



Habitat preferences of European Middle Miocene omnivorous ursids

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***Indarctos* spp. were the first large-bodied bears with omnivorous tendencies. Two *Indarctos* fossils assigned to *I. arctoides* ssp. by Bernor, Feibel, et al. (2003) and Viranta and Werdelin (2003) show that the genus had a wide geographic range in Europe in the Middle Miocene and was represented by at least two contemporaneous species. Present work shows that the two species of *Indarctos* lived in a mixture of environments, and were not clearly separated into distinct habitats. *Indarctos* seems to have evolved during an interval of faunal turnover in Europe. The appearance of *Indarctos* coincided with an extinction of small omnivorous mammals and was accompanied by the appearance of other large omnivores.**

Modern bears (Ursidae) have an omnivorous diet. Only the polar bear (*Ursus maritimus*), which is a very late descendent of a brown bear (*Ursus arctos*) like ancestor (Kurtén 1964), is a specialized hunter. Nevertheless, the first large bodied ursids in the early Neogene were all carnivorous. Vallesian (Late Miocene, 11.2–9 Ma) *Indarctos* spp. were the first bears showing a tendency towards bunodont dentition, that is typical of modern Ursidae and a clear adaptation to omnivory. *Indarctos* was probably part of the ancestral stock that gave origin to the modern ursine bears. Hunt (1998) included *Indarctos* in Ursavini, which is a sister tribe for the tribes of the modern bears. Alternatively, *Indarctos* is a sister taxon of *Ursus* and in the same clade with the modern great panda (*Ailuropoda melanoleuca*) (Ginsburg and Morales 1998; Ginsburg 1999).

Petter and Thomas (1986) reviewed the *Agriotherium* and *Indarctos* radiations in the Old World. They considered that there were only two *Indarctos* species in the Old World: *I. arctoides* (including subspecies *I. a. vireti* and *I. a. arctoides*) and *I. atticus* (*I. a. atticus*, *I. a. lagrelii*, and *I. a. punjabiensis*). *I. arctoides* had a limited distribution, occurring only in western and central Europe. *I. atticus* spanned from western Europe to China. According to this hypothesis *I. arctoides* was a forest dweller in the Vallesian (11.2–9 Ma) and *I. atticus* was associated with steppe and savanna in the Turolian (9–5.3 Ma). The two were considered to be chronospecies, with the open habitat *I. atticus* evolving from the closed habitat *I. arctoides*.

Material and methods

I extracted all mammalian species occurrence data from the NOW (Neogene of Old World) database (Fortelius, Andrews, et al. 1996) for Vallesian (MN 7/8–9) and Turolian (MN

10–12) fossil localities. The entire database is available online (www.helsinki.fi/science/now).

I recorded all the occurrences of the *Indarctos* spp. in western Eurasia and compared ecomorphological and taxonomic compositions of the mammalian faunas between contemporaneous localities with and without *Indarctos* spp. All localities from Vallesian and Turolian (MN 7/8–MN 12) with more than four recorded species were included. All mammal orders except Lagomorpha, Rodentia and Chiroptera were included. Small mammals were excluded because their ecomorphology is still wanting. Student's t-test was used to test for the significant differences between faunas.

All the species were classified as either plant eaters, animal eaters, or omnivores (NOW data field Diet 1). Plant eaters were further classified as hypsodont or non-hypsodont. A hypsodont dentition is defined as a dentition with molars with antero-posterior length exceeded by dorsoventral height (NOW data field tooth crown height).

Omnivore species (all members of Artiodactyla or Carnivora) were put in size categories based on their estimated body mass. Three categories were used: small (<20 kg), medium (20–80 kg), and large (>80 kg). Body mass estimates for the carnivores are based on the lower carnassial (Van Valkenburgh 1990) and performed by me. Body mass estimates for Artiodactyla are based on molars and performed by M. Fortelius (Fortelius, Made et al 1996). *Indarctos* were omitted from all analysis. All *Indarctos* localities were analyzed first collectively and then separately for each *Indarctos* species (*I. arctoides* vs. *I. atticus*) and geological age (Vallesian vs. Turolian). Following the taxonomy by Petter and Thomas (1980), I combined all the small *Indarctos* spp. (*I. vireti* and *I. arctoides*) into *I. arctoides* and large species *Indarctos* spp. (*I. atticus* and *I. anthracitis*) into *I. atticus*.

Results

The early Vallesian (11.2–9.5 Ma) is characterized by a decrease of medium and small-bodied omnivores and increase of large-bodied species (Fig. 1). At the same time the total number of all mammal species increased. This is also when the first *Indarctos* species appeared in the record. The increase of large omnivores continued until the beginning of the Turolian (9.0 Ma), when total numbers of omnivores started to decline. The localities with a record of *Indarctos* have an overall higher species count than localities without *Indarctos*, although the

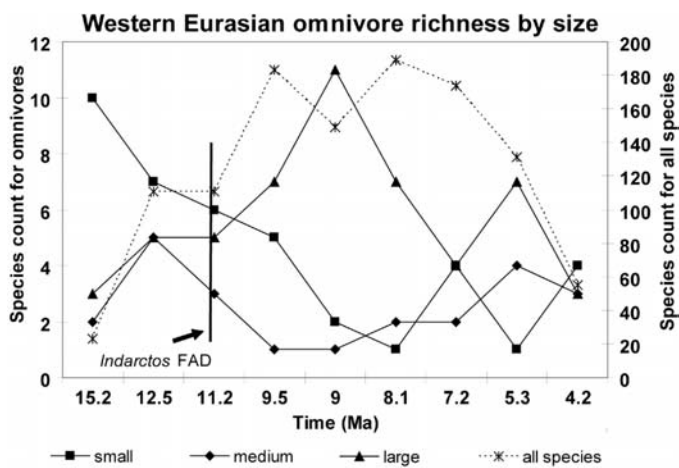


Fig. 1. Mammalian species richness in Middle and Late Miocene Europe. All species = all macromammals, small = small bodied omnivores, body mass <20 kg, medium = medium omnivores, 20–80 kg, large = large omnivores, >80 kg.

numbers of herbivores are almost the same (Table 1). Numbers of omnivores are higher, even when it is measured as a proportion of the total species count. Of the plant eaters, numbers of hypsodont species are similar in localities with and without *Indarctos*.

When the *Indarctos* localities of the two time periods or localities with different *Indarctos* species are contrasted, no significant differences arise (Tables 2 and 3). One locality (Dorn Dürkheim, MN 12) has a record of both *I. arctoides* and *I. atticus*. This locality was omitted from this analysis.

Table 1. Average mammalian species counts for NOW database localities with more than four species occurrences. Localities with *Indarctos* and without *Indarctos* are compared. Similarities are tested using Student's t-test. All species = all macromammal species, omnivore prop. = relative proportion of omnivores, hypsodont=hypsodont herbivores, hypsodont prop.=relative proportion of hypsodonts in herbivores.

	All species	Herbivores	Omnivores	Omnivore prop.	Hypsodonts	Hypsodont prop.
Localities w/ <i>Indarctos</i>	19.63	10.16	2.32	0.19	1.55	0.19
Localities w/o <i>Indarctos</i>	12.17	8.39	1.05	0.12	1.30	0.16
p-value	0.001	0.193	0.000	0.041	0.412	0.392

Table 2. Average mammalian species counts for Vallesian and Turolian NOW localities with *Indarctos*. For abbreviations see Table 1.

	All species	Herbivores	Omnivores	Omnivore prop.	Hypsodonts	Hypsodont prop.
Vallesian localities	22.71	11.71	3.29	0.21	1.44	0.18
Turolian localities	17.83	9.25	1.75	0.18	1.64	0.19
p-value	0.464	0.466	0.159	0.681	0.755	0.930

Table 3. Average mammalian species counts for NOW localities with the smaller and primitive *Indarctos* (*I. arctoides*) and the larger form (*I. atticus*). For abbreviations see Table 1.

	All species	Herbivores	Omnivores	Omni. prop	Hypsodonts	Hypsodont prop.
Localities w/ <i>I. arctoides</i>	22.88	10.88	3.50	0.25	1.14	0.14
Localities w/ <i>I. atticus</i>	19.00	10.25	1.67	0.14	1.67	0.21
p-value	0.553	0.848	0.071	0.113	0.415	0.433

Discussion

Two new *Indarctos* reports confirm a wider spatial and temporal distribution to *Indarctos* spp. than previously thought. *I. arctoides* has a temporal range from MN 7 to MN 12 (12.5–7.1 Ma) and *I. atticus* from MN 10 to MN 13 (9.5–5.3 Ma). Both species thus show overlap in temporal existence. In light of the Hatvan and Sinap *I. arctoides* findings it is apparent that *I. arctoides* and *I. atticus* are separate species, not chronospecies. In the present data even the habitat separation between the two is not obvious. Both species co-exist with a similar array of hypsodont herbivores. Hypsodonts are typical indicators of open environments.

Sinap locality 12 has a diverse fauna indicative of mixed vegetation. Several elements of more open habitat as well as forest are present in the ungulate fauna (Bernor, Scott, et al. 2003; Gentry 2003). Other species considered requiring forested areas are present too, such as a hominoid species, *Ankarapithecus meteai* (Alpagut et al. 1996). Geology reveals a riparian system for Sinap locality 12 (Lunkka et al. 2003).

The Hungarian Hatvan locality shows a mixture of species also. It includes primates and chalicotheres, both typical forest dwellers, but also hipparion, a typical inhabitant of more open areas. Hatvan has been interpreted to present a mixed forested woodland habitat that has some elements of the Pikermian fauna (Bernor, Feibel, et al. 2003).

Analyses in this report show that the appearance of *Indarctos* occurs at a time of change in omnivorous mammalian fauna in Europe. Smaller species are replaced by larger bodied ones. At a same time the diversity of all species increases. This has been shown to reflect a change in beta diversity rather than alpha diversity; in other words, western Eurasia became less

provincial and the faunas of different regions more similar (Fortelius, Werdelin, et al. 1996).

The origin of *Indarctos* appears to be part of a bigger transition in the fauna. The fact that the localities with *Indarctos* have higher species richness could mean that genus thrived in high diversity communities. However, this might also be due to sampling bias, as rare species are more likely to be discovered in rich fossil localities. The indication that localities with *Indarctos* have fewer herbivores and more omnivores is of interest. It may actually be an indication that *Indarctos* lived in environments that supported relatively more diverse omnivore faunas.

On the other hand, hypsodont herbivores are not rarer in the localities with *Indarctos*. In fact, localities with *Indarctos* have slightly more hypsodont species although this is not significant. An abundance of hypsodont species indicates open environments because high crowned teeth are an adaptation to various factors, which all are associated with dry climate and open landscape (Fortelius 1985; Janis 1988).

Today's omnivorous carnivores live in different types of environments. Large omnivorous carnivores are especially abundant in temperate forests with a single tree canopy (Viranta and Andrews 1995). Van Valkenburgh (1989) explained the abundance of omnivores in modern temperate Yellowstone by hibernation and food switching. Omnivores either hibernate through the lean season or switch to a more carnivorous diet. A scarcity of large omnivores in richer environments was explained by competition with ungulate and primate omnivores (Van Valkenburgh 1989).

It is apparent from this study that *Indarctos* already was flexible in its habitat use. Hibernation is unlikely to have originated in the Miocene when temperatures still were relatively warm. Seasonality however increased, and *Indarctos* may have been adapted to switch between a plant dominated and meat dominated diet.

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