

The European descendants of *Ursus etruscus* C. Cuvier (Mammalia, Carnivora, Ursidae).

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ABSTRACT

This paper deals with a review of the Pleistocene Bears origin, evolution, and stratigraphical distribution.

U. ruscinensis DEP. could be considered the common ancestor of all the European Pleistocene Bears, as the source of two evolutive lineages: one the more conservative, *U. mediterraneus* F. MAJOR, and another the more evolved which starts with *U. etruscus* G. CUV. and gave origin to two evolutive trends: the today vanished speloid one (*U. deningeri* V. REICH, and *U. spelaeus* ROS.-HEIN) and the still living arctoid one which is represented today in the true brown bear (*U. arctos* LIN.).

U. minimus DEV.-BOUILL. does not constitute a link between *U. ruscinensis* and *U. etruscus*: it is a lateral branch, in the general evolutionary schedule, more evolved than *U. etruscus*.

Recent findings of arctoid *Ursidae* remains in the Iberian Peninsula, ranging from Lower to the Middle (Upper) Pleistocene, allowed us to think that the general migration southwards of an Asiatic Brown bear population during the Würm glacial period beginning, superimposed on an autochthonous European Brown bear population (prearctoid): *U. prearctos* BOULE, which is the probable ancestor of the polar bear (*U. maritimus* PHIP.).

Key words: Ursidae, Phylogeny, Stratigraphy, Pleistocene, Europe.

RESUMEN

En este trabajo se revisan el origen, evolución y distribución estratigráfica de los osos del Pleistoceno.

U. ruscinensis DEP. puede considerarse como el ancestro común: de él derivaría un grupo muy conservador (*U. mediterraneus* F. MAJOR) y otro más evolucionado *U. etruscus* G. CUV. que será el origen de las dos principales líneas evolutivas de Ursidos pleistocenos en Europa: la línea espeloida (*U. deningeri* V. REICH. y *U. spelaeus* ROS.-HEIN.), muy bien conocida, y la línea arctoide, cuyo representante actual es *U. arctos* LIN.

U. minimus DEV.-DEBOUILL. no constituye un estadio intermedio entre *U. ruscinensis* y *U. etruscus*, debe tratarse de un representante lateral dentro del esquema evolutivo general, más evolucionado que *U. etruscus*.

Hallazgos recientes en la Península Ibérica, de osos arctoides con edades que van desde el Pleistoceno Inferior al Medio (Superior), permiten pensar que la gran migración hacia el sur de parte de la población asiática de oso pardo, que tuvo lugar a comienzos del Würm, se superpuso a una población europea autóctona de oso pardo (prearctoide): *U. prearctos* BOULE, de la cual derivó el oso polar (*U. maritimus* PHIP.).

Palabras clave: Ursidos, Filogenia, Bioestratigrafía, Pleistoceno, Europa.

1. FOREWORD

In spite of the fact that there are a very large amount of papers dealing with Pleistocene bears, there remain some gaps in the phylogeny and stratigraphical distribution of the different spe-

cies. To solve this will be the goal of this article.

2. PHYLOGENY

The genus *Ursavus* could be considered the common ancestor of the *Ursus* genus, the first representatives of which appeared at the Upper Pliocene.

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Figure 1.—Phylogeny and stratigraphical distribution of *Ursidae*. Logarithmic scale for time.

The *Ursavi* were Carnivora with a typical enough Ursoid dentition: there is a certain cusp duplicity in molars and the lower carnassials show a cutting-like paraconid, while the metaconid is very small and placed backward. They were not too different from true bears, but smaller, like the wolverine (*Gulo gulo*). This genus had a full Miocene development.

The first relatively well documented bear species are *Ursus ruscinensis* DEPERET and *Ursus minimus* DEVEZE-DEBOUILLET. Their first appearance was during the Pliocene.

U. ruscinensis was found in the Ruscinian locality of Perpignan (France). Very close to this species, if not the same, are *Ursus minutus* GERVAIS from the Pliocene of Montpellier (France); *U. wenzensis* STACH from the Polish site of Weze, of similar age to Montpellier, and *Ursus (Protursus) boeckii* SCHLOSSER from the Pliocene lignites of Barót-Kôpeck (Hungary) which in FICCARELLI's opinion (1979) is a *U. ruscinensis* synonymous.

Along the Lower Villafranchian, Villarroja (Spain), there appeared, for the first time, *Ursus etruscus* G. CUVIER, which reached its highest ecological development in the Middle Villafranchian: Val d'Arno (Italy), Tegelen (The Netherlands), Saint Vallier (France), La Puebla de Valverde (Spain) and a certain number of other minor localities. This species disappeared at the Upper Villafranchian, Venta Micena (Spain), and it is considered to be the ancestor of the main European Pleistocene bears.

Although it is possible that *U. minimus* and *U. etruscus* were related to *U. ruscinensis*, it seems difficult that they are both related, in spite of the fact that *U. minimus* has been considered an *U. etruscus* ancestor species, STEHLIN (1933), THENIUS (1959), KURTEN (1975), TORRES (1984, 1986). BERZI's analysis (1966) of Gaville *U. minimus* mandible morphology, and of this author's own data on unpublished material from Layna, proved that both species were unrelated, showing *U. minimus* mandibular characteristics more evolved than in *U. etruscus*; FICCARELLI (*op. cit.*) agrees on an early extinction of the former, but thought that this had more carnivorous characteristics than *U. ruscinensis*.

In the Cromer, for the first time, a bear of undoubted speloid characteristics was detected

with a heavily built skeleton and bunodont-sectorial cheek-teeth morphology: it is the Deninger bear, *Ursus deningeri* VON REICHENAU, which would be superseded by its descendent: the cave bear, *Ursus spelaeus* ROSEN-MÜLLER-HEINROTH, which finally vanished at the end of Würm without further descendants. In this species those morphological characteristics which were pointed in the Deninger bear appeared exaggerated.

In the Cromer, and until the Riss, there is a more conservative evolutionary lineage representing: *U. prearctos* BOULE, which retained very close similarities with its ancestor *U. etruscus*. In the Würm this species would be substituted by the still living brown bear: *Ursus arctos* LINNEO.

Although they will not be studied in this paper it is interesting to briefly cite a group of small sized Pleistocene bears very closely related to the *U. ruscinensis*, also known as *Plionarctos* group, of which the best known, and probably the only one representative was *U. mediterraneus* FORSYTH-MAJOR, in STEHLIN (1933)'s opinion, which KURTEN and POULIANOS (1977) called «European black bear», assuming a narrow parallelism with the Thibet bear *Ursus tibetanus* G. CUVIER.

The bear of Achenheim (France) *Ursus schertzi* DEHM, must be considered as a *U. mediterraneus* synonymous, in spite of MOTTI (1951)'s opinion that it was an arctoid lineage relation, like an intermediate stage between the brown bear of Repolust and *U. priscus*: «Der Braunbär der Repolust Höle also zwischen *Ursus schertzi* DEHM und *Ursus priscus* GOLDFUSS der Steiermark...».

Others representatives of this group of small sized bears, and probably *U. mediterraneus* synonymous too, are: *U. (Plionarctos) stehlini* KRETZOI from Gömbasszog (Hungary) of Riss (?) age, *Ursus (Plionarctos) telonensis* BONIFAY of Cimay (France) of Mindel age and *Ursus sackdillingensis* HELLER from Sackdillinger Höle (Austria) of doubtful age (Lower- Middle Pleistocene?).

The *Plionarctos* genus can not be employed in European bear description, mainly because it was employed by FRICK (1926-1929) to describe an *Ursus (Tremarctos) ornatus* F. CUVIER ancestor: *Ursus (Plionarctos) edensis* FRICK, it

was employed later by KRETZOI (1970-1971) as «*Plionarctos-group*» to describe some small sized species that he thought similar, ERDBRINK (1953), to *Ursus (Helarctos) malayanus* RAFFLES.

In short: since the Upper Villafranchian there has been a relatively net species distribution: some were big sized, *U. etruscus* derivated, coexisting with others clearly smaller and closely related to its ancestor *U. ruscinensis*. It is not necessary to invoke an *U. etruscus* invasion, as was suggested by FICCARELLI (*op. cit.*, p. 168): «Col Villafranchiano medio-superiore l'*Ursus etruscus* invade larga parte dell'Eurasia...». This species was already all over since the Lower Villafranchian, although its demographical boom took place at the moment indicated by the author.

There is also a co-existence of two evolutive lineages apart from the residual presence of *U. mediterraneus*: since the Cromer and until the Riss it was composed by *U. deningeri* and *U. prearctos*, since the Riss it was composed of *U. spelaeus* and *U. prearctos*. Later, during the Würm, *U. arctos* substituted *U. prearctos*. The former was an asiatic immigrant which at the end of Pleistocene times colonized the whole of Europe, North America and the Circunmediterranean border of Asia and Africa: KOBAYASHI (1955), KURTEN (1969), TORRES (1988). This emigration took place from a supposed species «ancestral stock» represented in the Niowan and Chou-K'ou-Tien materials, ZDANSKI (1928) and TEILHARD DE CHARDIN (1938), although in the opinion of PEI (1934, 1938) and ERDBRINK (*op. cit.*) the Chou-K'ou-Tien bear was related to the Deninger bear. An opposed opinion to *U. etruscus-U. arctos* relationship can be seen in ZAPFE (1946).

An European bear population development with net carnivorous affinities could explain the appearance of *U. maritimus* PHIPPS without needing an asiatic brown bear ancestral stock, KURTEN (1969, p. 25): «The ancestral population probably lay within the Asiatic Brown Bear population of this time, perhaps in the vast Siberian area».

In short: from an ancestral species, *U. etruscus*, two different evolutive lineages were derived: one, more evolved, changed into the speloid group: *U. deningeri* and *U. spelaeus*. The

other, more conservative (arctoid)), was composed of *U. prearctos* and *U. arctos*, showing a similar, but quite less marked, tendency; *U. maritimus* can be explained as result of an insularization period effecting a prearctoid population during an advance of the ice cap period.

A description and discussion of the six species before mentioned will be the central objective of the following.

3. DESCRIPTION AND DISCUSSION OF THE SPECIES

Ursus etruscus G. CUVIER 1823

Synonymous: *Ursus cultridens* NESTI 1826, *Thalassarctos etruscus* AIRAGHI 1922.

As stated before, this species appeared at the Lower Villafranchian (Villarroya), reached its population peak at the Middle Villafranchian (Val d'Arno, Saint Vallier) and disappeared during the Upper Villafranchian (Venta Micena, Spain).

It is anatomically characterised by a notably sized skeleton when compared with *U. ruscinensis*. In the humerus it is possible to observe a still developed entepicondilar foramen, a characteristic that links this species to *Ursavus*. It is moderately brachipodial, there are small articular facets in carpus and tarsus bones and the metapodial bones are slender.

This species usually shows a dental formula identical to *Ursavus*:

I	1, 2, 3	C	1	P	1, 2, 3, 4	M	1, 2
	1, 2, 3		1, 2, 3		1, 2, 3, 4		1, 2, 3

There is a single cheek teeth morphology, and its cusps are strongly convergent towards the inner part of the teeth. In the first upper molar there is a relatively small transversal development of the talus. When compared with the anterior lobe of the teeth and the heel of the second upper molar, it is relatively short. The fourth lower premolar is single built with a protoconid rising in the center of the crown. The first lower molar is also very simple and its paraconid looks like that of *Ursavus*, the metaconid is almost negligible and backward. The

third lower molar crown is almost circular shaped, without lateral troughs.

It seems highly possible that this species would be opportunist as is suggested by its having colonized fluvial regions (Valdarno, Italy), marshes (Tegelen, Holland), lacustrine areas (Venta Micena, Spain), arid sabana-like zones (La Puebla de Valverde, Spain) and steppes (as suggested by loess deposits from Saint Vallier (France)).

Ursus deningeri VON REICHENAU 1906

Synonymous: *Ursus savini* ANDREWS 1922, *Ursus arctos spelaeus* ERDBRINK 1953, *Ursus deningeri hundsheimensis* ZAPPE 1940, *Ursus süszenbornensis* SOERGEL 1912, *Ursus gombaszögensis* KRETZOI 1941, *Ursus etruscus gombaszögensis* KRETZOI 1945, *Ursus deningeri suevicus* KOBAY 1951, *Ursus arctos* (Hundsheim) FREUDENBERG, *Ursus taubachensis* RODE.

This species marks a dramatic change when compared with its ancestor *U. etruscus*: the skeleton became more heavily built, mainly at the bone epiphysis, while the diaphysis are still slender. There is a net length decrease in first metacarpals and metatarsals and an enlargement of the area of articular facets of tarsal and carpal bones articular facetts, which in some cases result merged.

The dental formula is simpler than in *U. etruscus*:

$$\begin{array}{ccccccc} 1, 2, 3 & & 1 & & (1), (3), 4 & & 1, 2 \\ I & \frac{\quad}{\quad} & C & \frac{\quad}{\quad} & P & \frac{\quad}{\quad} & M & \frac{\quad}{\quad} \\ 1, 2, 3 & & 1 & & (1), (3), 4 & & 1, 2, 3 \end{array}$$

That is: the second premolars are always absent, but the first and/or the third can randomly appear.

There is an important change in the dental morphology too and the old sectorial structure is changed into a very marked bunodontism. The first upper molar talus is wider than the trigon and there is a relative elongation on the second upper molar heel, where narrow forms dominate. In the paraconid-protoconid region of the fourth lower premolar there appear many cusplets and in the first lower molar the paraconid shows a morphology far enough from those of *Ursavus*,

and the metaconid has grown and moved towards the anterior part of the tooth. There is also a net length augmentation of the third lower molar, having frequent troughs on both sides of the tooth as in *U. etruscus* and is covered by cusplets. In spite of the appearance of strong speloid characteristics it is not infrequent, in large populations data to find 'atavistic' cases showing older morphologies.

Because of its high morphological variability German authors wrote about a «deningeri Formenkreis» and the French ones about «groupe deningeri». Some subspecies have also been defined, here they are considered as synonymous because they need a revision: *U. deningeri savini* ANDREWS (Bacton Forest, England), *U. d. suevicus* KOBAY (Jagsthausen, Germany), *U. d. hundsheimensis* ZAPPE (Hundsheim, Germany), *U. d. süszenbornensis* SOERGEL (Süssenborn, Germany). *U. d. romeviensis* PRAT (La Romieu, France) appears as the only recently described *U. deningeri* subspecies and represents a lateral branch of the normal species. This species appeared along the Cromer, KURTEN (1959), disappearing at the end of the Riss, BONIFAY (1971). In PRAT and THIBAUT's (1975) opinion they disappeared in La Romieu Cave at the Riss I while in the Riss II sediments there are remains of a *spelaeus*-like bear.

Although there are no doubts about the role played by this species as the cave bear ancestor, it seems probable that there was a development of lateral groups not directly linked with *U. spelaeus*, this is KOBAY's (1951, p. 403) opinion about *U. deningeri suevicus*: «Cette sous espèce ne paraît pas être l'ancêtre immédiat de l'ours des cavernes mais plutôt se trouver sur un rameau latéral...».

Although usually this species remains have been found in caves (that is: related to karst on calcareous rocks) it is interesting to note that in the oldest sites they are linked to open air environments, fluvial related in some cases, as Bacton Forest Bed (England), Cromer Forest Bed (England), Hundsheim (Germany), Mauer (Germany) and Süssenborn (Germany).

Ursus spelaeus ROSENMÜLLER-HEINROTH 1794

Synonymous: *Ursus arctoideus* BLUMENBACH 1799, *Ursus pitrori* DE SERRES 1930,

Ursus metoposcainus DE SERRES 1830, *Ursus neschersis* CROIZET 1839, *Ursus spelaeus major* SCHMERLING 1833, *Ursus giganteus* SCHMERLING 1833, *Ursus fornicatus maior* SCHMERLING 1833, *Ursus fornicatus minor* SCHMERLING 1833, *Ursus leodiensis* SCHMERLING 1833, *Ursus planus* OKEN, *Ursus spelaeus odessanus* VON NORDMANN 1858, *Ursus spelaeus raza minor* GAUDRY y BOULE 1892, *Ursus ligusticus* ISSEL 1885, *Ursus spelaeus var. ligustica* ISSEL 1890, *Ursus spelaeus var. sibyllina* FRAAS 1899, *Ursus dentifricus* MEYER, *Ursus ferreo-jurassicus* JAGER, *Ursus prespeleus* OSBORN, *Ursus Gaudryi* FILHOL, *Ursus spelaeus var. hercynica* RODE, *Ursus spelaeus forma nonata* EHEREMBERG 1935, *Spelaerctos spelaeus* BORSSIAK 1931.

There is a very important reduction in the number of premolars in this species, its dental formula being as follows:

$$\begin{array}{ccccccc} 1, 2, 3 & 1 & 4 & & 1, 2 & & \\ I & \text{---} & C & \text{---} & P & \text{---} & M & \text{---} & \\ 1, 2, 3 & 1 & 4 & & 1, 2, 3 & & \end{array}$$

This reduction in the number of teeth was accompanied by an enormous augmentation in the size of the premolars and molars, whose cusps are now more complicated and vertical. There is noticeable metrical growth in the total length of the fourth upper premolar, the first upper molar heel width, the second upper molar talus, length, the width of the fourth lower premolar, the talonid width in the first and second lower molars and a general size augmentation of the third lower molar. At the same time there is a shortening in the paraconid- protoconid distance (it marks the cutting portion of the teeth) in the first lower molar.

There are important changes in the skeleton too: an augmentation of the skull volume (in spite of intense pneumatization), the mandible *ramus ascendentis* became vertical and a general growth in the relative transversal measurements of postcranial bones (both diaphysis and epiphysis). In carpus and tarsus bones there is some growth and a frequent fusion of articular facets. The first metacarpal and metatarsal became relatively shorter than in *U. deningeri*.

This species seemed to have more morphological uniformity than its ancestor the Deninger

bear, so they only have a certain systematic significance *U. spelaeus var. hercynica* RODE., also known as, «Alpinenkleinenformen», the steppa bear from Krasnodar (URSS) and a strange vasque subspecies *U. s. parvilatipedis* TORRES 1991, characterized by extremely short and broad paws. It is necessary to take into account the enormous intersexual variability of this species, which appeared in a more or less marked way in the skeleton and dentition. There is a very high intraspecific variability too, of which a typical example was composed by a cave bear skull from Gaylenreunth employed by GOLDFUSS (1823) to describe a new species: *U. arctoides*, and is only a dolicocephalous extreme of a population with more normal brachicephalous representations, CORDY (1972). During Ontogeny there are also a lot of astonishing changes in skull morphology, TORRES (*op. cit.*).

The cave bear appeared at the end of Riss times, and vanished without further descendants at the end of the Würm III or a bit later, ALTUNA (1984).

In spite of the fact that this species was apparently linked to karstic zones, it also colonized fluvial — swampy zones, like the Brown Ridge soil in the North Sea where fishermen trap (in their nets) cave bear bones. It has been found also in steppe zones and in high mountain regions over 2.500 m.

Ursus prearctos BOULE 1919

Synonymous: *Ursus priscus (pro parte)*, *Ursus arctos (pro parte)* *Ursus prearctos* MIR y SALAS 1976.

This species has many affinities with its immediate ancestor *U. etruscus*. It has a noticeably marked dental conservatism in the oldest material where the second premolar still remains. This is usually absent in more modern material, where some of the other two remaining first premolars (first or third) could also be absent:

$$\begin{array}{ccccccc} 1, 2, 3 & 1 & 1, (2), 3, 4 & & 1, 2 & & \\ I & \text{---} & C & \text{---} & P & \text{---} & M & \text{---} & \\ 1, 2, 3 & 1 & 1, (2), 3, 4 & & 1, 2, 3 & & \end{array}$$

There is a certain, not profound, change in molar and premolar morphology, when compared with that of *U. etruscus*: the second upper molar heel became longer and was full of cusplets, in *U. etruscus* it was rudely draped. At the lower molars there is a limited duplication of some

cusps that become slightly verticalized, in relation with the convergency towards the antero-posterior axis of the teeth that appeared in *U. etruscus*, but are still convergent when compared with *U. arctos* ones. In the lower carnassial it is possible, in some cases, to observe *Ursavus*-like morphologies, which are absent in the majority of the other cases.

In the postcranial skeleton there is a visible augmentation of robustness.

This species creates some problems, in ERDBRINK (*op. cit.*): «In fact BOULE's theory that this small bear, which he described as *U. prearctos*, forms the link between the real *U. etruscus* and the Pleistocene Brown bear, *U. arctos* (with many sinonimia) does not seem improbable to me...». This species was first described by BOULE (1906) from the Grotte du Prince (Italian Liguria) material from bones and teeth as having an *etruscus*-like aspect, and being small sized. The author also found some remains of a bigger brown bear that was thought to be from *U. pris-cus*. Later BONIFAY (1965) ratified this species but also thought that there were two coeval brown bears of different sized species, pp. 69-70: «Il semble qu'à la Grotte du Prince nous soyons en présence de deux 'species': l'une l'ours brun typique qui est la mieux représentée; l'autre un petit ursidé que ne paraît pas être la forme de transition éminemment variable décrite par M. Boule». TORRES (1984) found that all this material, both big and small sized, were from a unique bear population. Size differences can be explained as sexual dimorphism reflect, with metrical relationships quite different from those of the recent brown bear population of the Iberian Peninsula. RENAULT-MISKOVSKY (1986) estimates an age of 85000-80000 years for the bony breccia underlying to tyrrhenian age marine deposits.

The oldest iberian material came from Gran Dolina, Atapuerca (Burgos). This paleontological locality was placed by the author in the Günz, TORRES (*op. cit.*). More recent datings placed it in the lower Cromer or a bit older, GIL et. al. (1987).

There are some remains of Mindel age from Mollet Racó (Banyoles, Girona) first described by MIR and SALAS (1976).

The most recent material comes from Pinilla del

Valle (Madrid), cited by ALFEREZ et. al. (1982), first described by TORRES (1984), later ALFEREZ et. al. (1985) published a skull from this site, of Uppermost Riss or Eem age, as *Ursus* sp.

Outside of Spain *U. prearctos* has been found in Mont Maurin (France), De SAINT PERIER (1922), it is similar in age to the one from Gran Dolina; in the Grotte du Prince, BOULE (1906), BONIFAY (*op. cit.*) a bit older than Pinilla del Valle. PRAT and THIBAUT (*op. cit.*) found in old levels an archaic brown bear p. 39: «...nous sommes en présence d'une forme arctoïde primitive qu'il faut peut être rapprocher d'*Ursus prearctos* M. BOULE... un Ours brun vivant déjà en Gers durant l'avant dernier interglaciaire...».

The time span covered by these finds allow us to doubt BONIFAY's (1971) suggestion of a post-Villafranchian stratigraphical hiatus lasting until the Riss glacial when prearctoid bears appeared in southern Europa that would be substituted by the true brown bear (*U. arctos* LIN) in the last glacial.

This species has only been found in karstic fillings.

Ursus maritimus PHIPPS 1774

Synonymous: *Ursus marinus* PALLAS 1776, *Ursus albus* MULLER 1776, *Thalassarctos maritimus* ERXLEBEN, *Thalassarctos eogroenlandensis* KONOTTNERUS-MEYER 1908, *T. labradorensis* K.-M., *T. spitzbergensis* K.-M., *T. jenäensis* K.-M., *T. maritimus* var. *ungavensis* K.-M. *Thalassarctos maritimus groenlandicus* BIRULA 1932, *T.m. marinus* BIRULA 1932.

The dental formula of this species is:

$$\begin{array}{ccccccc} 1, 2, 3 & & 1 & & 1, 3, 4 & & 1, 2 \\ I & \text{---} & C & \text{---} & P & \text{---} & M & \text{---} \\ 1, 2, 3 & & 1 & & 1, 4 & & 1, 2, 3 \end{array}$$

The first premolar is absent in most of the cases.

As is normal in a species with carnivorous habits an important amount of «primitive» characteristics remain in its dentition: small sized teeth, cusps with cutting edges, slightly convergent towards the anteroposterior axis of molars, and an uncomplicated morphology. The small development of the second upper molar heel is

noticeable and, consequently, that of the third lower molar, subcircular shaped and with scarce inner ridulae. The skeleton is quite similar to that of the brown bear, but more heavily built. In spite of its marine habits, its scapula does not differ from that of the brown bear, KOBY (1955).

In spite of KURTEN's (1964, p. 23) opinion about the ancient origin of some characteristics of this species, maybe as long ago as during the Cromer-Mindel: «...thus a *maritimus* like pattern seems to date back again to approximately the Cromer - Mindel stage», there is not any fossil remain until *Ursus maritimus tyrannus* KURTEN 1964, from the Lower Würm and some of those *maritimus* —like characteristics, mainly those of the dental morphology, can be recognized, in *U. prearctos* material, as in some second upper molar (unfortunately broken in part) from Mollet Racó, which have short and narrow heels.

This species is restricted today to the Arctic circle neighborhood. But at the maximum extent of the ice cap during the Würm, it probably could have reached the northern coast of the Iberian Peninsula, but its special habitat could make the preservation of bones and teeth difficult.

Ursus arctos LINNEO 1758

Synonymous of fossil and sub-fossil species from Europa and circummediterranean border.

Ursus fossilis GOLDFUSS 1821, *Ursus priscus* GOLDFUSS 1822 (1810?), *Ursus arctoides* DE SERRES, DUBREUIL & JEANJEAN 1829, *Ursus arctos subfossilis* von MIDDENDORFF 1851, *Ursus planifrons* DENNY 1864, *Ursus faidherbianus* BOURGUIGNAT 1867, *Ursus lartetianus* BOURGUIGNAT 1868, *Ursus letourneuxianus* BOURGUIGNAT 1868, *Ursus bourguignati* LARTET 1867, *Ursus rouvieri* BOURGUIGNAT 1868, *Ursus pomeilianus* BOURGUIGNAT 1868, *Ursus tarandi* FRAAS 1872 (teste PORTIS 1878), *Ursus ferox fossilis* (GOLDFUSS 1821) BUSK 1873, *Ursus horribilis fossilis* (GOLDFUSS 1821) LYDEKKER 1885, *Ursus arctos raza priscus* (CUVIER 1823) GAUDRY & BOULE 1892, *Ursus arctos* var. *isabellinus* (HORSFIEL 1827) von FRITSCH 1893, *Ursus arctus fos-*

silis (GOLDFUSS 1821) LYDEKKER 1897, *Ursus libycus* POMEL 1897, *Ursus syriacus* (HEMPER & EHEREMBERG 1828), ZUMOFEN 1900 (apud BATE 1927), *Ursus arctos antiqui* POHLIG 1909, *Ursus procerus* HAY 1911 (1912?) aut. MILLER 1899 (teste HAY 1923, FREUDENBERG 1918), *Ursus arctos* var. *priscus* (GOLDFUSS 1822) FREUDENBERG 1914, *Ursus arctos* var. *priscus* (CUVIER 1823) BOULE 1919, *Ursus anglicus* GUNTHER 1923, *Ursus arctos* subs. *nucifragus* LONNBERG 1923, *Ursus arctos raza libycus* (POMEL (1897) DEPERET 1928, *Ursus arctos* mut. *faidherbi* BOURGUIGNAT (1867) ARAMBOURG 1932, *Ursus arctos* mut. *larteti* (BOURGUIGNAT 1868) ARAMBOURG 1932, *Ursus arctos nemoralis* DEGERBOL 1933, *Ursus arctus priscus* (GOLDFUSS 1822), DEGERBOL 1933, *Ursus arctos fossilis* (GOLDFUSS 1821) KOBY 1944.

This list does not include the enormous amount of synonymia defined from living material, because this would make it too long. An example can be found in ERDBRINK (*op. cit.*) who gave a list of two hundred and thirty two «species» created by MERRIAM (1918 *non vidi*) from the present North American brown bear material. An implicit recognition of the unusfulness of these species proliferation was in COUTURIER (1953, p. 326): «cette partie du squelette (the skull) revêt une importance particuliere, car elle seule souvent constitue l'unique materiel pour décrire une espèce ou une sous - spèce. Je pense que MERRIAM aurait créé 17 espèces avec les 17 têtes osseuses d'Ours des Pyrénées de ma collection, car toutes sont différentes...».

The dental formula of the brown bear is as follows, TORRES (1984):

$$\begin{array}{ccccccc} & 1, 2, 3 & 1 & (1), (3), 4 & 1, 2 & & \\ \text{I} & \text{-----} & \text{C} & \text{---} & \text{P} & \text{-----} & \text{M} & \text{-----} \\ & 1, 2, 3 & 1 & (1), & 4 & 1, 2, 3 & & \end{array}$$

In spite of certain similarities with *U. etruscus* and *U. prearctos* morphologies, it shows its own evolved characteristics: cusp are usually duplicated, having lost their cutting appearance. The enamel was covered by small cusplets, while in the other two species it was ridulae draped. The cusp are almost vertical, having lost a net obliquity, mainly in their lingual walls, which was typical in the older species. The relative length

of the second upper molar grows significantly, and the paraconid in the first lower molar shows a «modern» habit. The «Ursavoid» morphologies which were present in all *U. etruscus* carnassials and in a certain number of specimens of *U. prearctos* are absent. There is a rather important augmentation of the third lower molar length.

As in the speloid evolutive lineage, there is a similar evolution in the postcranial skeleton of arctoid lineage representings. There is a growth of transversal measurements of long bones epiphysis, and in the extent of the articular facets of carpal and tarsal bones. There is not an entepicondilar foramen in the humerus, but a small apophysis still remains, a vestige of a bony bridge that defined the outer limit of the foramen.

It seems quite possible that in the Würm beginning a massive migration took place, due to an enormous enlargement of ice covered areas. *U. arctos* covered the whole of Europe, North America (Rancho La Brea, California) and the circum-mediterranean border of Africa and Asia. In North America giant forms appeared in favourable environments: *U.a. gyas* and *U.a. midden-dorffi*, that show a certain morphological convergence with the cave bear in its skull morphology.

The name of *U. priscus* has frequently been used to describe fossil and subfossil brown bear remains. In fact MUSIL (1985) still employs it, but today there are not too many reasons to continue its use, because the Gaylenreuth skull, on which Goldfuss based it, is from a normal brown bear, DE BLAINVILLE (1839) and GAUDRY (1867) were already of this opinion and GAUDRY (in KOBAYASHI 1944) wrote: «j'ai constaté que l'ours gris diffère plus que l'ours brun d'*U. priscus*, car notre squelette d'ours gris est plus massif que celui de l'ours brun et son humérus se distingue par une plus forte saillie de l'épicondyle... *U. priscus* paraît être simplement un *U. arctos* de grande taille...». This fact becomes more evident when the enormous intraspecific variability of this species is taken into account, of which ERDBRINK (op. cit.) stated (p. 384): «In view of the astonishing variability in size of teeth of *U. arctos* it may be clear that the value of formulae or indices based on combinations of measurements of teeth is almost negligible if

these formulae or indices were intended for use as determining factors...». It is evident that it is an extreme opinion which can be discarded by regression analysis.

4. ISSUES

- *U. ruscinensis* must be considered as the common ancestor of all European Pleistocene bears. From it, two evolutive lineages are derived: one, more conservative, represented by *U. mediterraneus*, had small teeth and a small-sized skeleton and had limited ecological success. The other one, more evolved, was represented by *U. etruscus* and showed an enormous size augmentation and ecological success.
- *U. minimus* seems to be linked to *U. ruscinensis* but not to *U. etruscus*, because of its more evolved characteristics. It could be taken as a first attempt of the general hipocarnivorous tendency of all Pleistocene bears.
- *U. etruscus* appears as the ancestor of two big sized evolutive lineages of Pleistocene bears: speloid and arctoid.
- The speloid lineage was composed by *U. deningeri* and *U. spelaeus*; both species have well defined metrical and morphological differential characteristics and net geographical and stratigraphical distributions. Both had an enormous ecological success.
- The whole of the arctoid lineage is less known because of the lesser frequency of finds. It is assumed a massive arrival of *U. arctos* at the Würm beginning being colonized North America, the whole of Europe and the Mediterranean Border of Asia and Africa. Continuous finds of etruscoid-arctoid like bears, covering the whole of middle Pleistocene times, support the hypothesis of a continuous presence of an arctoid—like bear all through the Pleistocene: *U. prearctos*. A highly adaptative potential in different ecological systems can be assumed for it.
- A continuous (in time), European etruscoid-arctoid bear population permits the *U. maritimus* origin to be placed in the European

arctoid stock, without an asiatic ancestor being necessary.

- It is evident that a continuity of an etruscoid-arctoid stock could cause taxonomic problems, because of evolutive convergence, there could appear remains of a «relatively modern» bear representing in fact indistinguishable from that of an ancient one of the speloid lineage, and still very closely, related to the common ancestor *U. etruscus*.
- The cronological interval covered by these etrusco-arctoid bears does not seem too big when compared with that of the *U. etruscus* (from Villarroya to Venta Micena), and taking into account its high morphological and metrical conservatism and its very probable ecological opportunism.
- It remains a certain nomenclatural uncertainty: *U. priscus* must be taken as *nomen delenda*, because the original material was from an animal indistinguishable from the modern *U. arctos*. *U. prearctos* could be an adequate denomination since it was established from true fossil material with more modern characteristics than *U. etruscus* but more archaic features than *U. arctos*.

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