILGRIM (1931: 23-29, text-figs 4-5)

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described some bone remains (an associated left radius and ulna) from Pikermi as *Indarctos* (?) cf. *atticus*. He had knowledge of the Samos specimens and noted the possibility of their belonging to *I. atticus*, but left HELBING to make the final decision. VIRET (1939: 23) mentioned the similarities between the Samos specimens and *I. atticus*, and ERDBRINK (1953: 576-578) considered that they should be named so. Other specimens of *I. atticus* from Samos are also cited by THENIUS (1949, 1959). Fossils attributed to *I. atticus* are known from Spain, France, Germany, Hungary, Libya, Iran (Maragha) and China, in addition to Pikermi and Samos.

Hyaenarctos maraghanus MECQUENEM 1925, from Maragha has been considered by FRICK (1926, in VIRET 1939: 23) a large individual of *"H." atticus* and this view is followed by most authors, such as ERDBRINK (1953: 580), THENIUS (1959: 285), HENDEY (1980: 101) and WERDELIN (1996: 280). Other authors however as BERNOR et al. (1996: 145) recognize *I. maraghanus* as a distinct species.

ZDANSKY (1924) described two species of *Indarctos* from China, *I. largelii* and *I. sinensis*, but ERDBRINK (1953: 580-581) regarded the validity of the latter one as doubtful. THENIUS (1959: 270, tab. 1) also considered the two Chinese forms identical, accepting only the first name (having page priority) as a subspecies of *I. atticus*, and is followed by ERDBRINK (1968: 23).

Indarctos salmontanus PILGRIM 1913, (genotype of *Indarctos*) from the Siwaliks, is thought by MATTHEW (1929: 479) to be identical with *Indarctos punjabiensis* (LYDEKKER 1884) from the same locality. ERDBRINK (1953: 569) followed that opinion, while THENIUS (1959: 270, tab. 1) considered *I. punjabiensis* (= *I. salmontanus*) a subspecies of *I. atticus*. According to THENIUS (1959) *I. atticus* contains three subspecies: *I. atticus atticus* (DAMES 1883) known from Hungary (Baltavar), Greece (Pikermi, Samos), Iran (Maragha); *I. atticus largelii* (ZDANSKY 1924) (= *I. sinensis* ZDANSKY 1924) from Shansi (China); *I. atticus punjabiensis* (LYDEKKER 1884) = (*I. salmontanus* PILGRIM 1913) from Siwaliks.

I. atticus is also reported from the Late Vallesian (MN 10) of Terrasa (ALCALÁ & MONTOYA 1989-1990) in Spain, from the Early Turolian (MN 11) of Crevillente 2 and Puente Minero (ALCALÁ & MONTOYA 1989-1990; FRAILE et al. 1997; ALCALÁ 1994) in Spain and Dorn-Dürkheim 1 (ROTH & MORLO 1997) in Germany, the Middle Turolian (MN 12) of Concud, Los Mansuetos, Valdecebro 5 and Cerro de la Garita (MORALES & SORIA 1979; FRAILE et al. 1997; ALCALÁ 1994) in Spain and Aubignas (AZANZA et al. 1993) in France. It is also known from Baltavar in Hungary (PETTER & THOMAS 1986; ROTH & MORLO 1997) and Sahabi (PETTER & THOMAS 1986) in Libya.

Various species of *Indarctos* are also known from the New World but their relationships to European or Asiatic forms remain obscure. Most important for the present study is the postcranial material found in Oregon and described first as *Indacrtos* (?) *oregonensis* by MERRIAM, STOCK & MOODY (1916).

Unfortunately, the remains attributed to *I. atticus* are mainly teeth or skull portions. Until now very little has been published on the postcranial skeleton of *Indarctos* or other Late Tertiary ursids, so the skeleton of *I. atticus* is very insufficiently known. As far as we know the only postcranial remains attributed to *I. atticus* are some from Pikermi, China and Spain.

PILGRIM (1931) described as *Indarctos* (?) cf. *atticus* an associated left radius and ulna from Pikermi. These remains belong to the WOODWARD collection of the British Museum (Natural History) and were found during the excavations made in Pikermi by WOODWARD and SKOUPHOS in 1901 (WOODWARD 1901). A left calcaneus and a (possibly pathological) left third metacarpal from S. E. Shansi (China) are described by ERDBRINK (1968) and attributed to *I. atticus* cf. *largelii*. Some bones and bone fragments from Concud are mentioned (but not figured) by CRUSAFONT-PAIRÓ & KURTÉN (1976); these specimens are two second metacarpals, an astragalus and two second metatarsals, all attributed to *I. atticus*. Finally, some remains of the pelvic region, from the locality of Valdecebro 5 in Spain are mentioned by ADROVER et al. (1986).

Material

The material listed below comes from the classical locality of Pikermi and it was found in the Pikermi collections stored in the Museum of Palaeontology Geology of Athens. These specimens were found in a wooden box, wrapped in newspapers of 1901. These specimens possibly come from the excavations made in the old locality of Pikermi in 1901 by WOODWARD and SKOUPHOS (WOODWARD 1901), since articles dedicated to these excavations were also found.

P.A. 1909/91: metacarpal V, left.
P.A. 1910/91: metacarpal IV, left.
P.A. 1911/91: metacarpal III, left.
P.A. 1912/91: metacarpal II, left.
P.A. 1909/91-1912/91 were found in life position in the same small ossiferous block.
P.A. 1944/91: humerus, right.
P.A. 1963/91: ulna, right.
P.A. 1964/91: radius, right.
P.A. 1963/91-1964/91 were found in life position in the same ossiferous block.
P.A. 2016/91: metacarpal I, right.
P.A. 2016b/91: radial sesamoid ?, right.
P.A. 2017/91: metacarpal II, right.
P.A. 2018/91: metacarpal III, right.
P.A. 2019/91: metacarpal, IV, right, the posterior part of the shaft is broken.
P.A. 2020/91: metacarpal V, right.
P.A. 2021/91: pisiform, right.
P.A. 2022/91: sesamoid bone.
P.A. 2023/91: cuneiform, right.
P.A. 2024/91: scapholunar, right.
P.A. 2025/91: magnum, right.
P.A. 2026/91: trapezoid, right.
P.A. 2027/91: trapezium, right.
P.A. 2028/91: unciform, right.
P.A. 2016/91-2028/91 were found in life position in the same ossiferous block.

From the above specimens, the left metacarpals (P.A. 1909/91-1912/91), the right manus (P.A. 2016/91-2028/91) and the right ulna and radius (P.A. 1963/91-1964/91), were found in three small ossiferous blocks where the bones were still in life position. The humerus (P.A. 1944/91) was found in the same wooden box, independent, but with sediment of the same type. Probably, all of the above specimens belong to the same individual. The associated radius and ulna described by Pilgrim (1931) as *Indarctos* (?) cf. *atticus* come from the same excavations, have the same dimensions as the present specimens, and represent the opposite member, the left. So, keeping in mind the rarity of that form, it is possible, even likely, that the specimens described by Pilgrim (1931) and the specimens under consideration here belong to the same individual.

Methods

The measurements taken on the long limb bones (humerus, radius, ulna) have the following abbreviations: Lmax: maximum length, DTpr.: maximum transverse diameter of the proximal end, DAPpr.: maximum anteroposterior diameter of the proximal end, DTdia: transverse diameter of the shaft at its middle, DAPdia: anteroposterior diameter of the shaft at its middle, DTdist.: maximum transverse diameter of the distal end, DAPdist.: maximum anteroposterior diameter of the distal end. In addition, at the humerus the transverse diameter of the distal articular surface (DTdist.art.) is also used. The same measurements have been applied to the radius and the ulna. Moreover, at the ulna the transverse (DTcor.pr.) and the anteroposterior (DAPcor.pr.) diameter at the coronoid process, as well as the transverse (DTst.pr.) and the anteroposterior (DAPst.pr.) diameter at the styloid process have been taken.

At the carpals (except the pisiform) the following measurements have been used: DTmax: maximum transverse diameter of the bone, DAPmax: maximum anteroposterior diameter of the bone, Hmax: maximum height of the bone. Additionally, for the scapholunar the anteroposterior diameter (DAPpr.art.) of the radial facet, the transverse (DTdist.art.) and the anteroposterior (DAPdist.art.) diameter of the distal articular part have been taken. For the pisiform the following measurements have been used: Lmax: maximum length, DTpr.: maximum transverse diameter of the base, Hpr.: maximum height of the base, DTdist.: maximum transverse diameter of the head, Hdist.: maximum height of the head.

The metacarpals have been measured as the long bones, except: DTdist.art.: transverse diameter of the distal articular condyle, DAPdist.art.: anteroposterior diameter of the distal articular condyle.

Description

Humerus (pl. 1 fig. 1): The greater tuberosity is situated lower than the head of the humerus. The biccipital groove seems more constricted than that of *I. oregonensis* (Merriam, Stock & Moody 1916: text-fig. 15a) and the depression for the infraspinatus is wide and deep. The head in rear view appears flattened and in side view semicircular. In these features the head of the humerus shows similarities with that of *Ailuropoda* which according to Davis (1964: 94) is more cylindrical than that of *Ursus*, as is the head of cursorial forms. However, on available specimens of *U. spelaeus* from Igricz (Hungary) the head is more cylindrical than that of *U. arctos*. The shaft of the humerus is not different in development than that of *U. arctos* and in side view shows an important angulation at the distal end of the deltoid ridge. Such an angulation is also present in *U. arctos*, *A. africanum* (Hendey 1980: text-fig. 15) and *I. oregonensis* (Merriam, Stock & Moody 1916: text-fig. 15c) but absent in *Ailuropoda* (Davis 1964: text-figs 47, 48). The pectoral and deltoid ridges extend distally to the lower third of the bone. An interesting observation concerns the torsion of the proximal part of the humerus in relation to the distal part. Comparison with one specimen of recent *U. arctos* and two of *U. spelaeus* from Igricz shows that with the trochlea axis medio-laterally oriented, the bicipital groove in all cases shows medially, but the torsion of the proximal part in *I. atticus* is stronger than that of the two other species. The stronger torsion of the shaft in *I. atticus* affects the orientation of the area between the deltoid and pectoral ridge, that seems to face anteriorly more than in *U. arctos*. At the distal part of the humerus and anteriorly the condyloid and the coronoid fossa are almost equally developed (the coronoid fossa is slightly less marked) but shallow. The sulcus for the ulnar nerve is small and shallow. The medial epicondyle and the olecranon fossa are like those of *Ursus*, in contrast with *Ailuropoda* where the medial epicondyle is vertically compressed and the olecranon fossa relatively wider (Davis 1964: text-fig. 49). The most important character of the distal part of the humerus is the presence of an entepicondylar foramen. That is absent in *U. arctos* except in very rare cases (Erdbrink 1953: 275), absent also in *A. africanum* (Hendey 1980: text-fig. 15), but present in *I. oregonensis* (Merriam, Stock & Moody 1916: text-fig. 15), *Tremarctos ornatus* and *Ailuropoda* (Davis 1964: 95). It is present also in a specimen of a young individual attributed to *I. vireti* by Crusafont-Pairó & Kurtén (1976: 11) but absent in *Ursavus primaevus* (Viret 1951: text-fig. 9). The entepicondylar foramen is present in some Amphicyoninae such as *Amphicyon major* (Ginsburg 1961: text-fig. 9.2, Bergounioux & Crouzel 1973: text-fig. 23), *A. giganteus* (Ginsburg & Telles Antunes 1968: text-fig. 20), *A. longiramus* (Olsen 1960: text-fig. 7), *Ysengrinia* (Hunt 1972: text-fig. 12) or *Cynelos lemanensis* (Ginsburg 1999: text-fig. 10.8) and some Hemicyoninae such as *Hemicyon sansaniensis* (Ginsburg 1961: text-fig. 31).

Tab. 1. Measurements of humerus.

	Lmax	DTpr.	DTpr.art.	DAPpr.	DTdia	DAPdia	DTdist.	DTdist.art.	DAPdist.
I. atticus, P.A. 1944/91, Pikermi	458.7	84.7	72.0	109.0	43.3	53.7	110.5	97.2	73.2
I. oregonensis (Merriam, Stock & Moody 1916), Oregon	(490)	(108.3)	—	(122)	—	—	—	—	—
I. vireti (juvenile) (Crusafont-Pairó & Kurtén 1976), Can Llobateres	(290)	—	—	—	24.3	—	75.4	50.6	—

Tab. 2. Measurements of radius.

	Lmax	DTpr.	DAPpr.	DTdia	DAPdia	DTdist.	DAPdist.
I. atticus, P.A. 1964/91, Pikermi	384.5	50.7	39.0	(37.0)	(26.5)	70.9	47.6
I. atticus, (Pilgrim 1931), Pikermi	381	50	38.5	35	—	72	—

Radius (pl. 2 fig.4): As described by Pilgrim (1931: 26), the cross-section of the shaft at about 50 mm on either side of the midpoint is sub-triangular. That is clearly visible on the present specimen but only at the proximal part because distally of the midpoint the shaft is slightly deformed. In that character the shaft of the radius resembles that of *Ailuropoda* where the section of the shaft is triangular (Davis 1964: 97), while in *U. arctos* the section of the shaft is ovoid. On the lateral side of the shaft and below the level of the radial tuberosity there is a feeble ridge, observable also in the cross section of the shaft given by Pilgrim (1931: text-fig. 5d). The head of the radius shows torsion in relation to the distal epiphysis, but that is not different from that of *U. arctos*. The articular surface for the humerus shows no differences to *U. arctos*. The radial tuberosity and the external tuberosity are well developed and the area between them is slightly swollen. The shaft on its distal part and laterally is characterised by a well developed groove, mentioned by Pilgrim (1931: 27), which starts above the articular surface for the ulna and continues proximally for about 10 cm. According to the same author, that groove also exists on the ulna from the Siwaliks attributed by Falconer to *Agriotherium sivalense*. As we see from Hendey (1980: text-fig. 17b), that groove may be present in *A. africanum*, contrary to the description given by that author (Hendey 1980: 36). Posteriorly, the surface for the pronator quadratus is almost flat while in one specimen of recent *U. arctos* and two specimens of *U. spelaeus* that surface is slightly concave. Distally, the articular surface for the scapholunar is like that of *U. arctos*, not deflected proximally towards the ulnar notch as in *Ailuropoda*, and the articular area on the styloid process is saddle shaped, as in *Ursus*, while in *Ailuropoda* it is scarcely developed (Davis 1964: 99). The articular surface for the ulna is transversally oval and concave. On the dorsal surface of the distal extremity, from the medial to the lateral side, there is one deep groove for the abductor pollicis longior, two shallow grooves for the extensores carpi radialis longior and brevior, and one deep groove for the extensor communis digirotum. Between the grooves for the extensor carpi radialis brevior and the extensor communis digitorum there is a wide (25 mm) median ridge, while the ridge that separates the grooves for the extensores carpi radialis longior and brevior is scarcely developed.

Ulna (pl. 1 fig. 2, pl. 2 fig. 3): The ulna of *I. atticus* is very similar with that of *U. arctos*. The anterior tuberosity of the olecranon process, which is the area for insertion of the most proximal part of the anconeus, is the higher part of the olecranon, equally developed as that of *U. arctos*, and knob-like. Also knob-like and extended medially is the area for insertion of the flexor carpi ulnaris muscle. On the ulna from Saharanpur (Siwaliks) described by Lydekker (1888: text-fig. 1) as *Hyaenarctos*, the anterior tuberosity is more developed than in *I. atticus*, and a very deep groove separates that tuberosity from the tip of the olecranon. In *A. africanum* (Hendey 1980: text-fig. 16) the anterior tuberosity is very small. In *I. oregonensis* the anterior tuberosity is also the higher point of the olecranon as in *I. atticus*, but the postero-medial angle of the olecranon process seems to be situated lower (Merriam, Stock & Moody 1916: text-fig. 16). The surface of the ulna opposite the sigmoid cavities is very wide, a result of the presence of a ridge posteriorly and laterally of the sigmoid cavities. The greater sigmoid cavity is almost semicircular in lateral view, unlike the specimen from Saharanpur where the greater sigmoid cavity in lateral view seems more restricted and low (Lydekker 1888: text-fig. 1). Distally, the crest that separates the area of attachment of the pronator quadratus muscle from that for the distal part of flexor digitorum profundus 5, is developed in the form of a high and lamelliform projection. A deep depression is visible between that and the styloid process. Such a depression is also present in *A. africanum* (Hendey 1980: 36). According to Hendey this depression is absent in ursines, but it was found present in specimens of *U. arctos* and *U. spelaeus*. The radial facet is proximodistally ovoid and slightly convex transversely. Compared with *U. arctos* and *U. spelaeus* this articular surface seems less set out from the shaft of the bone. The olecranon is inclined backwards equally as that of *U. arctos*. Pilgrim (1931: 24) states that the olecranon of *I. atticus* is longer than in *Ursus* and shorter than in *I. oregonensis*, but his view is not supported by metrical data. On the present specimen, the olecranon process is equally developed (in relation to the total length of the bone) as that of *U. arctos*. The olecranon length (measured from the lower lip of the anconeus process to the tip of the anterior tuberosity) is about 63 mm, 14% of the total length of the ulna. On a specimen of *U. arctos* the same proportion was found equal to 15.5%, a small difference. Comparison with the ulna of *I. oregonensis* described by Merriam, Stock & Moody (1916) cannot be made since that specimen is not completely preserved.

Carpalia (pl. 3 figs 5-6, 12): The carpals of *I. atticus* are very similar with those of *U. arctos*. The scapholunar is the

Tab. 3. Measurements of ulna.

	Lmax	DTcor.pr.	DAPcor.pr.	DTdia	DAPdia	DTdist.	DAPdist.	DTst.pr.	DAPst.pr.
I. atticus, P.A. 1963/91, Pikermi	443.4	63.4	87.5	28.9	50.5	33.8	49.9	23.5	34.3
I. atticus, (Pilgrim 1931), Pikermi	439	61	85	—	—	31	52	26	32
I. oregonensis (Merriam, Stock & Moody 1916), Oregon	—	—	98.6	—	—	—	—	—	—

Tab. 4. Measurements of scapholunar.

	DTmax	DAPmax	DAPpr.art.	DTdist.art.	DAPdist.art.	Hmax
I. atticus P.A. 2024/91, Pikermi	56.9	60.2	36.7	49.0	35.3	31.7

largest of the carpals. Its articular surfaces for the magnum and the unciform have almost the same width, are elongated and anteroposteriorly oriented. The articular surface for the magnum at its most anteromedial part is flattened. The articular surface for the trapezoid and the trapezoideum is slightly broken posteriorly, but seems to be of oval shape with its long axis obliquely oriented; it does not extend posteriorly to the posterior limit of the articular surface for the magnum and is convex in anteroposterior direction. The outline of the proximal articular surface for the radius is oblique medially. This facet is in contact anteriorly with the trapezium facet as in some specimens of *A. africanum* (Hendey 1980: 40) and some specimens of *Ailuropoda* (Davis 1964: 99). It was not possible to recognize an articular surface for the radial sesamoid at the scapholunar, but the specimen P.A. 2016b/91, found between the scapholunar and the first metacarpal could represent such a bone. This specimen is elongated (about 18 mm) and has a flat, almost circular articular surface with a diameter of 8 mm. Due to the absence of comparative material it is not certain whether it represents a radial sesamoid, but it is very possible since a similar circular articular surface is also observable at the medial side of the first metacarpal and proximally. In any case, if that specimen really represents a radial sesamoid, then it was not as that of *Ailuropoda* which is not only very large but is also movable and functional. A radial sesamoid is also present in *Ursus* but in this case it is relatively small (Davis 1964: 99-100). There are few data for the presence of that bone in extinct taxa since it is very often of small size and is hardly recognisable. According to Hendey (1980: 36, 40) in *A. africanum* the radial sesamoid is absent since that author could not recognize an articular surface for it at the scapholunar, but the possibility to be rudimentary cannot be excluded. Ginsburg (1961: 28) and Bergounioux & Crouzel (1973: 30) mention its existence in the amphicyonid *A. major*. The other carpals show no important differences from those of *U. arctos* except in details.

Tab. 5. Measurements of trapezium, trapezoid, magnum, unciform and cuneiform.

		Hmax	DTmax	DAPmax
I. atticus Pikermi	Trapezium, P.A. 2027/91	20.1	15.5	28.3
	Trapezoid, P.A. 2026/91	16.4	15.3	28.3
	Magnum, P.A. 2025/91	29.3	19.5	36.7
	Unciform, P.A. 2028/91	32.9	30.2	(33.9)
	Cuneiform, P.A. 2023/91	19.6	36.1	39.7

Tab. 6. Measurements of pisiform.

	DTpr.	Hpr.	Lmax	DTdist.	Hdist.
I. atticus P.A. 2021/91, Pikermi	36.3	21.2	49.0	24.0	(29.3)

Metacarpalia (pl. 3 figs 7-12): The metacarpals of *I. atticus* in their morphological characters are very similar to those of *U. arctos*. They appear straight in lateral view and only the first metacarpal is slightly curved. The distal articular surface of the first metacarpal is slightly narrow dorsally, while on the rest of the metacarpals these surfaces are wide. In these characters, the metacarpals of *I. atticus* differ from those of *Ailuropoda* where the distal articular surfaces are narrow (Davis 1964: 100). On the first metacarpal, the area for the insertion of the extensor ossis metacarpi pollicis is highly developed. As mentioned earlier, an articular surface at the medial and proximal part of the first metacarpal could represent a surface for the radial sesamoid. At the dorsal surface of the second metacarpal and above the middle of the shaft a scar marks the insertion of the extensor carpi radialis longior. At the fifth metacarpal the area for the insertion of the extensor carpi ulnaris is very well developed.

Tab. 7. Measurements of metacarpals.

	Lmax	DTpr.	DAPpr	DTdia	DAPdia	DTdist.art.	DAPdist.art.	DTdist.
Mc I, *I. atticus*, P.A. 2016/91, Pikermi	75.0	30.2	24.0	(14.2)	(14.8)	18.8	16.6	18.8
Mc II, *I. atticus*, P.A. 2017/91, Pikermi	89.4	19.3	31.2	18.4	15.6	21.6	—	22.0
Mc II, *I. atticus*, P.A. 1912/91, Pikermi	89.4	19.0	30.8	18.5	15.3	21.7	19.9	23.3
Mc II, *I. atticus*, (Crusafont-Pairó & Kurtén 1976), Concud	115	—	29.3	14.0	—	—	—	22.9
Mc II, *I. atticus*, (Crusafont-Pairó & Kurtén 1976), Concud	118	—	28.8	14.0	—	—	—	—
Mc II, *I. vireti*, (Crusafont-Pairó & Kurtén 1976), Can Llobateres	70	—	27.8	12.0	—	—	—	20.0
Mc II, *I. vireti*, (Crusafont-Pairó & Kurtén 1976), Can Llobateres	78	—	25.4	12.8	—	—	—	19.5
Mc III, *I. atticus*, P.A. 2018/91, Pikermi	98.1	22.5	31.8	19.4	15.9	21.8	—	22.7
Mc III, *I. atticus*, P.A. 1911/91, Pikermi	99.1	—	32.0	19.4	15.7	(22.8)	(20.4)	24.8
Mc III, *I. atticus* cf. *largelii*, (Erdbrink 1968), Shansi	81.2	20.0	30.0	19.0	14.8	23.5	30.0	—
Mc III, *I. vireti*, (Crusafont-Pairó & Kurtén 1976), Can Llobateres	—	—	25.5	14.4	—	—	—	—
Mc IV, *I. atticus*, P.A. 2019/91, Pikermi	105.3	22.9	31.2	(20.7)	(15.9)	24.0	21.0	24.5
Mc IV, *I. atticus*, P.A. 1910/91, Pikermi	105.6	22.8	31.0	19.7	16.9	25.3	21.6	26.0
Mc IV, *I. vireti*, (Crusafont-Pairó & Kurtén 1976), Can Llobateres	(83)	—	24.5	15.7	—	—	—	—
Mc V, *I. atticus*, P.A. 2020/91, Pikermi	102.0	29.7	31.5	17.4	18.5	(24.7)	20.6	25.7
Mc V, *I. atticus*, P.A. 1909/91, Pikermi	100.3	30.2	31.1	18.0	18.0	26.3	20.5	26.3
Mc V, *I. oregonensis*, (Merriam, Stock & Moody 1916), Oregon	103.6	(32.4)	39	21.5	—	—	—	(30)

Discussion

The humerus of *I. atticus* shows similarities with the humerus of *I. oregonensis* in the presence of an entepicondylar foramen and the strongly angled shaft. However, since the humerus of *I. oregonensis* is broken distally no accurate measurements for the total length and the distal width of that specimen are available. Its total length is estimated by Merriam, Stock & Moody (1916) to be 490 mm, larger than the humerus of *I. atticus*. The humerus of *I. atticus* is significantly longer than that of *U. arctos*, but as shown by the ratio DTdist. × 100/Lmax its distal end is less developed (tab. 8). The same ratio for Pleistocene remains of *U. arctos* (from various localities in Spain) varies according to Torres (1988: tab. 6) from 26.3-32.3 (n=24), larger again than the corresponding value of *I. atticus*. The brachial index is not different from that of *U. arctos* (tab. 9, ratio Lmax.Rad × 100/ Lmax.Hum).

As shown earlier, the shaft of the humerus of *I. atticus* is strongly angled, as in *U. arctos*. It seems, however, that it is characterised by the stronger torsion of the proximal extremity in relation to the distal one. Such an observation needs more comparative material to be proved. Another important character of the humerus of *I. atticus* is the presence of an entepicondylar foramen, absent in *U. arctos*. This seems to be the only significant character common between *I. atticus* and *Ailuropoda*. That foramen is also present in other extinct arctoid carnivores but its importance remains obscure. Olsen (1960: 9-10) comments on the various explanations that have been proposed for the presence or absence of that character. The presence of an entepicondylar foramen has been correlated with the development of the extensor musculature, while its absence has been related to the reduction of the medial epicondyle. Other authors have suggested a relationship with crouching life habits. Additionally, some authors suggest that the entepicondylar foramen may act as a retinaculum for the median nerve, to prevent it from slumping across the angle of the elbow when the humerus is abducted and the median nerve exposed. On the humerus of *I. atticus* the presence of an entepicondylar foramen does not seem to correlate with the development of the medial epicondyle. The trochlea of the humerus in *I. atticus* corresponds to 88% of the distal width of the bone, while in one specimen of recent *U. arctos* the same percentage is 80%. That means that the medial epicondyle of *I. atticus* is not more developed than that of *U. arctos*, so its development is probably not correlated with the presence of an entepicondylar foramen. Equally, Olsen (1960: 11) does not consider that the size of the medial epicondyle is related to the presence or absence of the entepicondylar foramen, or that the presence of such a foramen is indicative of a particularly strong muscle development. Its presence in many other groups of mammals (e. g. Felidae, Mustelidae) could indicate that it has functional and not phylogenetical significance.

From tables 2 and 8 it is clear that the radius P.A. 1964/91 is similar in dimensions and proportions to that described by Pilgrim (1931) and its other morphological characters are also in accordance with the description given by that author. As shown earlier, the distal end of the humerus is less developed than that of *U. arctos*, while the distal end of the radius is equally developed (tab. 8, ratio DTdist. × 100/Lmax). Ginsburg (1999: 122) seems to give special importance to the form of the grooves on the dorsal surface of the distal extremity of the radius. As he notes, *I. atticus* is like and is related to *Ailuropoda* in the development of a deep groove for the extensor carpi radialis brevior muscle, not observed in *Ursus*. Nevertheless, that view is not supported by the description given by Davis (1964: 99), according to which in *Ailuropoda* only the groove for the abductor pollicis longior is deep whereas the other grooves are shallow. *I. atticus*

Tab. 8. Limb indexes.
1: From Pilgrim (1931). – 2: From Crusafont-Pairó & Kurtén (1976). – 3: From Erdbrink (1968). – 4: From Merriam, Stock & Moody (1916). – 5: From Zapfe (1946). – 6: From Ehrenberg (1964). – 7: After the author.

		Humerus	Radius	Ulna	Mc I	Mc II	Mc III	Mc IV	Mc V
I. atticus Pikermi	Lmax	458.7	384.5	443.4	75.0	89.4	98.1-99.1	105.3-105.6	102.0-100.3
	DTdist. × 100/Lmax	24.1	18.4		24.0	24.6-26.1	23.1-25.0	23.3-24.6	25.2-26.2
	DTdia × 100/Lmax				(18.9)	20.6-20.7	19.6-19.8	18.7-(19.7)	17.1-17.9
I. atticus [1] Pikermi	Lmax	—	381	439	—	—	—	—	—
	DTdist. × 100/Lmax	—	18.9		—	—	—	—	—
I. atticus [2] Concud	Lmax	—	—	—	—	115-118	—	—	—
	DTdist. × 100/Lmax	—	—	—	—	19.9	—	—	—
	DTdia × 100/Lmax	—	—	—	—	11.9-12.2	—	—	—
I. a cf. *largelii* [3] Shansi	Lmax	—	—	—	—	—	81.2	—	—
	DTdist. × 100/Lmax	—	—	—	—	—	—	—	—
	DTdia × 100/Lmax	—	—	—	—	—	23.4	—	—
I. vireti [2] Can Llobateres	Lmax	(290)	—	—	—	70-78	—	(83)	—
	DTdist. × 100/Lmax	(26)	—	—	—	25.0-28.6	—	—	—
	DTdia × 100/Lmax	—	—	—	—	16.4-17.1	—	(18.9)	—
I. oregonensis [4] Oregon	Lmax	(490)	—	—	—	—	—	—	103.6
	DTdist. × 100/Lmax	—	—	—	—	—	—	—	(28.9)
	DTdia × 100/Lmax	—	—	—	—	—	—	—	20.8
U. arctos [5] recent, Europe	Lmax	290-353	272-306	311-358	66-76	74-78	76-84	77.5-83	76-88
	DTdist. × 100/Lmax	28.6-31.0	19.1-21.5		22.7-23.9	22.4-25.0	22.2-25.0	23.1-25.3	25.1-26.9
U. arctos [6] n = 3	Lmax	340-387	307-339	357-391.5	72.5-81.7	78-87.3	82.6-91.2	83-94	83.9-96
	DTdist. × 100/Lmax	28.7-32.1	18.9-21.2		23.4-23.9	24.6-25.6	23.9-24.8	23.6-26.4	25.4-26.2
U. arctos [7] recent, n = 1	Lmax	320.3	276.5	326.0	—	—	—	—	—
	DTdist. × 100/Lmax	32.6	22.6		—	—	—	—	—

Tab. 9. Limb proportions.

	Lmax.Radius × 100/ Lmax.Humerus	Proportions of Mcs I : II : III : IV : V	Lmax.Mc I × 100/ Lmax.Mc II	Lmax.Mc I × 100/ Lmax.Radius	Lmax.Mc V × 100/ Lmax.Radius
I. atticus, (dext.), Pikermi	83.8	73.5 : 87.6 : 96.2 : 103.2 : 100	83.9	19.5	26.5
U. arctos (NM 2570) (Ehrenberg 1964)	87.6	85.1 : 90.9 : 95 : 97.9 : 100	93.6	24.1	28.3
U. arctos (NM 2570) (Ehrenberg 1964)	93.5	86.4 : 94.2 : 98.5 : 100.4 : 100	91.8	26.4	26.4
U. arctos (No Num.) (Ehrenberg 1964)	86.1	86.4 : 88.6 : 94.3 : 94.3 : 100	97.4	24.8	28.7
U. arctos, recent (Zapfe 1946)	82-96	—	—	—	—
U. arctos, recent after the author	86.3	—	—	—	—

seems to be distinguished by the deep grooves of the abductor pollicis longior and the extensor communis digitorum, which are usually shallow in *U. arctos*. However, in specimens of *U. spelaeus* the situation was almost as in *I. atticus*, with deep grooves for the abductor pollicis longus and extensor communis digitorum, and developed "median ridge" as in *I. atticus*. From the above observations, it seems that such characters alone are not reliable for defining phylogenetic relationships. The radius of *I. atticus* is *Ursus*-like in the development of a saddle-like styloid process and different in that character from *Ailuropoda*. The articular surface for the scapholunar is not deflected proximally towards the ulnar notch as in *Ailuropoda* (Davis 1964: 99) but is *Ursus*-like.

The dimensions, the proportions and the other morphological characters of the ulna P.A. 1963/91 are similar (tabs 3, 8) to those of the specimen described by Pilgrim (1931). The observation of Pilgrim (1931: 24) that the olecranon of *I. atticus* is longer than in *Ursus* is not sufficiently supported, since, as shown here, the olecranon is almost equally developed with that of *U. arctos*.

The metacarpals of *I. atticus* are equally robust with those of *U. arctos* (tab. 8, ratio DTdist. × 100/Lmax) but their length proportions are different (tab. 9). Important is the fact that the first metacarpal of *I. atticus* is shortened relatively to that of *U. arctos*, compared to the fifth or the second metacarpal (tab. 9). In addition to the data given on table 9, for Pleistocene remains of *U. arctos*, Altuna (1973: tab. 3) gives for the ratio Lmax.Mc I × 100/Lmax.McV values that range from 79.3-85.9 (n=8), larger than that of *I. atticus*. That is also demonstrated from the ratio Lmax.Mc I × 100/ Lmax.Radius (tab. 9) where it seems that in *I. atticus* the Mc I is shortened. In contrast, the Mc V is not shortened but equally developed as that of *U. arctos* (tab. 9, ratio Lmax.Mc V × 100/Lmax.Radius).

As mentioned earlier, the postcranial skeleton of *I. atticus* is poorly known. In addition to the radius and ulna from Pikermi cited by Pilgrim (1931), Crusafont-Pairó & Kurtén (1976: 10, tab. 6) mention some postcranial remains of *I. atticus* from Concud. These postcranial remains are two second metacarpals, an astragalus and two second metatarsals. The occurrence of *I. atticus* in Concud, with the subspecies *I. atticus adroveri*, was first reported by Crusafont-Pairó (1962) and was based on some teeth remains. The postcranial material from Concud, however, has some differences from the present material. The two second metacarpals from Concud are significantly longer than the present specimens. The smaller Mc II from Concud has a length of 115 mm and the larger 118 mm, while the second metacarpals from Pikermi have a length of 89.4 mm (tab. 7). The difference in length between the larger specimen from Concud and the Pikermi specimens is about 32% and the difference between the smaller specimen from Concud and the Pikermi specimens is about 28.6%. The differences between the metacarpals from Concud and those from Pikermi are important. The Concud specimens are significantly more slender both in relative and absolute dimensions (tabs 7-8), even though they are larger. The ratio DTdia × 100/Lmax on the metacarpals from Concud is 11.9-12.2 and on the Pikermi specimens about 20.6 (tab. 8). The ratio DTdist. × 100/Lmax on the Mc II from Concud is 19.9, while on the two present specimens is 24.6 and 26.1 (tab. 8). These differences are important, but for Pleistocene remains of *U. arctos* from various localities in Spain, Torres (1988: tab. 18) gives for the first ratio a range equal to 15.0-19.0 (n=19) and for the second ratio a range 20.0-33.0 (n=17). From these figures it seems that ursines have important variation and despite the above mentioned differences, the possibility the specimens from Concud to belong really in *I. atticus* cannot be excluded. Moreover, the known postcranial material of *I. atticus* is inadequate and its size variation unknown.

Erdbrink (1968: pl. 2 figs 1-2) described some postcranial remains from Shansi under the name *I. atticus* cf. *largelii*. One of these is a Mc III, shorter than the present specimens (tab. 7). The Shansi specimen measures 81.2 mm in length, while the two third metacarpals from Pikermi measure 98.1 mm and 99.1 mm (tab. 7). So, the Pikermi specimens are 20.8%-22.0% larger in length than the specimen from Shansi. The ratio DTdia × 100/Lmax on the metacarpal from Shansi is 23.4, while on the two available specimens it is 19.6 and 19.8 (tab. 8). From the above, it seems that the Shansi specimen is smaller but more robust than the Pikermi specimens. These differences are not very important if we take into account that the Ursidae show a great degree of variation. We must also keep in mind that the metacarpal from Shansi probably represents a pathological individual (Erdbrink 1968: 23).

Crusafont-Pairó & Kurtén (1976: 5, tab. 6) mention some postcranial remains of *I. vireti* from Can Llobateres in Spain. For the present comparison, the most important specimen is a humerus from a juvenile individual which lacks the proximal epiphysis, two second metacarpals and one fourth metacarpal. The humerus is smaller in dimensions than our specimen (tab. 1) but has in common with *I. atticus* the presence of an entepicondylar foramen. Of the two second metacarpals, which Crusafont-Pairó & Kurtén (1976) attribute to *I. vireti*, the smaller one appears relatively more robust than the larger one and its proximal epiphysis has larger DAPpr. (tabs 7-8). While in *I. atticus* the second metacarpal is about 19.5% of the length of the humerus, the two second metacarpals of *I. vireti* represent about 24% and 27% of the length of the humerus. So, keeping in mind that the humerus of *I. vireti* comes from a juvenile individual, the second metacarpals of *I. vireti* seem relative longer. Important is the concept made by CRUSAFONT-PAIRÓ & KURTÉN (1976: 12), that *I. vireti* had less elongated external metacarpals, since the fourth metacarpal of *I. vireti* is only 6.4% larger than the second one. However, that is based on the assumption (CRUSAFONT-PAIRÓ & KURTÉN 1976: 12) that the available fourth metacarpal of *I. vireti* possibly comes from the same individual with the larger second metacarpal. The difference between the fourth metacarpal and the smaller second metacarpal of *I. vireti* is 18.6%, comparable with that between the fourth and the second metacarpal of *I. atticus* (about 18%).

Conclusions

The front limb of *I. atticus* is very similar to that of *U. arctos*. The most important character that distinguishes *I. atticus* from *U. arctos* and fossil forms such as *A. africanum* is the presence of an entepicondylar foramen at the humerus. Such a foramen is also present in *Ailuropoda* and *Tremarctos*, and fossil ursids such as *I. oregonensis*. Its presence, however, in many other groups that are not especially or closely related to each other could suggest that its significance is mostly functional. Like *U. arctos* and unlike *Ailuropoda* the humerus of *I. atticus* shows a strong angulation and an *Ursus*-like olecranon fossa. Its distal part however, seems less developed in relation to the total length of the humerus, than in *U. arctos*. Moreover, the humerus of *I. atticus* presents a clear torsion. That torsion seems stronger than that of *U. arctos* or *U. spelaeus*, but more comparative material is necessary to verify such an observation. The front limb of *I. atticus* is larger than that of *U. arctos*, but its brachial index is similar, as is the development of the metacarpals in relation to the radius or the humerus. The only exception is the first metacarpal that is shortened compared to the other metacarpals or the long bones.

The second metacarpals of *I. atticus* from Pikermi, compared with those from Concud attributed by CRUSAFONT-PAIRÓ & KURTÉN (1976) to *I. atticus*, show important differences in size and proportions. These differences concern the larger total length of the Concud specimens and their smaller robustness. However, it is very difficult to arrive to a conclusion for the metacarpals from Concud, since Ursidae show an important degree of variation. The differences from the third metacarpal from Shansi attributed by ERDBRINK (1968) to *I. atticus* cf. *largelii* are smaller, but in that case the problem is complicated, since the Chinese specimen is very probably a pathological one.

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Plate 1

Figs 1-2. *Indarctos atticus* (WEITHOFER 1888 *ex* DAMES MS).
Pikermi.

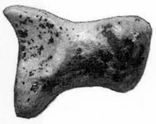
1. Right humerus. – P.A. 1944/91. – a) Anterior view, b) medial view, c) posterior view; × 1/4. d) Proximal view; × 1/3.
2. Right ulna. – P.A. 1963/91. – Proximal view; × 1/3.

Plate 2

Figs 2-3. *Indarctos atticus* (WEITHOFER 1888 *ex* DAMES MS).
Pikermi.

3. Right ulna. – P.A. 1963/91. – a) Lateral view, b) anterior view, c) medial view; × 1/4.
4. Right radius. – P.A. 1964/91. – a) Anterior view, b) lateral view, c) posterior view; × 1/4.

5a 5b 5c



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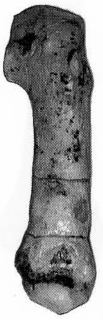

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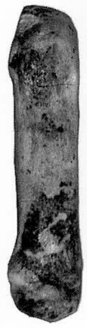

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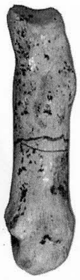

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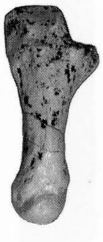

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Plate 3

Figs 5-12. *Indarctos atticus* (WEITHOFER 1888 *ex* DAMES MS).
Pikermi.

5. Right scapholunar. – P.A. 2024/91. – a) Proximal view, b) distal view, c) anterior view; × 1/2.
6. Right pisiform. – P.A. 2021/91. – Ulnar aspect; × 1/2.
7. Right Mc V. – P.A. 2020/91. – Anterior view; × 1/2.
8. Right Mc IV. – P.A. 2019/91. – Anterior view; × 1/2.
9. Right Mc III. – P.A. 2018/91. – Anterior view; × 1/2.
10. Right Mc II. – P.A. 2017/91. – Anterior view; × 1/2.
11. Right Mc I. – P.A. 2016/91. – Anterior view; × 1/2.
12. Right manus. – P.A. 2016/91-2028/91. – Anterior view; × 1/2.