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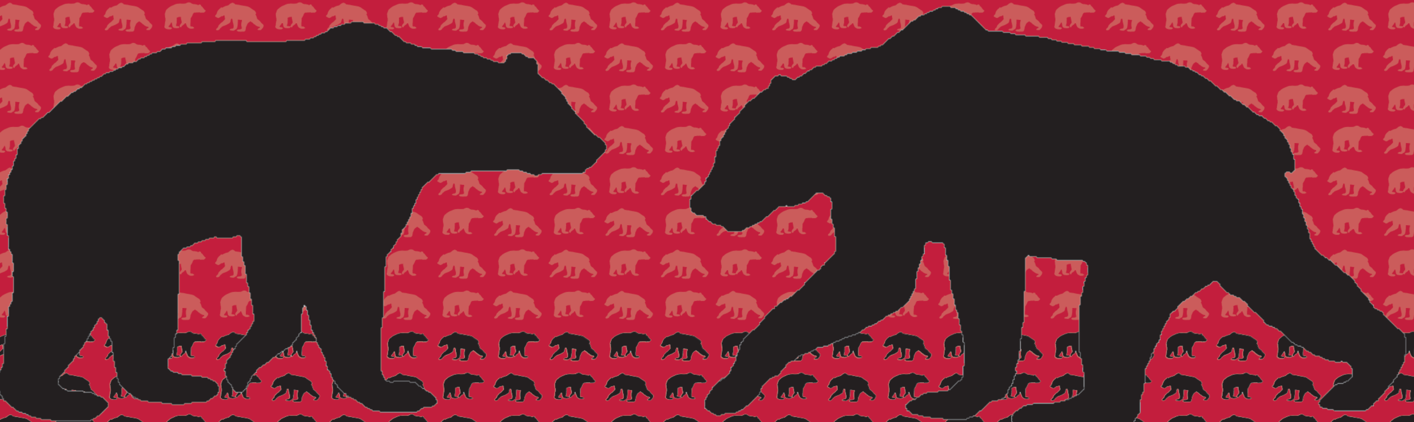

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The last record of an ailuropod bear from the Iberian Peninsula

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ABSTRACT

In this paper we describe Late Miocene (MN13) remains of the genus *Indarctos* Pilgrim, 1913 from the locality of Las Casiones (Teruel, Spain). Although the phylogenetic relationships of this genus are still controversial, the most recent phylogenetic analyses, based on cranial, mandibular and dental characters, include it in Ailuropodinae, thus making the relatives of the giant panda the predominant bears in the carnivoran assemblages for most of the Late Miocene in the Iberian Peninsula. These fossils of *Indarctos punjabiensis* (Lydekker, 1884) represent the last population of this subfamily from the Iberian fossil record, and possibly also from Europe, making this an important advance in our knowledge of the evolutionary history of this group. We also note the replacement of *Indarctos* by *Agriotherium* A. Wagner, 1837 in Iberian faunas, between *c.* 6.3 and *c.* 6.23 Ma.

KEY WORDS
Ursidae,
Ailuropodinae,
Late Miocene,
Las Casiones,
Teruel Basin.

RÉSUMÉ

Le dernier enregistrement d’un ours ailuropode dans la péninsule Ibérique.

Dans cet article nous décrivons les restes fossiles du genre *Indarctos* Pilgrim, 1913 du Miocène supérieur (MN13) de la localité de Las Casiones (Teruel, Espagne). Bien que les relations phylogénétiques de ce genre soient encore controversées, dans l’analyse phylogénétique la plus récente basée sur les caractères crâniens, mandibulaires et dentaires, ils sont inclus dans les Ailuropodinae. Ces parents des pandas géants étaient donc les ours prédominants dans les assemblages de carnivores pendant la majeure partie du Miocène supérieur de la péninsule Ibérique. D’autre part, ces fossiles d’*Indarctos punjabiensis* (Lydekker, 1884) représentent la dernière population de cette sous-famille dans les archives fossiles de la péninsule Ibérique, et éventuellement aussi d’Europe, ils contribuent de manière significative à l’avancement de la connaissance de l’histoire évolutive de cet groupe. En outre, nous signalons le remplacement de *Indarctos* par *Agriotherium* Wagner, 1837 dans les faunes ibériques entre 6.3 et 6.23 Ma.

MOTS CLÉS
Ursidae,
Ailuropodinae,
Miocène supérieur,
Las Casiones,
Teruel Basin.

INTRODUCTION

The Late Turolian (or Ventian, *sensu* Morales *et al.* 2013) fossil locality of Las Casiones, MN13 of the European Continental Neogene Mammal zonation (Mein 1990; Bruijn *et al.* 1992), is located 10 km north of the city of Teruel (Spain) in the district of Villalba Baja, on one of the slopes of a wide ravine near the villages of Celadas and Villalba Baja; more accurately at 40°26’10”N, 1°3’58”W (Alcalá 1994; van Dam *et al.* 2001; Pesquero 2003) (Fig. 1). This locality is included in the local zone M2 of van Dam (1997), and an age of 6.3 Ma has been proposed (van Dam *et al.* 2006: suppl. notes; Gibert *et al.* 2013). The fossils are found in a series of levels of lacustrine origin, mostly composed of green and black clays, with occasional intercalations of fine sand (Pesquero 2003). At least two different levels can be distinguished: Las Casiones (KS) and Las Casiones Superior (KSS), the first of which is the one that has yielded the majority of fossil remains. Several papers have been already written about this locality and its faunal composition. Its geology and stratigraphy was studied by Alcalá (1994) and later by Pesquero (2003), where a more detailed model was proposed.

The latest mammal faunal composition of Las Casiones (KS) is the following: The murids *Stephanomys ramblensis* van de Weerd, 1976, *Apodemus gudrunae* van de Weerd, 1976, *Occitanomys alcalai* Adrover, Mein and Moissenet, 1988, cf. *Rhagapodemus* sp.; the cricetids *Ruscinomys schaubi* Villalta & Crusafont, 1956, *Cricetus* cf. *C. kormosi* Schaub, 1930, *Blancomys sanzi* Adrover, Mein & Moissenet, 1993*;* the glirid *Eliomys truci* Mein & Michaux, 1970; the castorid *Dipoides problematicus* (Schlosser, 1902); the hystricid *Hystrix depereti* Sen, 2001; the erinaceid *Galerix* sp.; the talpids *Desmanella* sp., *Talpa* sp.; the soricids *Archaeodesmana* sp., *Paenelimnoecus* sp., *Blarinella* sp., *Amblycoptus jessiae* Doukas, van den Hoek Ostende, Theocharopoulos & Reumer, 1995; the vespertilionid chiropteran *Vespertilionidae* indet.; the ochotonid lagomorph *Prolagus* sp.; the proboscideans *Tetralophodon longirostris* (Kaup, 1832) and *Zygolophodon turicensis* (Schinz, 1824); the hyracoid *Pliohyrax* sp. cf. *P. graecus* (Gaudry, 1860); two species of the cervid *Pliocervus* Hilzheimer, 1922; the bovids *Tragoportax* sp. and two species of Boselaphini indet.; the hippopotamid *Hippopotamus crusafonti* Aguirre, 1963; the rhinocerotid *Dihoplus schleiermacheri* (Kaup, 1834); three species of the equid *Hipparion* Christol, 1832: *H. primigenium* (von Meyer, 1829), *H. mathewii* (Abel, 1926), and *H. periafricanum* Villalta & Crusafont, 1957; the mustelids *Plesiogulo monspessulanus* Viret, 1939, *Baranogale adroveri* (Petter, 1964), *Mustela* sp., and a Mustelidae indet. aff. *Sabadellictis* sp.; the ursid *Indarctos punjabiensis* (Lydekker, 1884); the hyaenids *Plioviverrops* sp. cf. *P. guerini* (Villalta & Crusafont, 1948) and *Thalassictis hipparionum* (Gervais, 1859); and the felids *Paramachaerodus orientalis* Kittl, 1887, *Amphimachairodus giganteus* Kretzoi, 1929, *Metailurus major* Zdansky, 1924, *Pristifelis attica* Wagner, 1857, and Felinae indet. (Cerdeño 1989; Alcalá 1994; Alcalá *et al.* 1994; van Dam 1997; Alcalá & Montoya 1998a, b; Pesquero 2003; van Weers & Rook 2003; Salesa *et al.* 2012).

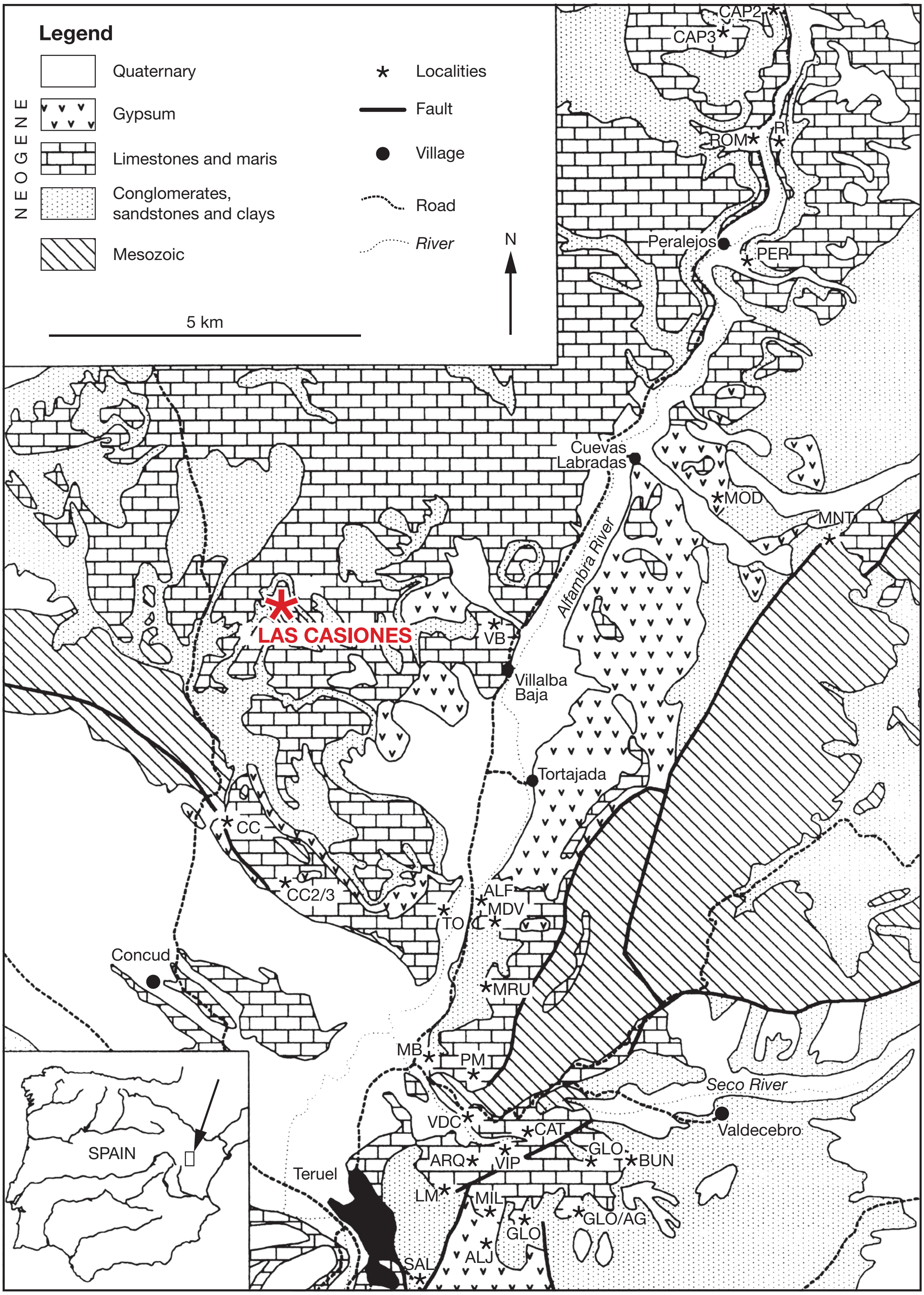

Fig. 1. — Schematic geologic map of the northern part of the Teruel basin with the paleontological localities indicated (after Pesquero *et al.* 2003 modified).

TABLE 1. — Measurements (in mm) of the dentition of the specimens of the genus *Indarctos* Pilgrim, 1913 from Las Casiones (length × width).

Specimens	P2	P4	M1	M2
K-174	10.45 × 7.42	–	–	–
K94-1733	–	32.01 × 22.51	–	–
K-162	–	–	29.21 × 28.98	–
K-161	–	–	× 26.89	–
KS-4316	–	–	28.62 × 27.01	–
KS-4315	–	–	–	31.34 × 27.79
KS-4317	–	–	–	31.49 × 28.06

The assignment of the bear fossil remains from Las Casiones to the genus *Indarctos* Pilgrim, 1913 might be considered as a novelty, since Alcalá (1994) described as *Agriotherium* Wagner, 1837 a very worn M1 and a fragment of M1, due to their large width. This identification has subsequently been repeated in many papers. The presence of *Indarctos* in Las Casiones was also tentatively noted by both Alcalá *et al.* (2005) and Salesa *et al.* (2012). This change in taxonomic determination has been possible due to the recovery of the new diagnostic remains described in this paper.

THE GENUS *INDARCTOS* IN THE FOSSIL RECORD

The genus *Indarctos* comprises medium to large-sized bears from the late Miocene, with an omnivorous diet (Montoya *et al.* 2001; Viranta 2004; Abella 2011; Abella *et al.* 2013; Monescillo *et al.* 2014; Domingo *et al.* 2016). Although comprehensively studied, there is not a full consensus about their phylogenetic relationships. Some authors (Hendey 1972; Qiu *et al.* 2014) relate them to the genus *Agriotherium* (considered a Hemicyonidae by the authors of the present paper) and others consider it to be a basal Ursidae (Abella *et al.* 2012, 2014). However, the most recent phylogenetic analyses, based on cranial, mandibular and dental characters, include *Indarctos* spp. in the Ailuropodinae (Abella *et al.* 2012; Qiu *et al.* 2014). This genus was indeed the predominant bear taxon during most of the late Miocene in the Northern Hemisphere (Abella *et al.* 2014).

The first specimen currently referred to the genus *Indarctos* consists of a left mandible fragment from the Greek locality of Pikermi identified as *Hyaenarctos* sp. by Dames (1883), with Weithofer (1888) later referring it to *H. atticus*. However, in 1884 Lydekker created the species *H. punjabiensis* based on a broken maxilla (which included P4-M1) from the Siwaliks in India. In that paper he also assigned a maxilla with P4-M2 and a skull with Upper canine and P4-M2 from other localities to the same genus. The latter specimen has been the cause of most of the later taxonomic confusion in comparisons among species since this skull clearly can be assigned to the genus *Agriotherium*, due to the lack of a clear talon and different relative development of the main cusps in the M2.

Pilgrim (1913) moved some of these remains from the junior synonym genus *Hyaenarctos* (also later synonym of *Agriotherium*) to the newly created genus *Indarctos* based on a maxillary fragment with M2 and broken M1 from the Siwaliks. However, it was not until a year later (Pilgrim 1913) that he measured, figured and compared this specimen to other, similar fossils, describing *Indarctos salmontanus* as the type species of the genus (Pilgrim, 1914). Later Baryshnikov (2002) accepted only two species of the genus *Indarctos*, literally he stated: "The genus *Indarctos* comprises two species. *I. arctoides* (Depéret, 1895) was found in Europe, northern Africa and Turkey, dating as the Vallesian (MN 9-11). *I. punjabiensis* (Lydekker, 1884) known from the Turolian (MN 10-13) had a Holarctic range, occurring in Europe, northern Africa, in the central, southern and eastern parts of Asia, and in North America". Therefore, although indirectly, he synonymized Pilgrim's type species with *Indarctos punjabiensis*.

The oldest record of *Indarctos* comprises some specimens from MN9 in the Vallesian basin of Vallès-Penedès, at the localities of Can Porull (Villalta & Crusafont 1943, 1948) and later from Can Llobateres (Crusafont & Kurtén 1976). These remains were assigned to *Indarctos vireti* Villalta & Crusafont, 1943, a small sized member of the genus, with elongated molars, more primitive (less reduced) premolars, and well-developed diastemas between them.

Indarctos arctoides (Depéret, 1895), is documented from MN10. This species was first described from the French locality of Montredon, and can be found along the northern edge of the Mediterranean Sea, including Spain, France and Turkey (Tobien 1955; Geraads *et al.* 2005; Abella 2011; Abella *et al.* 2014).

Finally, *Indarctos punjabiensis* (incl. *I. atticus*) has an extensive record in the Iberian Peninsula from MN10 to MN12. Most of these specimens were studied in detail by Montoya *et al.* (2001). Following the arguments of that paper we accept three species of *Indarctos*; four, if we take include the peculiar *I. anthracites* (Weithofer, 1889), which is thought to be an insular form and is only represented by a single published specimen. These are *I. vireti*, *I. arctoides* and *I. punjabiensis* with the last species having the temporal range. The present study increases the stratigraphic range of the genus *Indarctos* in the Iberian Peninsula to the lower part of MN13.

MATERIAL AND METHODS

The fossil remains of *Indarctos punjabiensis* from Las Casiones are part of the collections of the Gobierno de Aragón (Spain), and are housed at the Museo Aragonés de Paleontología, Fundación Conjunto Paleontológico de Teruel-Dinópolis (Teruel, Spain). The studied material was: KS-30: right IV metacarpal; K-162: left M1; K-161: distal fragment of right M1; KS-4315: right M2; KS-4316: left M1; KS-4317: left M2; K94-1733: right P4; K-174: maxillary fragment (P2, root of P1 and P3); KS-4314: premolar (p3?) (Figs 2; 3). Of the fossil remains studied here, only M1 K-161 and K-162 were originally described in Alcalá (1994). For comparison, we studied the the upper dentition of *Indarctos vireti* housed at the Institut Català de Paleontologia- Miquel Crusafont Museu (since the holotype consists of a mandible fragment with p4-m2), cast specimens of *Indarctos arctoides* (paratype) from Montredon housed in the Natural History Museum Basel – Naturhistorisches Museum

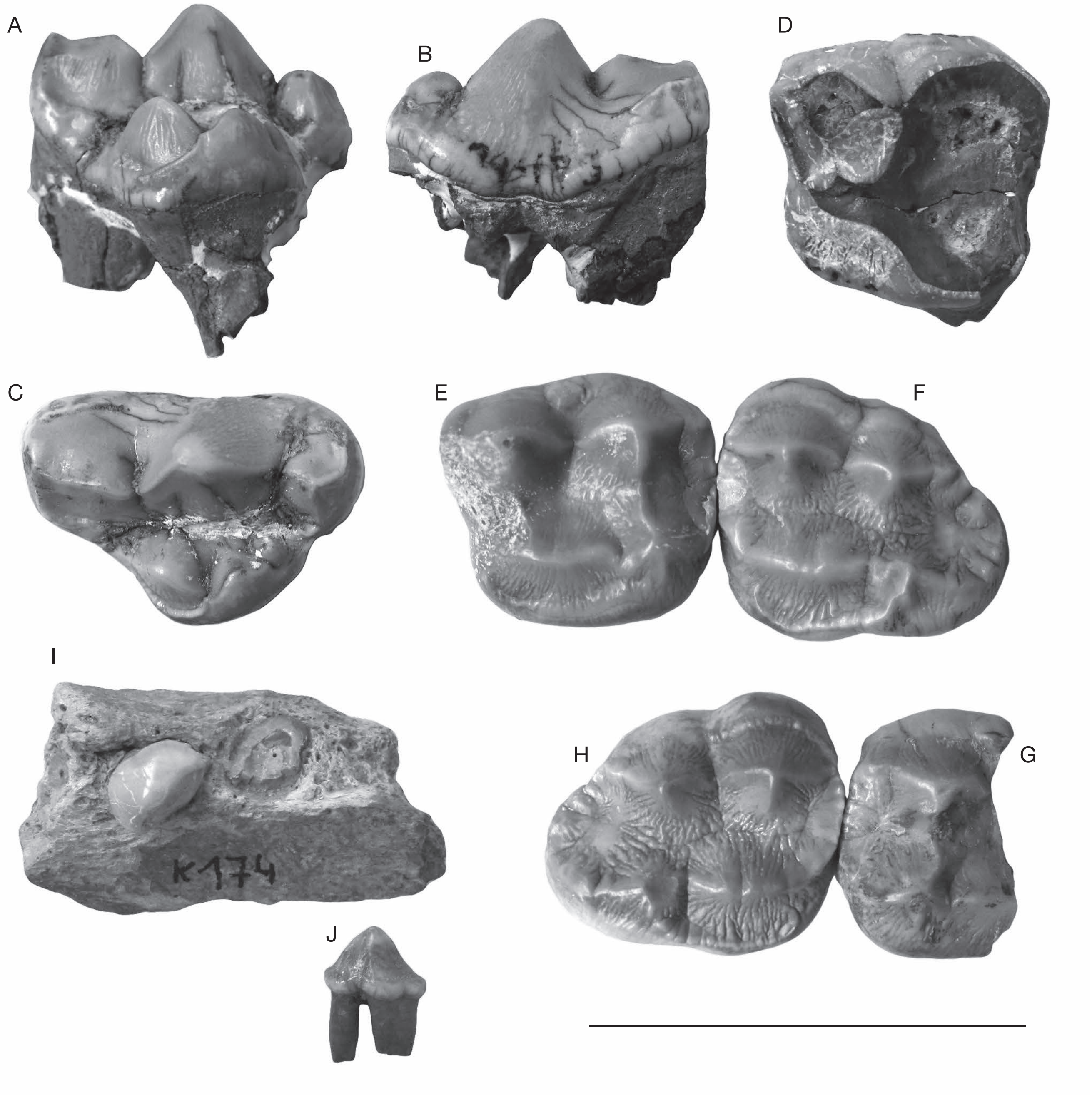

Fig. 2. — *Indarctos punjabiensis* (Lydekker, 1884) from Las Casiones: **A**-**C**, K94-1733, right P4: **A**, lingual view; **B**, labial view; **C**, occlusal view; **D**, K-162, left M1, occlusal view; **E**, KS-4316, left M1, occlusal view; **F**, KS-4317, left M2, occlusal view; **G**, K-161, distal fragment of right M1, occlusal view; **H**, KS-4315, right M2, occlusal view; **I**, K-174, left maxillary fragment with P2 and root of P1 and P3 (occlusal view); **J**, lower premolar, labial view. Scale bar: 5 cm.

Basel, the sample of *I. arctoides* housed at Museo Nacional de Ciencias Naturales-CSIC in Madrid, and the cast of the holotype of *I. punjabiensis* housed at the British Museum of Natural History, London.

The measurements were taken using Mitutoyo Absolute digital calipers to the nearest 0.1 mm (Table 1).

Institutional abbreviations

KS and K	Las Casiones;
MNCN	Museo Nacional de Ciencias Naturales;
NMB	Natural History Museum Basel – Naturhistorisches Museum Basel;
ICP	Institut Català de Paleontologia – Miquel Crusafont Museu.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Infraorder ARCTOIDEA Flower, 1869
Parvorder URSIDA Tedford, 1976
Superfamily Ursoidea Fischer von Waldheim, 1817

Fig. 3. — *Indarctos punjabiensis* (Lydekker, 1884) from Las Casiones, right IV metacarpal: **A**, plantar view; **B**, medial view; **C**, dorsal view; **D**, lateral view. Scale bar: 5 cm.

Family Ursidae Fischer von Waldheim, 1817
Subfamily Ailuropodinae Grevé, 1894
Tribe Indarctini Abella, Alba, Robles, Valenciano, Rotgers, Carmona, Montoya & Morales, 2012
Genus *Indarctos* Pilgrim, 1913

Indarctos punjabiensis (Lydekker, 1884)

Hyaenarctos punjabiensis Lydekker, 1884: 226.

Agriotherium cf. *A. roblesi* – Alcalá 1994: 103, 104, pl. 3, fig. o.

Syntype. — Fragments of the left and right maxillae with P4-M1, figured by Lydekker (1884: pl. XXX, fig. 2).

Type locality. — Hasnot Siwaliks. Salt Range, Jhelum District. Punjab.

Age. — Late Miocene. MN 10-13.

Emended diagnosis. — Medium to large sized Ursidae, with marked sexual dimorphism. Plantigrade. Dolichocephalic skull, base of the zygomatic arch coincides with the M1 and the mesial part of M2. The premolars are smaller in relative size and number compared to the other members of the genus, being crowded to some degree. Both the P2 and the P3 are double rooted, with the tendency to be fused in some individuals. The mesio-distal length of the P4 is equal to that of M1, and it has a quite developed parastyle, with two crists, une lingual and one labial. Wide upper molars, almost as wide as they are long; from sub-rectangular to trapezoid in shape. The talon in M2 is large, but not as long as in the derived Ursinae. Generally low, but robust jaw. Relatively long m1, with equally long talonid and trigonid; tall entoconid, taller than the hypoconid; m1 talonid similar to that of m2. The m3 morphology varies from rounded to elongated.

Description

Upper dentition

The description has been carried out on the possibly associated upper dentition, using both sides when possible.

P1 (Fig. 2I). Only a single root is preserved. Smallest of the upper premolars.

P2 (Fig. 2I). Reduced, ovoid premolar, with only one root. Single cusp with two ridges, one mesial and one distal, that curve towards the lingual side; the distal cusp is blunter than the mesial one. This tooth is rotated relative to the main axis of the maxilla and somehow crowded, due to the shortening of the muzzle.

P3 (Fig. 2I). Only a single root is preserved. Larger than the preceding upper premolars.

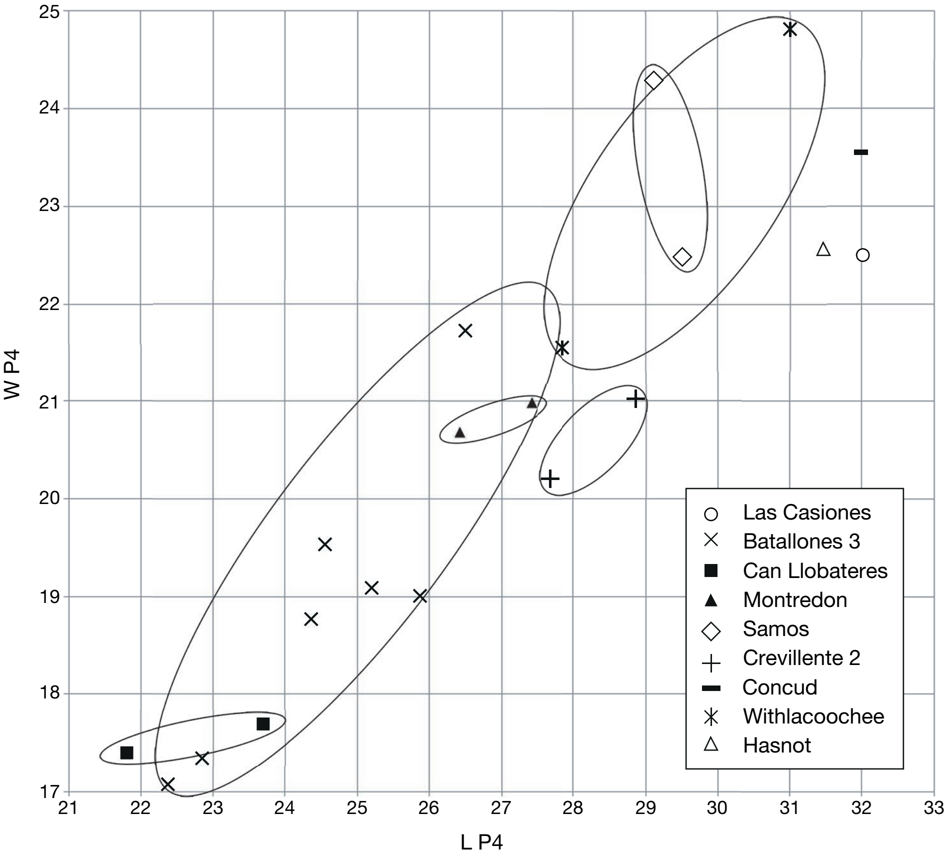

FIG. 4. — Bivariate plot of the P4 of different *Indarctos* Pilgrim, 1913 species from various sites.

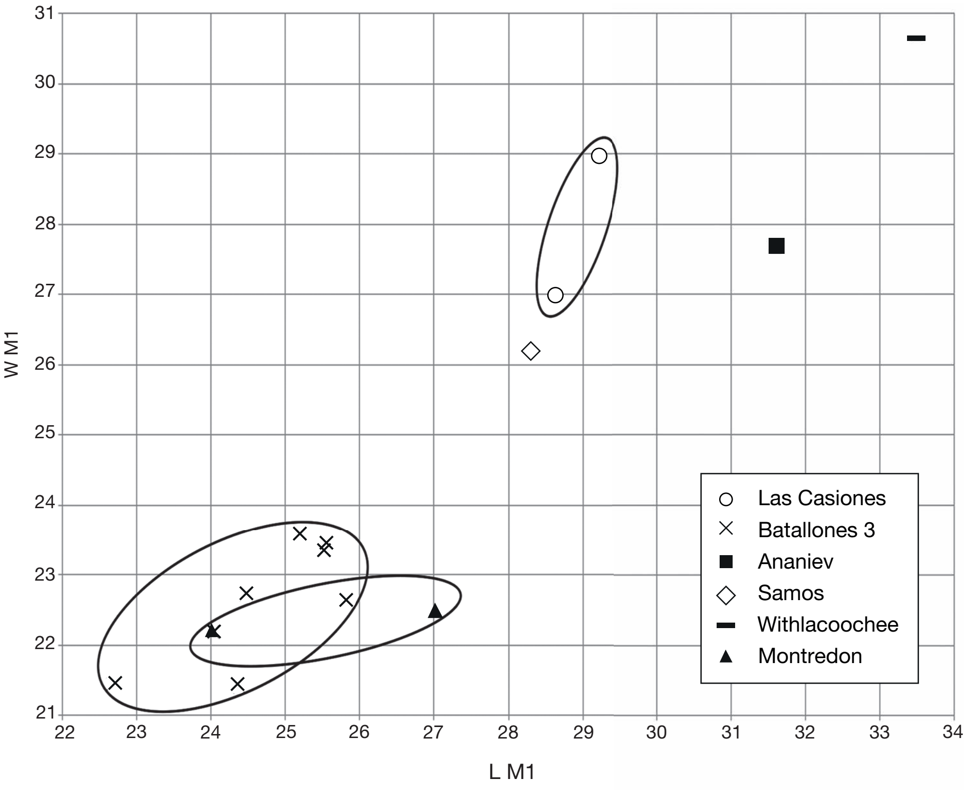

FIG. 5. — Bivariate plot of the M1 of different *Indarctos* Pilgrim, 1913 species from various sites.

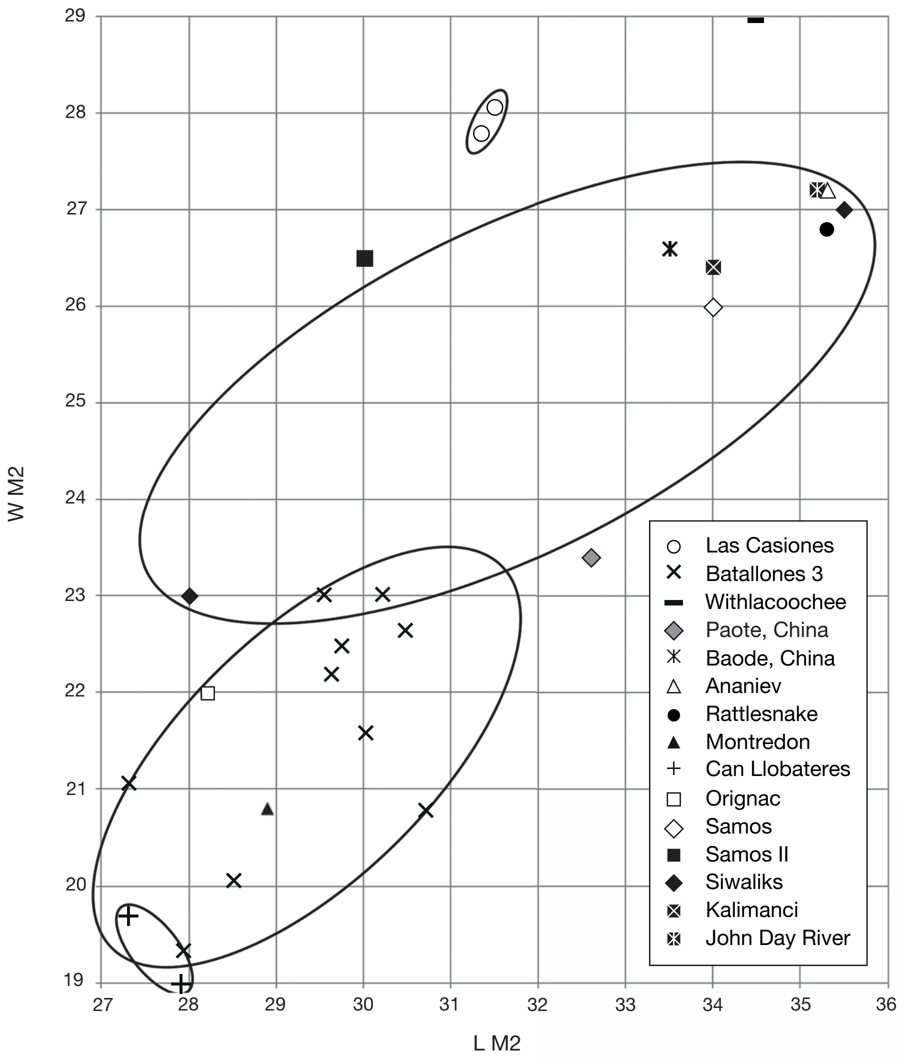

Fig. 6. — Bivariate plot of the M2 of different *Indarctos* Pilgrim, 1913 species from various sites.

P4 (Fig. 2A-C). Complete upper carnassial. Deeply wrinkled enamel. Well-developed parastyle with two ridges, one labial and one lingual. High paracone, almost flat in its lingual part but convex in the labial one. Metastyle lower than paracone, but more sectorial; wide at its base, with two cingula, a weak one in the labial part and a slightly more developed one in the lingual part. Where the two cingula join they create a distal pointed edge. The protocone is complex. It has three cusps, which grow taller towards its distal part, with the latter being the tallest, practically at the level of the notch between paracone and metastyle, and the only one partly surrounded by the labial cingulum of the cusp. The protocone occupies an intermediate position with respect to the paracone, and is projected lingually.

M1 (Fig. 2D). Very worn first upper molar, much more in the distal than in the mesial part. This kind of asymmetric wear is quite common in ursoids, and in this case prevents the description of many of the dental features. It is nearly square in shape. The contact facet for P4 is relatively large and concave instead of flat, while that for the M2 is located almost at the labio-distal corner of the tooth. Towards the labial side, between the paracone and the metacone, there is an expansion zone that widens towards the metacone; this structure has a slight vertical wear facet.

M1 (Fig. 2E-G). Molars with a clear quadrangular shape, almost as wide as long. The enamel has the typical young ursid roughness. It is barely worn and the roots were not completely formed before death and are not recovered. As in the worn M1, these two also have a medial-lingual thickening of the labial cingulum between the paracone and metacone. The paracone is larger (in both width and height) than the metacone. Both parastyle and metastyle are present, although these are very weak compared to the main cusps. There is a well-developed cingulum occupying almost all of the lingual face. The contact with P4 is vertical and straight. The protocone is large and cristiform. Distal to the protocone there is a robust hypocone, which is taller than the protocone, and although being the small-

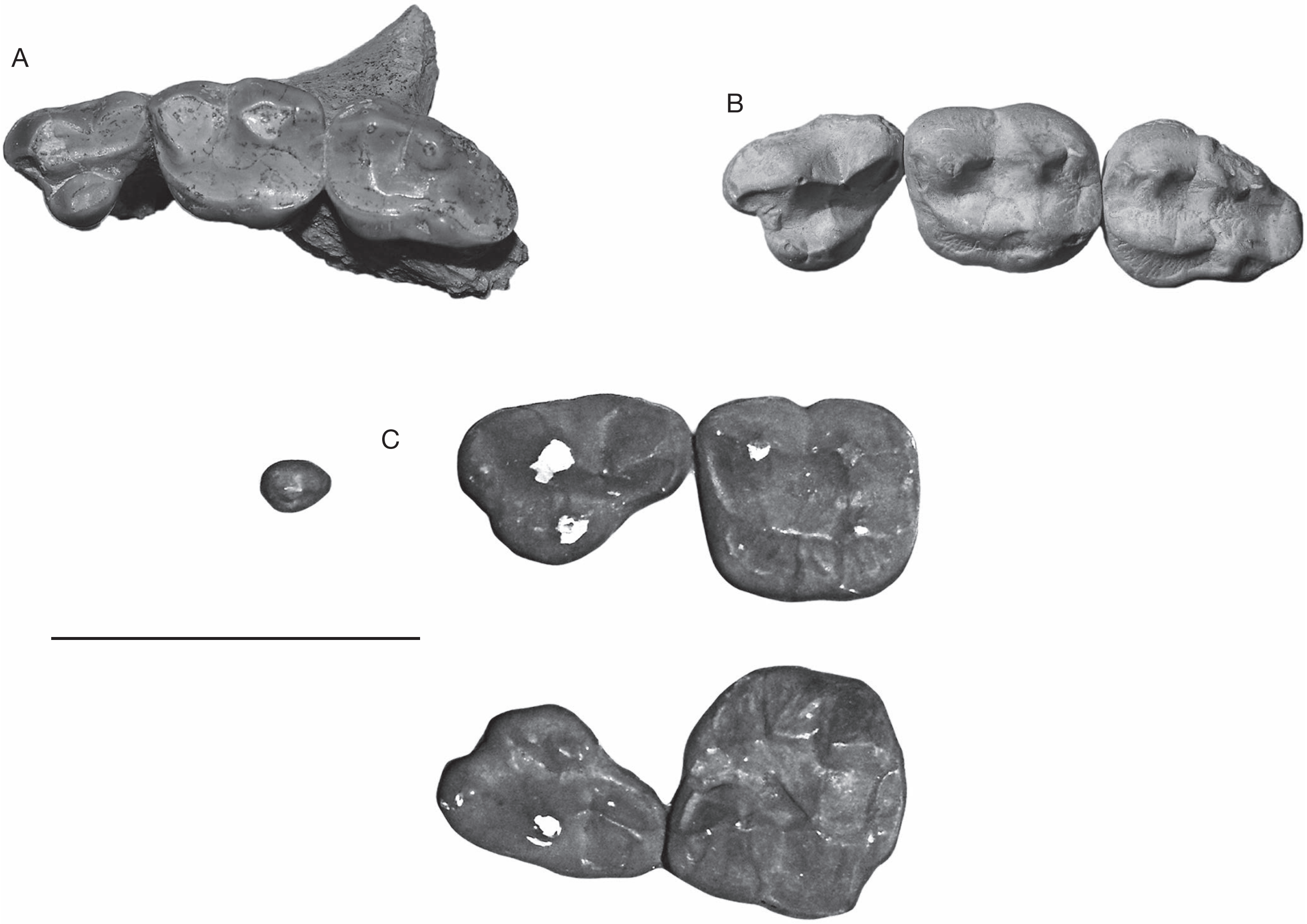

Fig. 7. — Other *Indarctos* species for comparison with *I. punjabiensis* (Lydekker, 1884) of Las Casiones: **A**, *I. vireti* Villalta & Crusafont, 1943; **B**, *I. arctoides* (Depéret, 1895) (from type locality); **C**, *I. punjabiensis* (syntype). All images are in occlusal view. Scale bar: 5 cm.

est of the four main cusps. Hypocone is more complex, having a ridge on each side. The mesial ridge is close to the protocone, whereas the lingual one joins the lingual cingulum. The medial one meets the ridge coming down the central valley of the tooth from the metacone and the distal ridge ends at the most distal edge of the tooth. In the labial side there is other cingulum, which is considerably thickened in the distal region.

M2 (Fig. 2F, H). A wide tooth, with large cingula on both in its labial and its lingual side, with the latter the most developed. In occlusal view the talon is slightly rotated labially while the labial cingulum is labially tilted, giving the teeth two different crushing surfaces. The tooth enamel is clearly rough, which is most evident on the lingual surface. The protocone is continued by the ridge that originates at the front of the paracone, continuing throughout the mesial part of the molar towards the lingual side, but not forming a clear parastyle. Unlike M1, the M2 protocone is slightly bilobed in its central part. The paracone is taller than the metacone although the difference is slightly smaller than in the M1. The talon is very rounded and relatively short, and although it joins the metacone, it has a more labial position. It has a ridge that runs from the hypocone to the metacone, forming a distal semicircle divided into at least six small cusps.

Lower Dentition

px (Fig. 2J). Biradicular premolar. Longer than wide. It has only one cusp in the center of the crown, with two cristids, one slightly mesio-lingual, which approaches the mesial edge, and other one distal.

Postcranial skeleton

Right Mc IV (Fig. 3). This metapodial has a robust general morphology. Epiphyses are wider than the diaphysis, the latter having a homogeneous width in dorsal view throughout its length. However, in lateral view, there is a difference in height because the distal part of the diaphysis is clearly flatter. The proximal epiphysis is robust, convex in the most proximal zone, the surface that serves as articulation for the unciform. Its contact facet for the Mc III has two lobes, a convex dorso-proximal one and a flat palmar-proximal one. The articulation for the Mc V has also two facets, a slightly convex dorsal one and a noticeably concave palmar one. The distal epiphysis is slightly wider and somewhat rounded in its dorsal view, thus being more flattened in lateral view.

SYSTEMATIC DISCUSSION

The fossil remains from Las Casiones show the following features in the dentition that clearly match the morphology of *Indarctos*:

1) A two-ridged parastyle on the P4. A mesially complex protocone;
2) Complex hypocone on M1;
3) Relatively short and robust Mc IV, with relatively large proximal and distal epiphyses that are equal in size. Medial and lateral contact facets of proximal epiphysis separate and distinct from proximal contact facet.

The fossil remains from Las Casiones are amongst the largest of the genus (Figs 4, 5 and 6), and in the Iberian Peninsula second only to the huge remains from Concud. Therefore, they are easily included in *Indarctos punjabiensis*, a species that was probably present in the Iberian Peninsula from MN10 and certainly from MN11: Masia la Roma 604, Terrassa, Crevillente 2, Concud, Rambla de Valdecebro 5 (Montoya *et al.* 2001; Alcalá *et al.* 2005; Abella *et al.* 2012, 2014).

COMPARISON WITH OTHER *INDARCTOS* SPECIES

Indarctos punjabiensis exhibits considerable morphological variability in the dentition, even within samples from the same site (Montoya *et al.* 2001), as shown by the measurements in Table 1 and the size comparison in Figures 4, 5, and 6. We can, however, distinguish it from other species of the genus on to the criteria presented below.

The remains from Las Casiones differ from *Indarctos vireti* (Fig. 7) in the following features (the holotype of this species is a mandible (Can Purull, Villadecavalls, Spain) so the comparison has been carried out using the upper dentition from Can Llobateres):

Overall, the dentition from Las Casiones is much larger than that of *Indarctos vireti*; the P4 of the latter is more elongated, without parastyle and much simpler in terms of the number of cusps in the protocone; the M1, although similar in cusp disposition, is more elongated in the Vallesian species, especially in the talon; the M2 is much more elongated in *I. vireti* than in the Las Casiones specimen.

The fossil remains from Las Casiones differ from the holotype of *Indarctos arctoides* (Montredon, France, MN10), and from the spectacular sample of *Indarctos arctoides* from Batallones 3 (Madrid, Spain) (Fig. 7) in the following features:

The dentition from Las Casiones is larger than that of *Indarctos arctoides*; the P4 of *I. arctoides* (same locality as the holotype) is already as wide as that of Las Casiones or relatively wider, due to the lingual widening of the wall between the paracone and metastyle; the parastyle is not as large and the protocone has fewer cusps, with only two cusps instead of the three in the P4 from Las Casiones; the M1 of both species are almost identical in shape, but the M2 from Las Casiones seems relatively much wider than that of the holotype of *I. arctoides*.

The dentition from Las Casiones is almost identical in size as that of the holotype of *Indarctos punjabiensis* (Hasnot Siwaliks, India. MN10-13) (Fig. 7). Both the P4 and M1 are very similar in morphology, though the paracone of P4 has fewer cusps in the holotype of *I. punjabiensis*. Comparison of the M2 from Las Casiones to that published by Pilgrim in 1914 under the name of *I. salmontanus* (now *I. punjabiensis*) leads to the conclusion that the latter is slightly more elongated, due to the lesser development of the labial and lingual cingula, but it has almost the same cusp disposition.

BIOSTRATIGRAPHY

As already mentioned, the fossil record of the genus *Indarctos* in the Iberian Peninsula covers much of the late Miocene. Thus, it is represented by *I. vireti* in the Vallesian (MN9 and MN10) of the Vallès-Penedès (Catalonia), by *I. arctoides* in the Vallesian (MN10) of the Batallones sites (Madrid) and by *I. punjabiensis* (formerly *I. atticus*) in the late Vallesian of Terrassa (Vallès-Penedès, Catalonia) and Masía de La Roma 604 (Teruel basin). It is also recorded from the early Turolian (MN11) of Crevillente 2 (Alicante), as well as in other Turolian (MN11 and MN12) localities from the Teruel basin. In addition, the range is now extended to the late Turolian or Ventian (MN13) also from the Teruel basin. More detailed information on the Spanish record of the genus *Indarctos* can be found in Montoya (1994), Montoya *et al.* (2001), Alcalá *et al.* (2005), Abella (2011) and Abella *et al.* (2013, 2014, 2015).

From a biostratigraphic point of view, the material of *Indarctos punjabiensis* in Las Casiones represents the youngest appearance of the genus in the fossil record of the Iberian Peninsula (and perhaps also of Europe), just before its replacement by the hemicyonid *Agriotherium*. Should be mentioned that the *Indarctos* record from Ananiev (Ukraine) could be more or less of the same age (Baryshnikov 2002). Recent works allow us to date, with relatively good precision, the moment of this substitution and its relationship to the faunistic events that took place during the Messinian, although prior to the Messinian Salinity Crisis.

The Las Casiones site lies within MN13, in local zone M2 of van Dam (1997), and van Dam *et al.* (2006: suppl. notes), where it is assigned an age *c.* 6.3 Ma. In addition, it is the reference site for the so-called First African-Iberian Dispersal (Gibert *et al.* 2013) because it records the FAD of Hippopotamidae in Western Europe from Africa. Furthermore, the entry of eastern immigrants, such as the genus *Plesiogulo* and *Hystrix depereti*, takes place during this period.

On the other hand, the FAD of the genus *Agriotherium* in Europe is recorded at the Venta del Moro site (Cuenca del Cabriel, Valencia) (Morales 1984; Montoya *et al.* 2006), with *A. roblesi* Morales & Aguirre, 1976. This deposit is located within MN13 in local zone M3, and a recent paleomagnetic study has allowed dating it to *c.* 6.23 Ma (Gibert *et al.* 2013). Because Venta del Moro also records the FAD in Europe of *Paraethomys* and *Paracamelus*, taxa most likely coming from North Africa, it is the reference site for the so-called Second African-Iberian Dispersal (Gibert *et al.* 2013). This dispersal coincides with the so-called '*Paraethomys* event' or 'Second Messinian mammalian event' of Agustí *et al.* (2006) and with

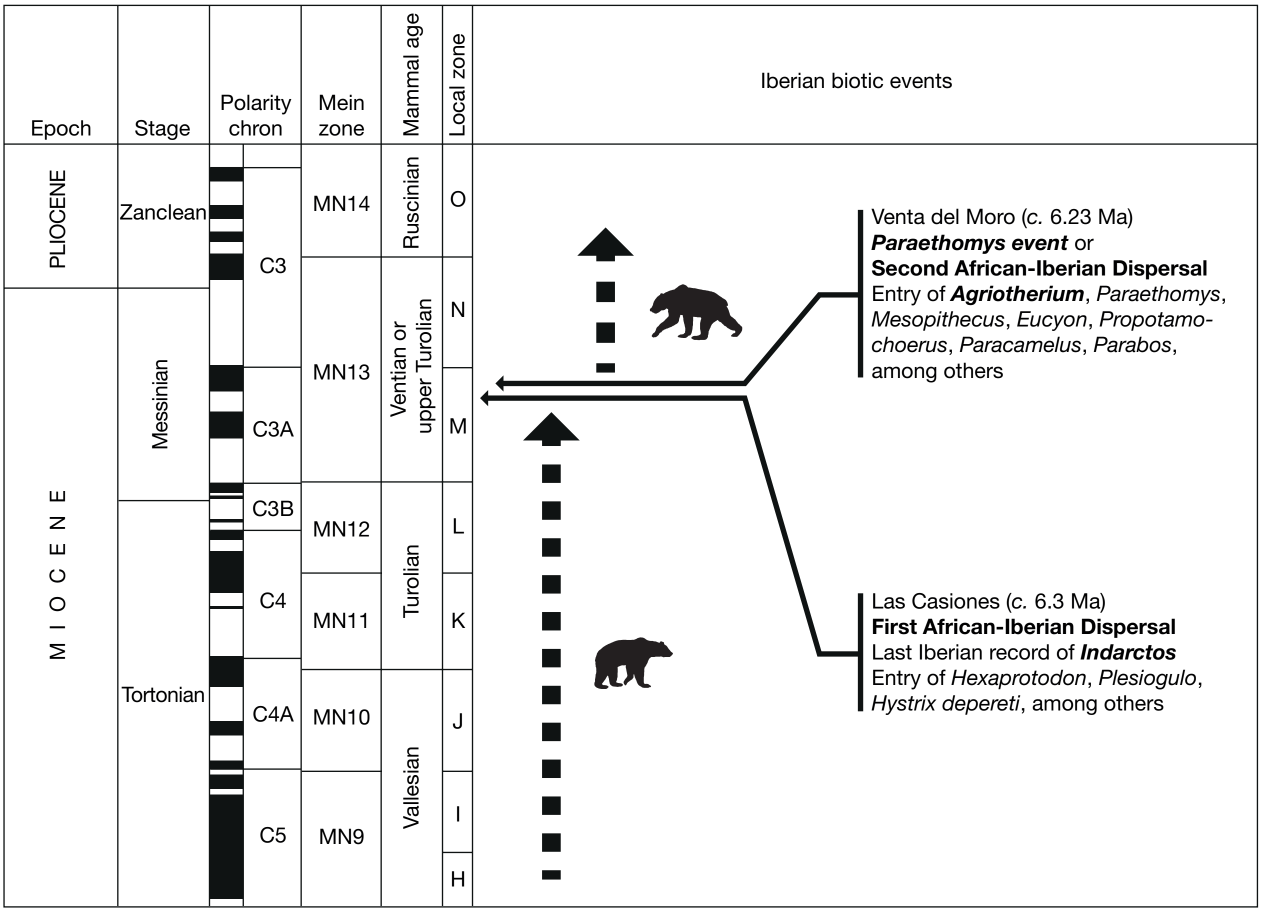

Fig. 8. — Biochronology showing the stratigraphic ranges of the genera *Indarctos* Pilgrim, 1913 and *Agriotherium* A. Wagner, 1837 in the Iberian Peninsula, related to the two biotic events recorded during the Messinian. Mammal ages and local zones according to Morales *et al.* 2013. Absolute age after Gibert *et al.* 2013.

the 'Third dispersal event' by Made *et al.* (2006). The fact that this faunal event has been evidenced, and named differently by different authors tells us of its importance.

The mammalian fauna with *Agriotherium* from Venta del Moro is, as far as large mammals are concerned, composed of a mixture of taxa already present in the Western European Turolian, together with a contingent of more than 50% that appear first in the fossil record of the Iberian Peninsula (Morales *et al.* 2011), and who are immigrants from the east or from Africa. Thus, the Euroasiatic provenance of *A. roblesi* cannot be disregarded. Therefore, the replacement of *Indarctos* by *Agriotherium* could be linked to this great faunal renewal event, which we now know took place 250 000 years before the onset of the Messinian Salinity Crisis (Agustí *et al.* 2006; Gibert *et al.* 2013) (Fig. 8).

FINAL REMARKS

Although some of the dental features may converge towards those present in some species of *Agriotherium* species, it seems clear that the studied dental remains represent a large-sized *Indarctos*, similar in both size and morphology to the syntype of *I. punjabiensis*. Moreover, the population from Las Casiones marks the upper range of the record of the genus *Indarctos* in the Iberian Peninsula and probably also in Europe. It belongs to the faunal assemblage prior to the entrance, at *c.* 6.23 Ma, of the rodent *Paraethomys* and many other immigrants, including the hemicyonid ursoid *Agriotherium*.

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