Indarctos (Ursidae, Mammalia) from the Spanish Turolian (Upper Miocene)

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Key words: Mammalia, Ursidae, Miocene, Spain.

Abundant fossils of the bear *Indarctos atticus* (Weithofer, 1888) from the Lower Turolian (MN11) site of Crevillente 2 (Alicante, Spain) and some new material from the Middle Turolian (MN12) of Concud and Valdecebro 5 (Teruel, Spain) are described. On the other hand some dental remains from Crevillente 2 are identified as *Indarctos* sp. cf. *I. vireti* Villalta & Crusafont, 1943 on the basis of their small size. The status of different *Indarctos* species are discussed.

Contents

Introduction

In Spain, *Indarctos atticus* has been published and described mainly from several localities of the Lower and Middle Turolian (MN11 and MN12) in the Teruel Basin: Concud (Hernández Pacheco, 1930a; Crusafont, 1962; Alcalá, 1994), Los Mansuetos (Adrover, 1963), Valdecebro 5 (Adrover et al., 1986) and Puente Minero (Alcalá et al., 1991; Alcalá, 1994). Outside the Teruel Basin it has only been reported from the Late Vallesian of Terrassa (Pons Moyà, 1989-90) and from Crevillente 2 (Alcalá et al., 1987; Alcalá & Montoya, 1989-90; Montoya, 1994). In this paper we describe the material from Crevillente 2, consisting of a relatively rich sample of dental and postcranial remains, and also some unpublished material from Valdecebro 5 and Concud (Cerro de la Garita). We also study a jaw fragment, and an incomplete lower carnassial, from the lower levels of Crevillente 2, which are clearly smaller than those of *I. atticus* and, on the other hand, very similar to those of *I. vireti*; they are assigned with some reserves to that species.

The mammals from Crevillente (prov. Alicante, Spain) have been studied in numerous papers, among others Montenat & Crusafont (1970), Montenat (1973), de Bruijn et al. (1975), Alcalá et al. (1987), Alberdi & Montoya (1988), Cerdeño (1989), Alcalá & Montoya (1989-90), Freudenthal et al. (1991, 1998), Montoya & Morales (1991), van der Made et al. (1992), Martín Suárez & Freudenthal (1993, 1998), Montoya (1990, 1993, 1994, 1997), Azanza & Montoya (1995), Montoya & Alberdi (1995), Momparler (1996), Montoya & Momparler (1996), van Weers & Montoya (1996), and Azanza (2000).

Crevillente 2 has provided a rich association of both micro- and macromammals, which indicates an Early Turolian age, zone MN11 of Mein (1975, 1990). According to the biozonation proposed for the area of Crevillente by Martín Suárez & Freudenthal (1998), Crevillente 2 is included in the *sondaari* Biozone. In recent biochronological papers on the Mediterranean Neogene, Crevillente 2 has been designated as the reference locality for zone MN11 (Mein, 1990, 1999; de Bruijn et al., 1992). Furthermore, it is the type locality of two taxa: *Neocricetodon occidentalis* (Aguilar, 1982), and *Lucentia iberica* Azanza & Montoya, 1995. Among the macromammal fossils found in Crevillente 2, the genus *Indarctos* is, after *Machairodus*, the second best represented carnivore in the locality, not only in number but also in variety of skeletal and dental remains.

Hernández-Pacheco (1924) was the first to report the locality Cerro de la Garita (Concud, prov. Teruel, Spain), and since then, this locality has provided a great quantity and variety of mammal fossils. It is included in zone MN12 of Mein (1975, 1990) and in the upper part of zone L of van Dam (1997). Cerro de la Garita is the type locality of four taxons: *Canis cipio* Crusafont, 1950, *Hipparion concudense* (Pirlot, 1956), *Turiacemas concudensis* (Hernández-Pacheco, 1930), and *Hispanodorcas torrubiae* Thomas, Morales & Heintz, 1982. There are many papers about the mammals of this locality, listed in Alcalá (1994).

Valdecebro 5 is a locality in the Rambla de Valdecebro (Teruel), first published by Adrover et al. (1986). It is included, as the previous one, in zone MN12 of Mein (1975, 1990) and in the upper part of zone L of van Dam (1997). This poor fauna, only 10 mammal species, is remarkable, because half of the taxons belong to carnivores (*Indarctos*, *Baranogale*, *Thalassictis*, *Lycyaena*, and *Felis*) (Alcalá, 1994).

The studied *Indarctos* material belongs to the following Spanish collections:

COT: Orihuela del Tremedal (A. Marcet) Collection
DGUV: Departament de Geologia, Universitat de València
GCPE: Grupo Cultural Paleontológico de Elche, Alicante
IPS: Institut de Paleontologia 'Miquel Crusafont', Sabadell
MCNV: Museu de Ciències Naturals, Valencia
MHMN: Museu Històric Municipal de Novelda, Alicante
MNCN: Museo Nacional de Ciencias Naturales (CSIC), Madrid

For comparison, specimens of *Indarctos* and *Agriotherium* have been studied in the collections of the Museo Nacional de Ciencias Naturales (Madrid, Spain), Institut de Paleontologia 'Miquel Crusafont' (Sabadell, Spain), Université Claude Bernard (Lyon, France), and Muséum National d'Histoire Naturelle (Paris, France).

Systematics

Order Carnivora Bowdich, 1821
Family Ursidae Gray, 1825
Genus *Indarctos* Pilgrim, 1913
Indarctos atticus (Weithofer, 1888)
Figs. 1-2, 7; Pl. 1, figs. 1-5; Pl. 2.

1883 *Hyaenarctos* sp. — Dames: 132.

1884 *Hyaenarctos punjabiensis* — Lydekker: 49-55, text-fig. 6; pl. 30, fig. 2; pl. 31, figs. 1, 1a.
*1888 *Hyaenarctos atticus* Dames — Weithofer: 231, pl. 12, figs. 1-2.
1913 *Indarctos salmontanus* — Pilgrim: 281, 290.
1914 *Indarctos salmontanus* — Pilgrim: 226, pl. 20.
? 1916 *Indarctos (?) oregonensis* — Merriam, Stock & Moody: 106, text-figs. 1-4, 8, 9, 13, 15-22.
1924 *Indarctos lagrelii* — Zdansky: 16-22, pl. 4, figs. 1-4.
1924 *Indarctos sinensis* — Zdansky: 24-26, pl. 5, figs. 1-8.
1925 *Hyaenarctos maraghanus* — Mecquenem: 19, pl. 5, fig. 8.
1926 *Indarctos atticus* Dames — Frick: 88.
1930 *Hyaenarctos* sp. — Hernández-Pacheco: 154, figs. 7-10.
? 1931 *Indarctos* (?) cf. *atticus* — Pilgrim: 23, figs. 4-5.
1932 *Indarctos* sp. — Helbing: 2-10, text-figs. 1-6, pls 1-3.
1932 *Indarctos salmontanus* — Pilgrim: 43-44, pl. 3, fig. 9.
? 1935 *Indarctos punjabiensis* (Lydekker) — Colbert: 90-92, figs. 43-44.
1949 *Indarctos* sp. — Thenius: 649-651, figs. 1-2.
1959 *Indarctos atticus atticus* — Thenius: 276-281, text-figs. 2-8.
1962 *Indarctos atticus adroveri* — Crusafont: 188, pl. 1.
? 1975 *Indarctos oregonensis keithi* — Schultz & Martin: 47, text-figs. 1-2.
1976 *Indarctos atticus* — Crusafont & Kurtén: 7-14.
? 1978 *Indarctos* — Wolff: text-figs. 2-6, pls 1-5.
1986 *Indarctos atticus* (Weithofer ex Dames MS) — Adrover et al.: 500-502, pl.1, figs. a-b.
1986 *Indarctos atticus* (Dames) — Petter & Thomas: 578-579, text-fig. 4.
1987 *Indarctos atticus* — Alcalá et al.: 25-26.
? 1988 *Indarctos bakalovi* — Kovacev: 66, pls. 1-2.
1989-1990 *Indarctos atticus* — Pons-Moyà: 200.
1991 *Indarctos atticus* (Weithofer, 1888 *ex* Dames) — Alcalá et al.: 225, pl. 3, fig. 1.
1994 *Indarctos atticus* (Weithofer, 1888 *ex* Dames) — Alcalá: 100-102, pl. 3, figs. j-ñ.
1997 *Indarctos atticus* (Weithofer 1888 ex Dames 1883) — Roth & Morlo: 59-60, text-figs. 23-32, pl. 2, figs. 19-20.

Type locality — Pikermi (Greece), Middle Turolian (MN12).

Other localities — Samos (Greece), Baltavar (Hungary), Aubignas (France), Dorn-Dürkheim 1 (Germany), Maragheh (Iran), Shansi (China), Hasnot (Pakistan), Crevillente 2, Terrassa, Puente Minero, Concud, Valdecebro 5 (Spain).

Differential diagnosis — *Indarctos* clearly larger than *I. vireti*, *I. arctoides* and *I. anthracitis*. P^4 with generally well developed parastyle, in contrast to *I. vireti* and *I. arctoides*. M^2 relatively shorter than in *I. vireti*. M_1 often shows an additional cusp between protoconid and hypoconid, and M_2 is relatively elongated, like in *I. vireti* and *I. anthracitis*, whereas *I. arctoides* does not show this cusp in M_1, and its M_2 is shorter. The basicranial and facial regions of the skull of *I. atticus* are clearly shorter than in *I. vireti*.

Studied material

Crevillente 2 (CR2)

I^3: MHMN CR2-S-251, MHMN CR2-S-288, MCNV CR2-873
upper canine: MHMN CR2-S-303, MCNV CR2-490
P^2: MHMN CR2-S-302
P^3: MHMN CR2-S-291
P^4-M^2: MHMN CR2-S-292, 293, 294 (right series), MHMN CR2-S-304, 289, 290 (left series, P^4-M^1 and talon of M^2)

left jaw with canine and P_1-M_3: MHMN CR2-S-250
I_1 and/or I_2 ?: MHMN CR2-S-252
P_1 ?: DGUV CR2-833
P_4: DGUV CR2-720
M_1: DGUV CR2-874 (incomplete)
M_3: DGUV CR2-876, GCPE CR2-2
left metacarpal II: MHMN CR2-S-459
left metacarpal III: MHMN CR2-S-474 (incomplete)
left metatarsal II: DGUV CR2-601
left scapholunar: DGUV CR2-S-475
third phalanx: MHMN CR2-M251

The specimens with the numbers CR2-S-250, 251, 252, 288, 289, 290, 291, 292, 293, 294, 302, 303, and 304, were found in association and very probably belong to a single individual.

Concud, Cerro de la Garita (CG)
left jaw: IPS
P^4: COT CG-78-AM (fragment)

Rambla de Valdecebro 5
M_1: COT RV5-50-AM
M_2: COT RV5-55-AM
left scapholunar: COT RV5-31-AM
third phalanx: COT RV5-30-AM

Description — We follow, with some variations, the nomenclature and way of measuring as defined by de Torres (1988).

Crevillente 2

I^3 — Two specimens are a bit more robust, but very worn, above all CR2-S-288, in which there is only a very small part of the crown left on its external face. We base our description on the third specimen (CR2-873), which has a subtriangular root section; the crown presents its maximum height on its postero-external border, where it is almost twice as high as on its internal border. There are two ridges, one postero-external and the other one antero-internal, as well as a strong postero-internal cingulum. The maximum height of the crown is almost half the total height of the tooth.

Upper canine — Tooth of big size, with very robust root of oval section. The crown shows an anterolingual ridge and a posterior one, which is approximately a third of the total length of the tooth. The external face of the crown is the highest.

P^2 and P^3 — Through comparison with material of *I. vireti*, we suppose that the longest specimen (CR2-S-291) is a P^3, and specimen CR2-S-302 is a P^2. Both teeth are reduced and biradiculated. They have only one cusp, stronger in P^2, shifted towards one of the extremes. They show a longitudinal ridge and a weak basal cingulum, surrounding the tooth.

P^4 — There is a well-formed parastyle in the anterior part of the tooth, with a lingual and a labial ridge. The paracone has an anterior ridge descending towards the parastyle. The protocone is clearly split into two cusps; the posterior one is more developed, and has a basal cingulum. The metacone presents a weak lingual cingulum reaching the protocone, and another one along its labial face. There is also a labial cingulum starting at the parastyle, but the two cingulums do not meet (Fig. 1 and Pl. 1, fig. 2).

M^1 — Rectangular tooth, clearly longer than wide with similar internal and external lengths. Paracone with a weak parastyle in its anterior part. There is a well-developed basal cingulum along the elongated protocone. Robust metastyle, but poorly individualized. The hypocone (or metaconule, according to de Beaumont, 1982) is worn and is less developed than the other cusps. The external border of the tooth is almost straight and the internal one convex (Fig. 1 and Pl. 1, figs. 1, 3).

M^2 — Clearly elongated tooth, with a robust talon. The valley between the four principal cusps is less deep than in the first molar. The metacone is shifted forwards, in comparison with M^1, so that the metacone and the the paracone are facing the elongated protocone. There is a weak lingual cingulum running from the anterior border of the tooth towards the base of the metaconule. The talon presents a flat and oblique occlusal surface, sloping down towards the postero-external end of the tooth (with respect to the occlusal plane of the tooth). The most robust cusp is the paracone (Fig. 1 and Pl. 1, fig. 1).

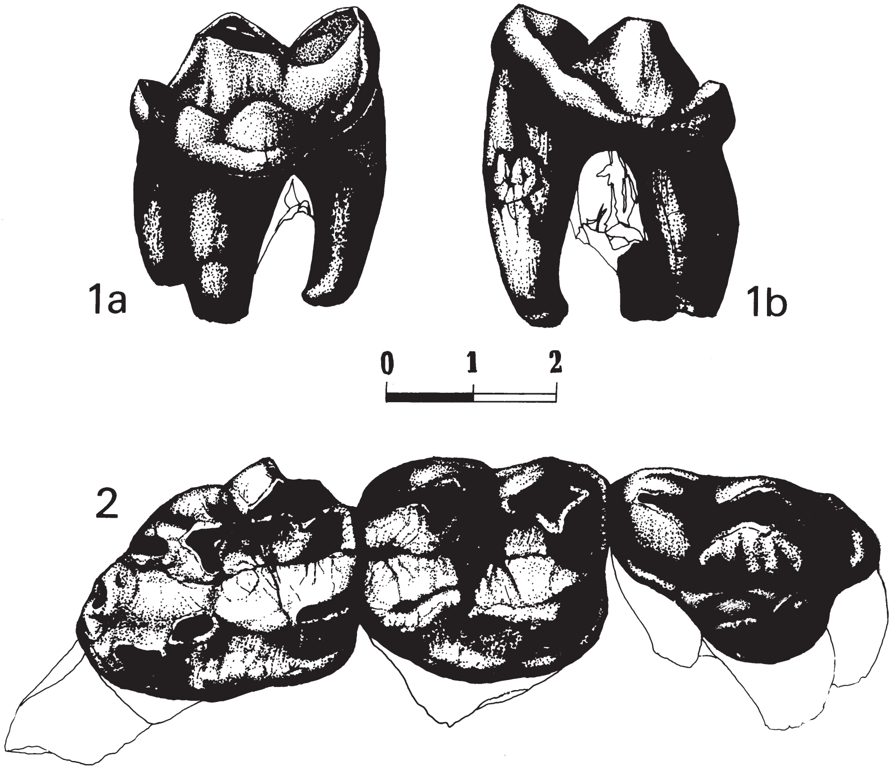


Fig. 1. Upper dentition of *Indarctos atticus* from Crevillente 2. a: left P^4 (CR2-S-304), lingual side; b: labial side of the same specimen; c: rigth upper dental series P^4-M^2 (CR2-S-292, 293, 294), occlusal view; drawing by Emilio Cortés.

Left jaw — The specimen is fairly complete, with almost all the teeth, but it presents a high degree of cracking and corrosion (Pl. 2, fig. 1). Furthermore, there are deformation signs, especially in the ascending branch, which has lost the angular process and the cusp of the coronoid process. The area of the symphysis is bulky, with a slight inclination of its lower edge. The height of the horizontal branch increases progressively from the symphysis backwards. Its lower edge is arched, except in the area under P_2-P_4, where it is straight, or even concave. Although the poor conservation of the branch of the mandible makes observations difficult, it seems not to have a premasseteric fossa. The incisors are broken, and we can only see the root of I_2. The canine is worn down completely, but its root indicates it was a very robust tooth. P_1 is not separated from the canine, and between P_1 and P_2 there is a short separation, of about 6 mm. The lower carnassial is nearly destroyed, there are only some fragments that give an idea of the high degree of wear of that tooth. M_3 is placed obliquely, with respect to M_2, ascending towards posterior. The characteristics of the teeth will be described hereafter.

P_1 — Tooth with apparently only one root. It is elongated and shows a low crown, without a defined cusp but with a weak lingual cingulum.

P_2 and P_3 — P_3 is larger than P_2; morphologically they are almost identical. They are biradiculated with only one cusp in a central position, a posterior cingulum, and a longitudinal ridge along the tooth.

P_4 — It is clearly larger than the other premolars. It shows a clear central cusp with a less-inclined anterior ridge, which nearly reaches a vestigial cusp on the anterior border of the tooth. The posterior ridge is steeper and slightly convex, and does not reach the posterior end of the tooth, since there is a strong basal widening, with a small cusp in its posterior end.

M_1 — This fragmentary specimen (CR2-874) consists of an almost complete protoconid. It is a robust cusp with one anterior and two posterior ridges.

M_2 — Rectangular tooth with weakly marked cusps. In its occlusal surface there are two valleys separated by a transversal crest that connects protoconid and metaconid, which are the best marked cusps of the tooth. The posterior valley is approximately double the size of the anterior one. The hypoconid is more robust than the entoconid, and both these cusps are elongated. The enamel of the labial wall is rough, with vertical grooves.

M_3 — This is a uniradiculated tooth, oval-shaped with the vertex in posterior position (Pl. 2, figs. 2-3). The cusps are not very marked, so its occlusal surface appears rather flat. Specimen CR2-876 shows an elevated edge all around the tooth, so the interior valley is deeper than in the other two specimens. The protoconid is the most prominent cusp in the three specimens.

Scapholunar — This specimen presents a broken palmar protuberance. It is more robust than the homologous element in *U. spelaeus* and *U. arctos*. The proximal face is very convex and on the distal one, there are two well-marked crests, which are perpendicular to the anterior and posterior edges of the bone. These two crests delimit a deep groove, which articulates with the magnum. On each side of this groove there is another, shallower, joint facet. The internal facet, which articulates with the trapezium and the trapezoid, is very wide, concave lateromedially, and convex in anteroposterior direction. The external facet, which articulates with the unciform, is narrower than the internal one, and very concave in anteroposterior direction.

Mc II — The proximal surface is trapezoid, with the longer side externally. Both the external and the internal edges are concave in proximal view. The facet for the cuneiform is concave in dorsal view, and sloping down towards the internal face. In the ventral part of the proximal end there is a not very prominent thickening. In the external face of that end, there is a large dorsal facet, which is slightly concave, for the third metacarpal. This facet seems to be extended on the ventral prominence. In the internal face, and shifted towards the shaft, there is a longitudinal tuberosity of oval shape. The shaft presents the biggest dorsoventral diameter in its proximal part; its distal part is dorsoventrally flattened.

Mc III — This is an incomplete bone, missing its distal one third, as well as the ventral vertex of the proximal extremity. The joint facet for the third carpal is clearly concave and subtriangular, with a concave external face, and the internal face like an inverted and open 'S'. The external dorsal vertex is the most prominent one. In the external face of the proximal end, there is a wide concavity, with a big facet for the fourth metacarpal, placed towards the dorsal edge. In the internal face, there is a central depression, and a prominent facet for the second metacarpal near the dorsal edge. Underneath the articular surface of the dorsal face there is a transversal depression, which is deep and extended longitudinally, and which progressively tapers out, and disappears at about 25 mm under the dorsal edge. The section of the shaft in the breakage zone, at c. 60 mm of the proximal extreme, is triangular, with very blunt vertices.

Mt II — The proximal surface is taken up by the facet for the second cuneiform. This facet is an isosceles triangle, with the sharp angle, in ventral position, passing into a robust cusp. The surface of that proximal facet is fairly convex, with a small concavity at the ventral vertex, precisely where the prominence starts. In dorsal view, the proximal surface has a clear inclination towards the internal edge. On the internal face of the proximal end, there is a facet for the first metatarsal, a bit elongated in longitudinal direction. On the external face, there are two facets for the third metatarsal which are nearly fused, the ventral one of which is the largest. The ventral edge is extended by the external surface of the ventral prominence. The shaft becomes flattened, in dorsoventral direction, towards the metapodial distal extreme. The distal end is flattened, too.

Third phalanx — This phalanx shows a typically ursid morphology. The articulation facet is very concave, almost semicircular in lateral view. Its surface is practically smooth, with a very slight medial crest. We can see a sharp palmar tuberosity and the shaft of the bone, slightly curved, becomes very rough in its distal half.

Concud (Cerro de la Garita)

Left jaw — This jaw (Fig. 2) has lost its incisors, P_1, M_3 and the ascending branch. It is clearly more robust than the jaw from Crevillente 2, and than the other known jaw (from Concud), described and figured by Alcalá (1994). The lower edge of the mandible branch is curved, except under P_3-P_4, where it is straight. The dentition is larger than that of the two other jaws. P_1 is uniradiculated. Between P_2 and P_3 there is a separation and both present a more conical shape than the ones from Crevillente. Especially P_2 is practically circular, with a central cusp shifted towards the labial face.

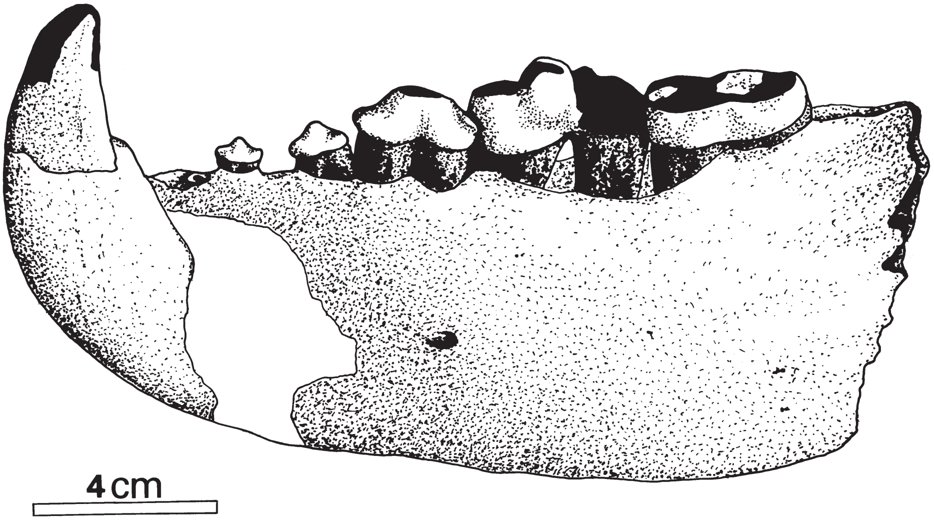


Fig. 2. Left jaw (IPS) of *Indarctos atticus* from Concud (Cerro de la Garita), labial side.

P_4, though worn, shows a morphology similar to the one described from Crevillente, but it is clearly larger. M_1 is worn, mainly in the talonid, and a cingulum is not observed. M_2 is very much worn.

P^4 — An incomplete left carnassial, without metacone (Pl. 2, fig. 5). The protocone presents a well-developed basal cingulum and a very weak bifurcation. The parastyle is very much reduced. The paracone has an anterior ridge connected to the parastyle.

Valdecebro 5

M_1 — This is a complete left carnassial (Pl. 2, fig. 4). The trigonid constitutes more than half of the tooth and the talonid is clearly wider and presents a weak basal labial cingulum. A robust paraconid and a more developed protoconid can be observed in the trigonid. The paraconid has a weak lingual cingulum. The protoconid shows two posterior ridges, one lingual and the other one labial. The lingual ridge is sharp and it is joined to a practically conical metaconid. The labial ridge is continues to the hypoconid, which has an elongated and slightly bifurcated crest, though it does not form an accessory cusp between protoconid and hypoconid. The entoconid is formed by two conical cusps, the posterior one of which (the entoconulid) is a bit smaller than the anterior one. The central part of the talonid is bears a wide, longitudinal valley with almost semicircular section.

M_2 — This is a subrectangular tooth, slightly wider anteriorly than posteriorly (Pl. 2, fig. 4). The elongated protoconid forms a longitudinal crest, connected in its centre to the metaconid by a transversal crest. The metaconid is the highest cusp of the tooth. In front of the protoconid and the metaconid there are small vestigial cusps. In the talonid, we can see a clearly bifurcated entoconid, the anterior cusp being sharper. The hypoconid is slightly bifurcated, with a vestigial hypoconulid in its posterior part.

Scapholunar — The morphology is identical to the one described for the specimen from Crevillente.

Third phalanx — This is an incomplete specimen, and we can only mention the absence of a medial crest in the articular facet, the presence of a robust palmar tuberosity, as well as a distally very rough bone shaft.

Discussion — There has been a long-lasting discussion about which dental characters would serve to distinguish between the genera *Indarctos* Pilgrim, 1913 and *Agriotherium* Wagner, 1837 (Pilgrim, 1914; Depéret & Gómez Llueca, 1928; Erdbrink, 1953; Tobien, 1955; Stach, 1957; Crusafont, 1962; Hendey, 1972, 1980; Morales & Aguirre, 1976; Qiu & Schmidt-Kittler, 1983; Petter & Thomas, 1986; Kovacev, 1988; and others). We consider the following the most useful:
- In *Agriotherium*, the dentition uses to be strongly developed in width. This means that the teeth are relatively shorter than in *Indarctos*. The upper molars in *Agriotherium* are, generally, wider than long, while in *Indarctos* the length is always the predominant dimension. This argument was already applied for M^2 by Morales & Aguirre (1976).
- In *Indarctos* M^2 is always longer than M^1, in contrast to *Agriotherium*. This criterion, proposed by Hendey (1972, 1980), relies on the greater development of the talon in *Indarctos*.
- The M_1 of *Agriotherium* has a more prominent protoconid, and a more developed metaconid with a larger separation from the protoconid than in *Indarctos*. This can be well observed in the M_1 of the jaw no. 467 of *A. insigne* from Montpellier, described by Viret (1939), who proposed this characteristic as a diagnostic for the distinction of the two genera. For Hendey (1980), that cusp would actually be a modified entoconid, and the M_1 of *Agriotherium* would not have a metaconid.
- Not only the M_1 but also the M_2 shows a more-developed and complex talonid in *Indarctos* than in *Agriotherium*.
- The *Agriotherium* jaw shows a premasseteric fossa while it laks in *Indarctos*, according Hendey (1980).

In view of these considerations, it is logical to assign our material to the genus *Indarctos*. The clearly elongated upper molars and the M^2, which is longer than the M^1 (Table 1), with a very well developed talon in the former, are clear characteristics in the ursid from Crevillente 2 (Fig. 1; Pl. 1, fig. 1). Furthermore, the absence of a premasseteric fossa in the jaw is another argument for assigning our material to the genus *Indarctos*, although this feature could not be observed unambiguously in the specimen from Crevillente 2. As regards the incomplete P^4 from Concud (Pl. 2, fig. 5), the presence of a reduced parastyle shows that it does not belong to *Agriotherium*, which always has a well-developed parastyle in the upper carnassial. With respect to the material from Valdecebro 5 (Pl. 2, fig. 4), the strong union of the metaconid to the protoconid in M_1 is a strong argument to assign it to *Indarctos*. Furthermore, M_1 as well as M_2, present a more complex talonid than the one observed in the homologous teeth of *Agriotherium*.

Our material is assigned to *I. atticus* (Weithofer, 1888), which is the characteristic ursid of the Lower and Middle Turolian in the Mediterranean area, though there are some differences due to the intraspecific variability. For the specific assignment of our material, we have compared it with remains of various *Indarctos* species:

Table 1. Dimensions of the studied dental remains of *Indarctos*. CR2: Crevillente 2; CG: Concud (Cerro de la Garita); RV5: Valdecebro 5; APD: anteroposterior diameter; TD: transverse diameter; t: talonid.

		cf. *I. vireti*	*I. atticus*			*I. atticus*	*I. atticus*
		CR2	CR2			CG	RV5
I^3	APD		15.1	14.5	14.4		
	TD		16.7	20.0	—		
C/	APD		24.0	28.8			
	TD		20.6	21.4			
P^2	APD		12.9				
	TD		8.3				
P^3	APD		12.7				
	TD		7.5				
P^4	APD		27.8	28.3		—	
	TD		20.2	21.0		24.7	
M^1	APD		27.7	27.9			
	TD		24.9	25.2			
M^2	APD		32.5				
	TD		24.1				
/C	APD	(22)				28.4	
	TD	14.8				21.2	
P_1	APD		11.4				
	TD		7.4				
P_2	APD	9.6	10.2			8.8	
	TD	6.0	7.0			8.5	
P_3	APD	11.8	13.6			12.6	
	TD	7.2	8.5			9.8	
P_4	APD	17.7	20.5	19.2		25.7	
	TD	10.0	10.8	11.4		14.5	
M_1	APD	—				40.0 ap.	39.4
	TDt	16.8				—	20.9
M_2	APD		30.2			33.9	29.5
	TD		19.8			22.5	21.0
M_3	APD		16.9	18.6	17.5		
	TD		15.0	17.6	15.1		

Our material is clearly different from *I. vireti* from Can Llobateres (Crusafont & Kurtén, 1976) and Can Purull (Villalta & Crusafont, 1943, 1948) by its larger size (Figs. 3-4; Tables 2-4). Additionally, the upper carnassial of the ursid from Crevillente has a markedly bifurcated protocone and a well-developed parastyle (though the specimen from Concud does not), whereas in *I. vireti* the protocone shows only a slight bifurcation, and there is no parastyle (see Fig. 5a). In the upper molars from Crevillente there is a far weaker lingual cingulum. Furthermore, in the M^1 of *I. vireti* from Can Llobateres, that cingulum is converted into a posterolingual accessory cusp, as observed in specimen IPS VP 646. In addition, the M^2 from Crevillente is relatively shorter than the M^2 of *I. vireti* (see Fig. 6). Apart from the great size difference, there are slight morphological differences between the lower dentitions.

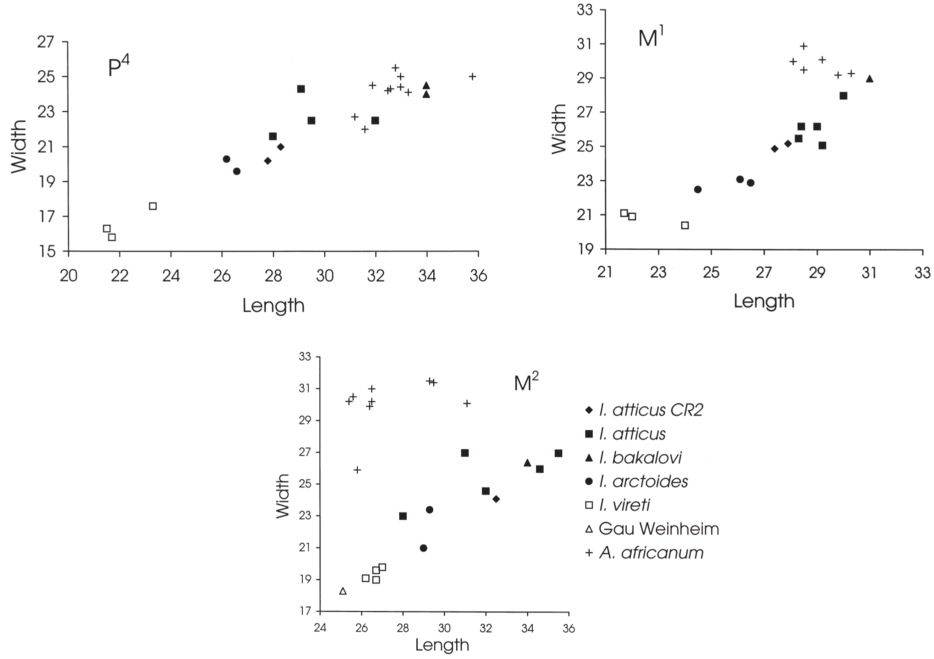


Fig. 3. Scatter diagrams of the upper dentition of the species of *Indarctos* and *Agriotherium africanum*; data, in part, from Deperet & Gómez Llueca (1928), Helbing (1932), Colbert (1935), Weitzel & Tobien (1952), Thenius (1959), Crusafont (1962), Hendey (1980), Kovacev (1988), and Roth & Morlo (1997).

With regard to *I. arctoides*, we have compared our material with the sample from Montredon (Depéret & Gómez Llueca, 1928; Helbing, 1932; de Beaumont, 1988), kept at the 'Université Claude Bernard', Lyon. The teeth from Crevillente present, apart from a larger size (Figs. 3-4; Tables 2-3), some morphological differences: The P^4 from Montredon has a rudimentary parastyle (see Fig. 5b), so this tooth has a wider aspect. The jaw from Montredon (213081 Mtn 14), which is the species holotype (Depéret & Gómez Llueca, 1928), is very close in size to the one from Crevillente, but the dentition shows significant differences. The P_4 in the jaw from Montredon is a shorter tooth and far more robust, with a very wide posterior part, and it is triangular in occlusal view. Besides, it has an anterior ridge only. M_2 is a very short tooth, compared with the ones from Crevillente and Valdecebro 5 (see Fig. 4 and Table 3), and it does not present accessory cusps in front of protoconid and metaconid.

Through revision of the material of *I. atticus* from various Spanish localities, kept at the 'Museo Nacional de Ciencias Naturales', Madrid, and at the 'Institut de Paleontologia', Sabadell, we have come to the conclusion that there are no significant morphological differences between those remains and the material from Crevillente, Concud and Valdecebro 5. Thus, the dental remains of *I. atticus* from the Teruel Basin, described by Hernández Pacheco (1930a), Crusafont (1962), Adrover et al. (1986), Alcalá et al. (1991), and Alcalá (1994) are biometrically and morphologically similar to our material. Comparison with bibliographical data of other material assigned to *I.*

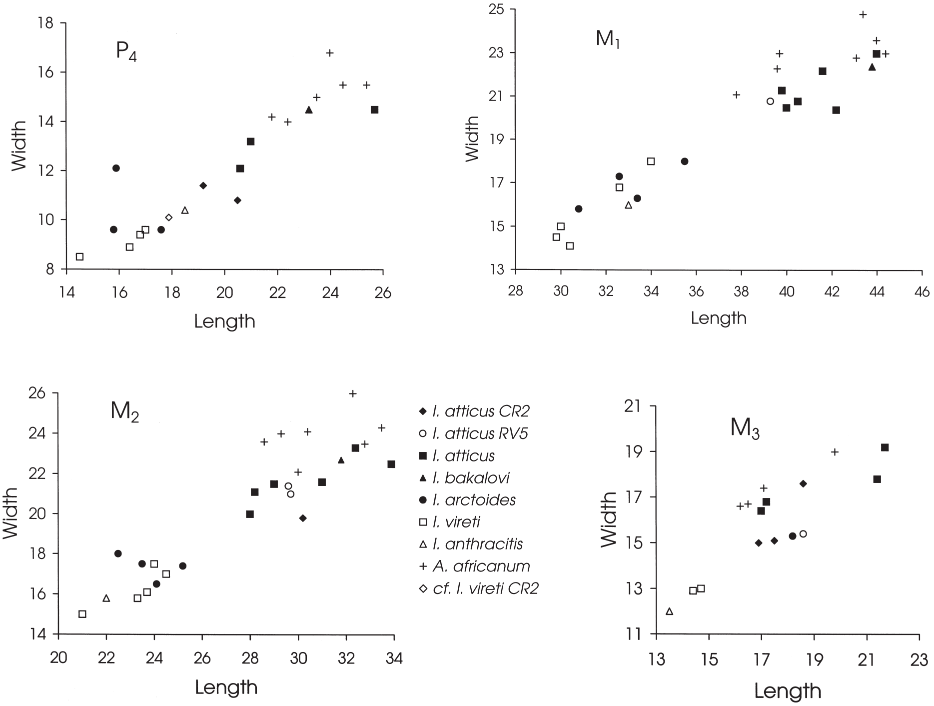


Fig. 4. Scatter diagrams of the lower dentition of the different species of *Indarctos* and *Agriotherium africanum*; data, in part, from Helbing (1932), Villalta & Crusafont (1943, 1948), Tobien (1955), Thenius (1959), Hendey (1980), Petter & Thomas (1986), Kovacev (1988), and Roth & Morlo (1997).

atticus gives the same result (Helbing, 1932; Erdbrink, 1953; Thenius, 1959; Petter & Thomas, 1986; Roth & Morlo, 1997, considering *Hyaenarctos punjabiensis* (Lydekker, 1884), *H. maraghanus* (Mecquenem, 1925), *I. salmontanus* (Pilgrim, 1914), *I. sinensis*, and *I. lagrelii* (Zdansky, 1924) as synonyms of this species). E.g. the upper carnassials from Crevillente have a well-developed parastyle, as do the specimens from Samos (Helbing, 1932; Thenius, 1959) and the Siwaliks (Lydekker, 1884). This, and the big size, are distinctive characters of the species (see Fig. 5). In any case, the P^4 from Concud here described, (Pl. 2, fig. 5) presents a smaller development of the parastyle, just like another, incomplete, upper carnassial from the same locality described by Crusafont (1962). On the other hand, a complete upper carnassial, also from Concud (CG-4M), described by Alcalá (1994), shows a strong development of the parastyle (see Fig. 5e), as is normal in *I. atticus*. This shows the variability of this species, even among individuals from the same locality.

In North America, material assigned to *Indarctos* has been described from several Hemphilian localities, which can roughly be correlated to the European Turolian (see Lindsay & Tedford, 1989). Thus, the species *I. oregonensis* has been described in the Rattelsnake Formation (Merriam et al., 1916), and it has also been mentioned in the Coffee Ranch (Dalquest, 1969) and in the Kimball Formation (Schultz & Martin, 1975). *I. nevadensis* has been described in Smiths Valley (Macdonald, 1959). Finally, a skull of

Table 2. Dimensions of the upper dentition of *Indarctos atticus* from Crevillente 2 (CR2-S-292, 293, 294) and Concud (CG 78-AM, CG-4M), compared with those of *I. arctoides* from Montredon (cast, Univ. Claude Bernard de Lyon 210059) and *I. vireti* from Can Llobateres (IPS VP646d). L: length; W: width; H: height; D: distance. The numbered categories follow the terminology proposed by Torres (1988).

		I. atticus	*I. atticus*		*I. arctoides*	*I. vireti*
		CR2	CG78-AM	CG-4M	210059	VP646d
P^4	1. total L	27.8		28.2	26.2	21.5
	2. total W	20.2	24.3	21.5	20.3	16.3
	3.paracone H	14.1	19.5	16.1	15.7	12.3
	4. metacone H			9.0	10.3	9.4
	5. protocone H	9.0	10.3	9.5	9.0	7.1
	7. paracone-metacone D	13.4		13.6	10.5	7.4
	parastyle L	4.6	4.5	6.1	1.3	—
	parastyle H	6.1	8.3	8.2	5.0	—
M^1	1. total L	27.9			26.3	21.9
	6. anterior W	23.4			22.6	19.7
	7. posterior W	25.2			23.1	20.9
	8. central narrow W	24.3			23.0	19.6
	10. paracone H				12.6	9.2
	11. metacone H				13.0	9.7
M^2	1. total L	32.5			29.3	26.8
	4. anterior W	24.5			23.4	19.6
	5. posterior W	22.9			21.1	17.7
	6. paracone-protocone D	12.4			10.3	10.7

Indarctos sp. has been described in Withlacoochee River (Wolf, 1978). It would be necessary to review of all these materials in order to clarify their taxonomic status. In some cases, even the generic assignment is doubtful. For example, the lower carnassial of the holotype of *I. nevadensis* (Macdonald, 1959) shows a morphology closer to the characteristics previously mentioned for *Agriotherium*. The trigonid is very much developed with respect to the talonid, though the jaw does not present a premasseteric fossa, which appears in the sample of *A. africanum* (Hendey, 1980). Neither is the generic assignment of the jaw fragment TMM 41261-1, classified as *I. oregonensis* by Dalquest (1969), very clear. The morphology of M_1 and M_2 is very similar to that of *Agriotherium*, though another M_1 of the same locality (TMM 41261-2) shows characters of *Indarctos*. The rest of the American material of *Indarctos* falls within the morphological and biometrical range of *I. atticus*, and part of the material ascribed to *I. oregonensis*, and the skull determined as *Indarctos* sp. might well belong to *I. atticus*.

We have not seen the material of *I. bakalovi*, a species described by Kovacev (1988) for a skull and a mandible from the Upper Miocene of Bulgaria. According to the description and the dimensions, *I. bakalovi* might well be referred to *I. atticus* (Figs. 3-4).

Weithofer (1888) classified a jaw from Monte Bamboli as *Hyaenarctos anthracitis*. The measurements given by Petter & Thomas (1986) show, that the molar series of this specimen is biometrically similar to *I. vireti*, but that the premolars are outside the range of the Vallesian species (Fig. 4). On the other hand, in figs. 34 and 41 of Frick

Table 3. Dimensions, according the terminology of Torres (1988), of the M_1 and M_2 of *Indarctos* here described, compared with those of *I. arctoides* from Montredon (Univ. Claude Bernard de Lyon 213081), *I. vireti* from Can Llobateres (IPS VP647d) and *Agriotherium insignis* from Montpellier (Univ. Claude Bernard de Lyon 467). CR2: Crevillente 2; CG: Concud (Cerro de la Garita); RV5: Valdecebro 5; L: length; W: width; D: distance; H: height.

		cf. *I. vireti* CR2	*I. atticus* CR2	*I. atticus* CG	*I. atticus* RV5	*I. arctoides* 213081	*I. vireti* VP647d	*A. insignis* 467
M_1	1. total L			40 ap.	39.3	35.9	29.8	40.5
	2. labial trigonid L			21.5	22.5	19.6	15.0	21.1
	3. labial talonid L			18.5	15.9	16.3	14.8	19.4
	4. protoconid L			14.3	14.9	12.0	9.8	15.6
	5. metaconid L			7.6	7.7	6.0	5.1	7.9
	6. entoconid L	10.0			12.3	11.9	8.3	8.3
	7. hypoconid L	12.6			14.1	13.5	7.8	14.4
	8. trigonid L	12.7		17.7	15.5	15.0	11.7	18.7
	9. talonid W	16.8			20.3	17.9	14.5	22.6
	10. central narrow W			17.2	15.2	14.3	10.9	16.6
	11. hypoconid-entoconid D	9.8			10.6	8.7	8.9	10.9
	12. metaconid-protoconid D				9.7	7.0	6.6	12.3
	13. protoconid-paraconid D				12.9	9.9	10.2	16.0
	14. protoconid-hypoconid D				18.6	15.5	13.4	20.0
	15. paraconid L	8.2		10.5	8.5	9.0	7.7	10.2
	16. D protoconid top to anterior end				15.5	16.5	11.9	18.8
	17. D metaconid top to anterior end				22.0	21.9	16.7	26.9
	18. paraconid H	11.8			15.8		10.2	16.7
	19.protoconid H		17.0		19.5		12.1	20.0
	20. metaconid H				12.3		8.1	12.5
	21. entoconid H	8.6			11.3		7.5	9.3
	22. hypoconid H	12.0			13.9		8.5	14.5
M_2	1. total L		30.2		29.5	23.9	23.7	31.2
	2. labial trigonid L		18.2		17.4	14.4	14.7	18.6
	3. labial talonid L		12.0		10.2	9.5	9.0	12.6
	4. lingual trigonid L		15.6		14.1	12.4	11.9	14.9
	5. lingual talonid L		14.6		13.1	11.5	11.8	16.3
	6. trigonid L		19.8		21.2	18.7	16.1	23.9
	7. talonid W		18.7		18.8	17.4	14.9	21.5
	8. central narrow W		18.9		18.6	16.8	14.5	21.3
	9. hypoconid-entoconid D		11.6		10.5	8.3	9.8	10.2
	10. metaconid-protoconid D		9.5		10.4	9.0	8.4	9.9
	11.protoconid H				13.5		8.4	13.6
	12. metaconid H				12.1	9.7	8.5	12.9
	13. entoconid H				8.5		6.7	8.7
	14. hypoconid H				12.9		7.2	12.5

Table 4. Main dimensions of the jaws of *I. atticus* from Crevillente 2 (CR2-S-250) and Concud (IPS), compared with those of *I. vireti* from Can Llobateres (Institut de Paleontologia 'Miquel Crusafont', in Sabadell), *Agriotherium africanum* (Hendey, 1980) and *Ursus arctos* (Torres, 1988). CR2: Crevillente 2; CG: Concud (Cerro de la Garita); L: length; H: height. The numbered categories follow the terminology proposed by Torres (1988).

	I. atticus	*I. atticus*	*I. vireti*		*A. africanum*	*U. arctos*
	CR2	CG	VP633	VP647	L45062	mean
1. L max	285.0			228.0	296.0	236.3
2. H under P_4	59.0	64.0	50.7	43.4		45.8
3. H under M_1	61.0	67.0	55.0	42.5	69.0	44.4
4. H under M_3	74.0		55.5	48.5		48.8
L rear C-M_1	103.0	110.0	94.2	85.5		
L P_4-M_2	87.0	96.8	72.7	70.3		
9. L P_4-M_3	103.5		87.6	82.4	104.0	76.9
11. L M_1-M_3			72.2	66.5		66.5

(1926) of the same specimen, under the name *Hyaenarctos laurillardi*, we can see that M_1 has an additional cusp between protoconid and hypoconid, as in *I. vireti* and often in *I. atticus*, whereas the known M_1 of *I. arctoides* does not present that cusp. The assignment of the ursid from Monte Bamboli to *I. vireti* cannot be certain without the additional material, e.g. the upper dentition. Furthermore, the Monte Bamboli lignites can be correlated with the Middle Turolian fauna V1 or more probably V2 of Baccinello. We prefer to maintain the specific status of *I. anthracitis*, given the strong endemic character of faunas V1 and V2 (Hürzeler & Engesser, 1976; Rook, 1993).

The postcranial skeleton of the Upper Miocene and Pliocene Ursidae is only documented by a large collection of bones of *Agriotherium africanum* from South Africa (Hendey, 1980); the metapodials, according to this author, are similar to those of *Ursus arctos*, though slightly more robust. Because of the limited knowledge of the postcranial skeleton of the genus *Indarctos* we are not sure whether the postcranial remains from Crevillente 2 belong actually to *I. atticus*. In any case, the scapholunar and the third phalanx from Crevillente are very similar in size to the specimens from Valdecebro 5.

The metapodials from Crevillente 2 (Fig. 7) are larger in size than the ones of *I. vireti* from Can Llobateres, but show a great size disparity with respect to the metapodials of *I. atticus* from Concud (Crusafont & Kurtén, 1976). Perhaps some of the postcranial elements from Crevillente belong to *Indarctos* sp. cf. *I. vireti*, to be described hereafter (see Table 5).

We have compared our material with the metapodials of the Spanish Pleistocene ursids described by Torres (1988). In spite of the strong sexual dimorphism and/or intraspecific variability observed in that material, we have observed a considerable morphological similarity between our material and the metapodials of *Ursus arctos*, *U. deningeri* and *U. spelaeus*. In size and robustness, they are more similar to the first one of these species. The most siginificant differences are:

In the Mc II and Mc III from Crevillente, the external and internal edges of the proximal end are clearly concave; in the three species of *Ursu*s studied, those edges are nearly straight.

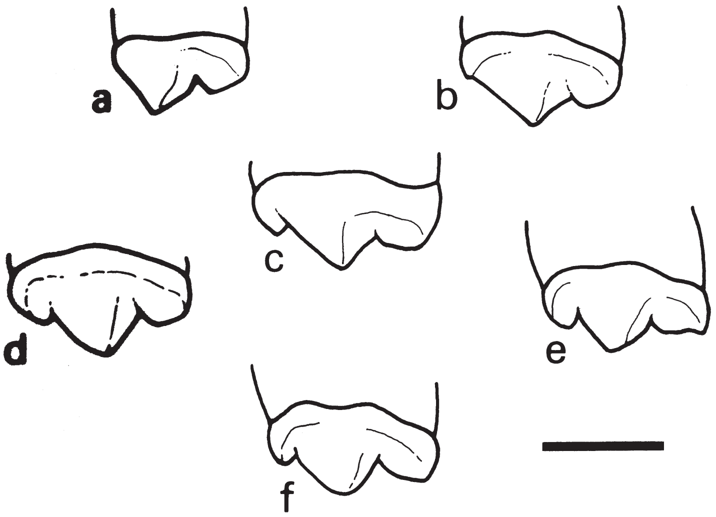


Fig. 5. Degree of development of the parastyle in the P^4 of *Indarctos*; a: *I. vireti* from Can LLobateres (IPS VP646); b: *I. arctoides* from Montredon (cast, Univ. Claude Bernard de Lyon 210059); c: '*I. punjabiensis*' from The Siwaliks (Lydekker, 1884); d: *I. atticus* from Samos (Helbing, 1932); e: *I. atticus* from Concud (CG-4M); f: *I. atticus* from Crevillente 2 (CR2-S-304). Scale bar is 2 cm.

Table 5. Main dimensions of the metapodials of *Indarctos atticus* from Crevillente 2, compared with those of *I. vireti* and *I. atticus* (Crusafont & Kurtén, 1976), *Agriotherium africanum* (Hendey, 1980) and *Ursus arctos* (Torres, 1988). APD: anteroposterior diameter; TD: transverse diameter; L: length. The numbered categories follow the terminology proposed by Torres (1988).

		I. atticus CR2	*I. vireti* Can Llobateres		*I. atticus* CG		*A. africanum* mean	*U. arctos* mean
Mc II	1. total L	86.2	70.0	78.0	115.0	118.0		77.8
	2. max. prox. TD	20.4					34.6	16.8
	3. max. prox. APD	28.5	27.8	25.4	29.3	28.8	24.8	23.8
	4. diaph. TD	16.2	12.0	12.8	14.0	14.0		13.0
	5. diaph. APD	14.0						12.5
	6. max. dist. TD	22.3	20.0	19.5				19.6
Mc III	1. total L						117.5	78.0
	2. max. prox. TD	20.5					21.9	17.0
	3. max. prox. APD		25.5				34.4	24.1
	4. diaph. TD	15.5	14.4					12.8
	5. diaph. APD	13.6						11.5
	6. max. dist. TD							19.9
Mt II	1. total L	75.9	>85.0		87.0	86.0	96.5	73.3
	2. max. prox. TD	17.4					17.4	13.8
	3. max. prox. APD	26.8	28.0		31.0	30.5	31.4	23.5
	4. diaph. TD	16.1	14.5		15.0	17.8		12.6
	5. diaph. APD	10.8						9.9
	6. max. dist. TD	21.7						18.6

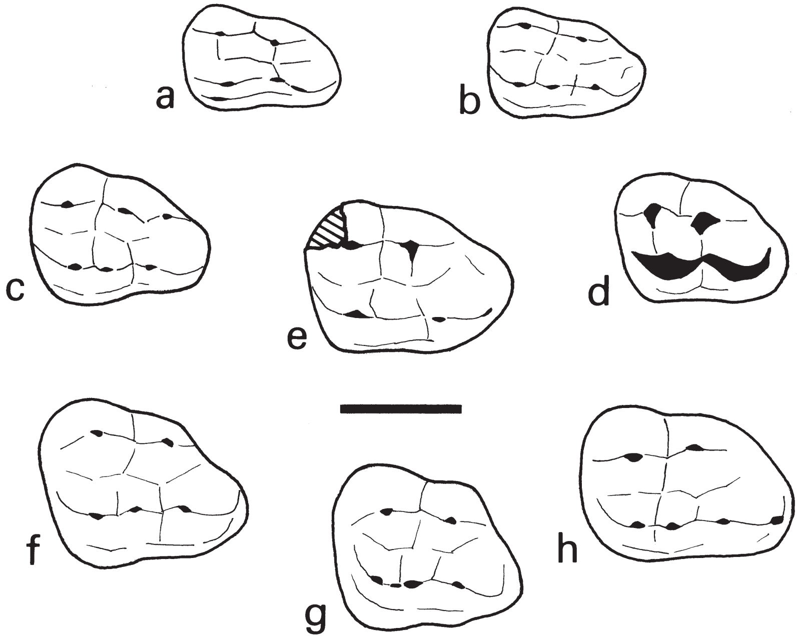


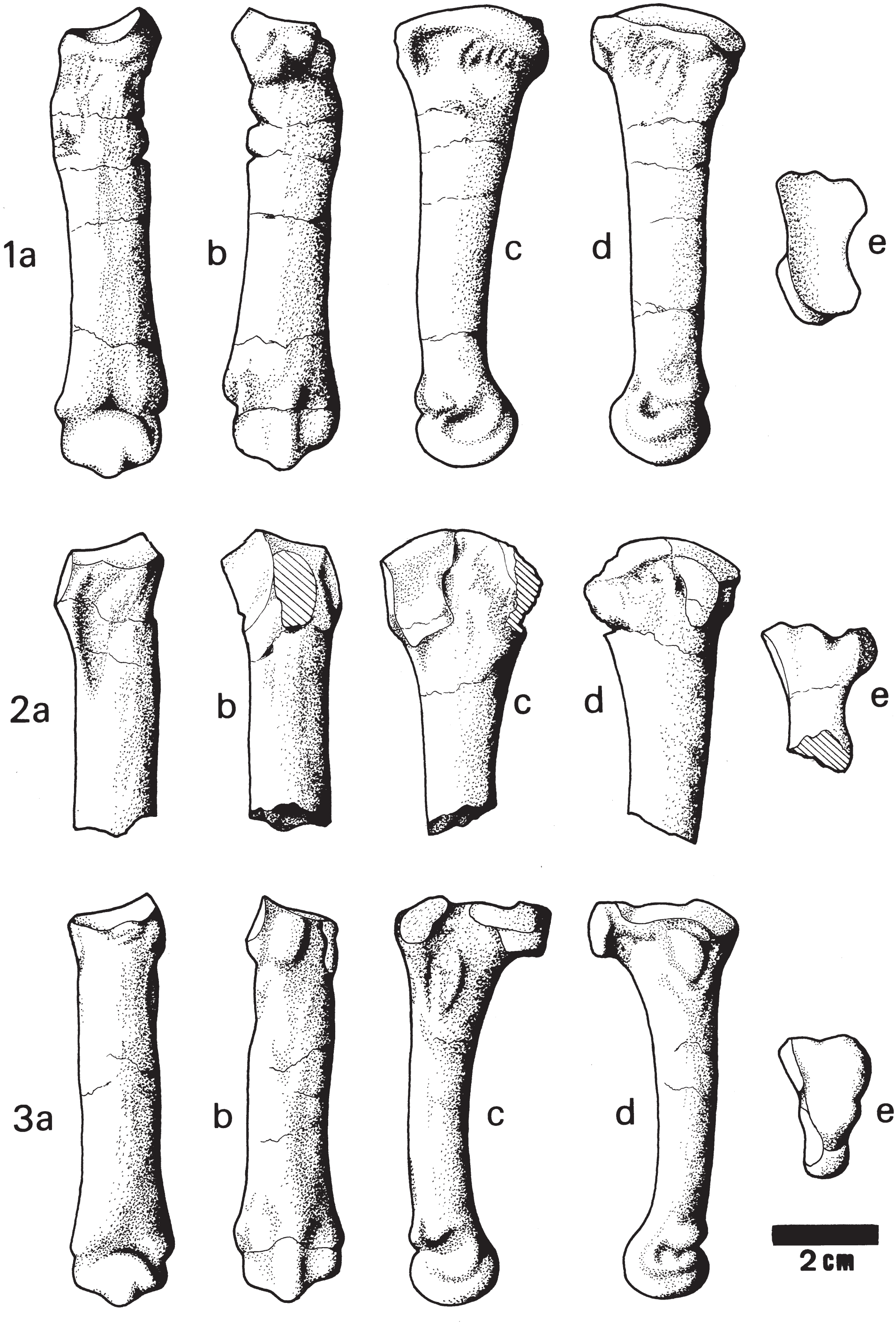
Fig. 6. Morphology of the M^2 of *Indarctos*; a: *I. vireti* from Can Llobateres (IPS VP646); b: *Indarctos* sp. from Gau-Weinheim (Weitzel & Tobien, 1952); c: *I. arctoides* from Montredon (cast, Univ. Claude Bernard de Lyon 210059); d: *I. arctoides* from Orignac (Helbing, 1932;); e: *I. atticus* from Crevillente 2 (CR2-S-294; figure reversed); f: *I. atticus* from Samos (Helbing, 1932); g: '*I. punjabiensis*' from the Siwaliks (Lydekker, 1884); h: '*I. salmontanus*' from Hasnot (Erdbrink, 1953). Scale bar is 2 cm.

In the Mt II from Crevillente the external edge of the proximal end is slightly concave, whereas in the three mentioned species of the genus *Ursus* this edge is always convex.

Morphological variability in I. atticus — Within the genus *Indarctos*, *I. atticus* is the species whith the widest stratigraphical and geographical distribution. Together with, or perhaps as a consequence of, this wide distribution, it shows a remarkable morphological variability.

As for its size, *I. atticus* is clearly the largest species of the genus. In fact, some teeth of the largest specimens exceed the measurements of the elements of *Agriotherium*. On the other hand, the dimensions of the smallest specimens of *I. atticus*, overlap those of the largest specimens of *I. arctoides*.

The premolar series has a great intraspecific variability that affects the number, morphology and arrangement of these teeth. There is also a certain morphological variability in M3, even within the same locality, e.g in Crevillente 2. Thenius (1959) already mentioned that there is a wide variation range in the genus *Indarctos*, above all in the anterior premolars and posterior molars, like in other ursids. Thus, in the jaws from Crevillente, Samos (Helbing, 1932) and Concud (IPS) the lower premolar series is complete, while in another jaw from Concud (Alcalá, 1994) and in the type of


1a
b
c
d
e
2a
b
c
d
e
3a
b
c
d
e
2 cm

'*punjabiensis*' (Lydekker, 1884), there are only three premolars.

The development of the talon in the M^2 is also variable. The morphology of this tooth shows various stages, from '*I. punjabiensis*', with a short M^2 similar to some specimens of *Agriotherium*, to '*I. salmontanus*', whith a very elongated M^2. The M^2 from Crevillente 2 described in this paper is morphologically close to the type '*salmontanus*' (see Fig. 6).

With regards to the morphology of the carnassials, the typical characteristics of *I. atticus* are the presence of a P^4 with a well-developed parastyle and a more or less bifurcated protocone, as well as a complicated M_1, with an additional cusp between protoconid and hypoconid. But, the P^4 from Concud show a poorly bifurcated protocone or even only an trace of bifurcation, whereas in Crevillente that cusp is clearly bifurcated. The same can be said about the parastyle, which is normally well developed, but in two of the three known specimens from Concud a reduced parastyle is observed. Besides, in the M_1 from Valdecebro 5, the additional cusp between protoconid and hypoconid is absent (Pl. 2, fig. 4).

Indarctos sp. cf. *Indarctos vireti* Villalta & Crusafont, 1943
Pl. 1, fig. 6.

*1943 *Indarctos vireti* — Villalta & Crusafont, 54: text fig. 1, pl. figs. 1-3.
1948 *Indarctos vireti* Villalta et Crusafont — Villalta & Crusafont: 87, text fig. 2, pl. I, figs. 2, 2a, 2b.
1948 ?*Agriotherium* sp. — Villalta & Crusafont: 89, text fig. 3, pl. II, figs. 1, 1a-b.
1959 *Indarctos arctoides vireti* — Thenius: 284.
1976 *Indarctos vireti* Villalta & Crusafont — Crusafont & Kurtén: 5, text figs. 1-5.
1986 *Indarctos arctoides vireti* Villalta & Crusafont, 1943 — Petter & Thomas: 576.

Type locality — Can Purull (Viladecavalls) (Spain), Upper Vallesian (MN10).

Other localities — Can Llobateres and Crevillente 2 (Spain).

Studied material from Crevillente 2

Canine and mandible fragment with P_2-P_4: MHMN CR2-A94
M_1 (incomplete): MHMN CR2-M321

Description

Lower canine — Only the crown is preserved. It shows an anterolingual ridge and a less-marked posterolingual ridge, which make the lingual face a rather flat surface.

P_2, P_3 and P_4 — They are similar to the homologous elements of *I. atticus* from Crevillente 2, but of smaller size.

M_1 — This is an incomplete tooth, which lacks nearly all the entire protoconid and the metaconid too. The paraconid is robust, and in the talonid there is a simple and wide hypoconid, as well as an entoconid formed by a conical main cusp and a small posterior cusp. Between hypoconid and entoconid, there is a marked valley. It cannot be decided whether there is an additional cusp between protoconid and hypoconid.

Fig. 7. Metapodials of *Indarctos atticus* from Crevillente 2; 1: left metacarpal II (CR2-S-459); 2: left metacarpal III (CR2-S-474); 3: left metatarsal II (CR2-601); a: dorsal view; b: ventral view; c: external view; d: internal view; e: proximal view.

Discussion — This material comes from the lower beds of Crevillente 2 (Montoya, 1990, 1994), and the dimensions are clearly smaller than in *I. atticus.* On the other hand, they are far closer to the small-sized species of the genus (*I. vireti* and *I. arctoides*) (Table 3, Fig. 4). In the absence of more material, we have decided to assign it, with some reserves, to *I. vireti*, which is the only *Indarctos* of small size quoted from the Iberian Peninsula. We cannot reject the possibility that in the Lower Turolian of Crevillente 2 *I. atticus* coexisted with an *Indarctos* of smaller size, like in Dorn-Dürkheim 1 (MN11), where *I. atticus*, *I. arctoides* and a lot of material of *Ursavus* are found together (Roth & Morlo, 1997). Neither can we exclude the possibility that we are dealing with a small individual of *I. atticus*, perhaps a case of sexual bimodality. In fact, *I. atticus* from Crevillente shows a small size, compared to mean values of this species (see Figs. 3-4).

The species *I. vireti* was created by Villalta & Crusafont (1943) on the basis of a jaw fragment found in the locality of Viladecavalls (Can Purull). Later, more material from this site was published (Villalta & Crusafont, 1948). Afterwards, Crusafont & Kurtén (1976) assigned a large sample from Can Llobateres to this species. The latter locality is of Early Vallesian age (MN9), and Viladecavalls is Late Vallesian (MN10) (Agustí et al., 1984), or, respectively the *Cricetulodon sabadellensis* and *Cricetulodon-Progonomys* Zones of the biozonation of Agustí & Llenas (1994) for the Catalonian Neogene basins.

Thenius (1959) regards *I. vireti* as a subspecies of *I. arctoides*. This was contested by Crusafont & Kurtén (1976), though other authors have afterwards followed Thenius's interpretation. In any case, there is not only an evident disparity in size between *I. vireti* and *I. arctoides* (Tables 2-3, Figs. 3-4), but there are morphological differences too, especially in the dentition: the P^4 of *I. vireti* has not even a trace of a parastyle, in contrast with the P^4 of *I. arctoides*, which already presents a vestigial parastyle (see Fig. 5), as can be observed in the sample from Montredon and in the recently described material from Dorn-Dürkheim 1 (Roth & Morlo (1997). The upper molars of *I. vireti* present a very strong lingual cingulum, which can develop into accessory cusps. Furthermore, it has a more elongated M^2 (Fig. 6a) than any other species of the genus *Indarctos*.

The morphology of M_1 and M_2 is closer to *I. atticus* than to *I. arctoides*. M_1 is 'complex' with an additional cusp between protoconid and hypoconid, and M_2 is not shortened. On the contrary, the samples of *I. arctoides* from Montredon and Küçükcekmece present the typical morphology of the species: a 'simple' M_1, without the mentioned additional cusp, and a relatively short M_2.

We think that these differences are sufficient to maintain *I. vireti* as a separate species. It is possible, as pointed out by Crusafont & Kurtén (1976), that *I. atticus* is a descendant of *I. vireti*. Until now, the latter species had only been mentioned from the Catalonian basin of Vallès-Penedès, though perhaps an M^2 from the German locality of Gau-Weinheim (Fig. 6b), described by Weitzel & Tobien (1952), and cited by de Beaumont (1988), also belongs to it. Its dimensions (APD: 25.1; TD: 18.3) make it biometrically close to the material from Can Llobateres (see Fig. 3); Roth & Morlo (1997) considered it an *I. arctoides*.

With the occurrence in the lower beds of Crevillente 2, the known stratigraphic range of *I. vireti* can be extended from the Vallesian into the Lower Turolian.

Stratigraphic and geographic distribution of the species of the genus Indarctos — So far *I. vireti* has been found in Can Llobateres (MN9), Viladecavalls (MN10) and possibly in Crevillente 2 (MN11). If the molar of *Indarctos* sp. from Gau-Weinheim (Deinotheriensande) (MN9) corresponds to *I. arctoides*, as suggested by Roth & Morlo (1997), the distribution of *I. vireti* is restricted to eastern basins of the Iberian Peninsula. In fact, *I. vireti* has not been found in the rich Vallesian localities of the central Spanish basins, e.g. Los Valles de Fuentidueña (MN9) (Ginsburg et al., 1981), and, especially, in Cerro de Batallones (MN10) (Morales et al., 1992) which shows an exceptional abundance of carnivora in its fossil assemblage. This distribution agrees well the subdivision of the Iberian Peninsula in two paleobiogeographical provinces, proposed by Agustí et al. (1984), based on the study of the micromammal assemblages. According to this hypothesis, during the Miocene, the eastern basins developed more humid climatic conditions than the interior basins, with a maximum of faunal differentiation in the Vallesian. This would indicate a clear preference of *I. vireti* for more wooded environments, as is the case for *I. arctoides* in the rest of Europe (Roth & Morlo, 1997).

I. arctoides shows a stratigraphical distribution which resembles that of *I. vireti* and which covers the Vallesian and the Lower Turolian, but it occupies a wider geographical area. Thus, it has been cited in the German sites of Westhofen (MN9), possibly in Gau-Weinheim (Deinotheriensande) (MN9), and in Dorn-Dürkheim 1 (MN11), in Pfaffstetten (Austria) (MN11), in the French sites of Montredon (MN10) and Orignac (Vallesian, according to Ginsburg & Boulot, 2000), and also in Küçükcekmece (Turkey) (MN11).

I. anthracitis has been cited from the Italian sites of Monte Bamboli (Baccinello) and Fiume Santo (Sardinia). Both sites, which can be correlated with the V2 level of Baccinello, were insular areas during the Middle Turolian (Rook, 1993; van der Made, 1999). We must therefore consider *I. anthracitis* as an endemic form, restricted to these insular zones of the Italian Upper Miocene.

In Europe, *I. atticus* is present in the Spanish sites of Terrassa (MN10), Crevillente 2, Puente Minero (MN11), Concud, Los Mansuetos, and Valdecebro 5 (MN12), in the the Greek sites of Pikermi and Samos (MN12), in Baltavar (Hungary) (MN13), in Aubignas (France), and in Dorn-Dürkheim 1 (Germany) (MN11). It is present as well in the Asiatic localities of Maragheh (Iran) (MN11), Shansi (China) and Hasnot (Pakistan). The Chinese *Indarctos* localities which have been reliably dated are Lufeng (Baode fauna) (Qiu, 1990) and Mahui (Yushe Basin) (Flynn et al., 1991) in the province of Shansi. Mahui has been dated as c. 6 Ma (Flynn et al., 1997), whereas Lufeng would be older, c. 8 Ma (Qiu, 1990). On the other hand, the presence of *Indarctos* in the Siwaliks is dated at c. 6.5 Ma (Barry & Flynn, 1990). Thus, at least during the Middle-Late Turolian *I. atticus* shows a wide distribution in Eurasia.

I. atticus probably also reached the Northern Africa at the end of the Miocene. In the fragmentary remains from Menacer (Algeria), described and figured by Petter & Thomas (1986), and assigned to *I.* aff. *arctoides*, the P^4 has a very well individualized parastyle. Unfortunately the remains are very scarce, but this feature, and the age of the outcrop (MN13 according to Mein, pers. com.), indicate that it might be a small-sized specimen of *I. atticus*.

In addition, we know, that *Indarctos* reached North America at the end of the Miocene (Hemphilian). At least some of the remains described as *I. oregonensis*, and a skull described as *Indarctos* sp., might well be ascribed to *I. atticus*. According to Roth & Morlo (1997) too, *I. atticus* s.l. would have arrived in North America at the end of the Miocene, coming from Eastern Asia.

Confirmation of these considerations would mean, that *I. atticus* had a vast geographical distribution at the end of the Miocene, which covered Eurasia, North America and the North of Africa.

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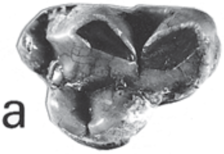
Plate 1

Figs. 1-5. *Indarctos atticus* (Weithofer, 1888) from Crevillente 2.
1: Rigth upper series P^4-M^2 (CR2-S-292, 293, 294).
2: Left P^4 (CR2-S-304); a: occlusal view; b: labial view.
3: Left M^1 (CR2-S-289).
4: Upper canine (CR2-S-303).
5: Upper canine (CR2-490).

Fig. 6. *Indarctos* sp. cf. *I. vireti* Villalta & Crusafont, 1943 from Crevillente 2.
Jaw fragment with P_2-P_4 (CR2-A94); a: labial view; b: occlusal view.

Scale with centimetric divisions.

1



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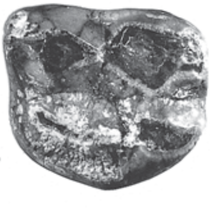

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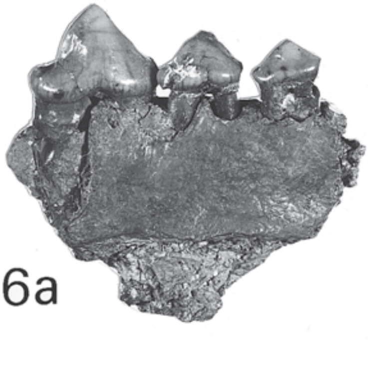

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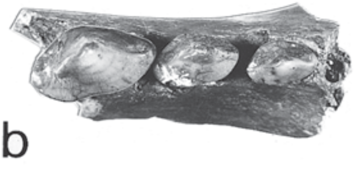


6b

Plate 2

Figs. 1-5. *Indarctos atticus* (Weithofer, 1888)
1: Left jaw (CR2-S-250), from Crevillente 2, labial view.
2: M_3 (CR2-876), same loc.
3: M_3 (GCPE CR2-2), same loc.
4. left series M_1-M_2 (RV5-50-AM, RV5-55-AM), from Rambla de Valdecebro 5; a: occlusal view; b: lingual view; c: labial view.
5. Incomplete left P^4 (CG-78-AM), from Concud (Cerro de la Garita); a: occlusal view; b: lingual view; c: anterior view; d: labial view.

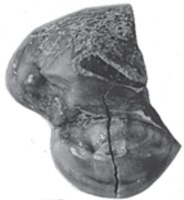
Scale with centimetric divisions. The small scale bar only for fig. 1.

2

3

1

4a



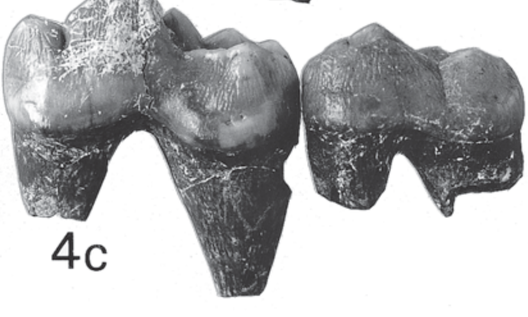
5a

5b

4b

5c

5d



4c