

Sus meum script

SOCIETAS PRO FAUNA ET FLORA FENNICA

ACTA
ZOOLOGICA FENNICA

144

Miguel Crusafont Pairó and Björn Kurtén:
Bears and Bear-Dogs from the Vallesian of the Vallés-Penedés
Basin, Spain

**Helsingin Yliopiston
Metsäkirjasto**

HELSINKI—HELSINGFORS
1976

K

ACTA ZOOLOGICA FENNICA

1—45 vide Acta Zoologica Fennica 45—50.
46—59 vide Acta Zoologica Fennica 60—93.
60—99 vide Acta Zoologica Fennica 100—125.

100. MARIA REUTER: Untersuchungen über Rassenbildung bei *Gyatrix hermaphroditus* (Turbellaria Neorhabdoceola). 32 S. (1961).
101. MARIA REUTER: Index Generalis Seriei Acta Zoologica Fennica 51—100 (1948—1961). 63 S. (1964).
102. WALTER HACKMAN: Studies on the dipterous fauna in burrows of voles (*Microtus*, *Clethrionomys*) in Finland. 64 pp. (1963).
103. A. M. J. EVERS: Über die Entstehung der Excitatoren und deren Bedeutung für die Evolution der Malachiidae (Col.). 24 S. (1963).
104. JOHAN REUTER: The international concentration in some hypotrichous Ciliates and its dependence on the external concentration. 94 pp. (1963).
105. GÖRAN BERGMAN and KAI OTTO DONNER: An analysis of the spring migration of the Common Scoter and the Long-tailed Duck in southern Finland. 59 pp. (1964).
106. HENRIK ÖSTERHOLM: The significance of distance receptors in the feeding behaviour of the Fox, *Vulpes vulpes* L. 31 pp. (1964).
107. BJÖRN KURTÉN: The Carnivora of the Palestine caves. 74 pp. (1965).
108. BJÖRN KURTÉN: The evolution of the Polar Bear, *Ursus maritimus* Phipps. 30 pp. (1964).
109. FRANK S. TOMPA: Factors determining the numbers of song sparrows, *Melospiza melodia* (Wilson), on Mandarte Island, B. C., Canada. 73 pp. (1964).
110. PONTUS PALMGREN: Die Spinnenfauna der Gegend von Kilpisjärvi in Lappland. 70 S. (1965).
111. BJÖRN KURTÉN: On the evolution of the European Wild Cat, *Felis silvestris* Schreber. 29 pp. (1965).
112. PAUL KRÜGER: Über die Einwirkung der Temperatur auf das Brutgeschäft und das Eierlegen des Rebhuhnes (*Perdix perdix* L.) 64 S. (1965).
113. SAMUEL PANELIUS: A revision of the European gall midges of the subfamily Porricondylinae (Diptera: Itonididae). 157 pp. (1965).
114. BO-JUNGAR P. WIKGREN: The effect of temperature on the cell division cycle in *Diphyllobothrid* plerocercoids. 27 pp. (1966).
115. BJÖRN KURTÉN: Pleistocene bears of North America. 1. Genus *Tremarctos*, spectacled bears. 120 pp. (1966).
116. TOR G. KARLING: On nematocysts and similar structures in Turbellarians. 28 pp. (1966).
117. BJÖRN KURTÉN: Pleistocene bears of North America. 2. Genus *Arctodus*, short-faced bears. 60 pp. (1967).
118. FRANK S. TOMPA: Reproductive success in relation to breeding density in pied flycatchers, *Ficedula hypoleuca* (Pallas). 28 pp. (1967).
119. ANN-MARIE FORSTÉN: Revision of the Palearctic *Hipparion*. 134 pp. (1968).
120. CHARLES HIGHAM: Size trends in prehistoric European domestic fauna, and the problem of local domestication. 21 pp. (1968).
121. ANITA ROSENGREN: Experiments in colour discrimination in dogs. 19 pp. (1969).
122. TOM REUTER: Visual pigments and ganglion cell activity in the retinae of tadpoles and adult frogs (*Rana temporaria* L.). 64 pp. (1969).
123. GÖRAN GYLLENBERG: The energy flow through a *Chorthippus parallelus* (Zett.) (Orthoptera) population on a meadow in Tvärminne, Finland. 74 pp. (1969).
124. PAUL KRÜGER: Zur Rassenfrage der nordeuropäischen Igel (*Erinaceus europaeus* L.). 15 S. (1969).
125. BRIT GODSKE ERIKSEN: Rotifers from two tarns in southern Finland, with a description of a new species, and a list of rotifers previously found in Finland. 36 pp. (1969).

ACTA ZOOLOGICA FENNICA 144
EDIDIT
SOCIETAS PRO FAUNA ET FLORA FENNICA

BEARS AND BEAR-DOGS FROM THE
VALLESIAN OF THE VALLÉS-PENEDÉS
BASIN, SPAIN

Miguel Crusafont Pairó and Björn Kurtén

Helsingin Yliopiston
Metsäkirjasto

HELSINKI—HELSINGFORS
March 1976

Abstract

CRUSAFONT PAIRÓ, MIGUEL & KURTÉN, BJÖRN: Bears and bear-dogs from the Vallesian of the Vallés-Penedés basin, Spain. — Acta Zool. Fennica 144:1—29. 1976.

A revised list of mammalian fossils from the Vallesian localities Can Llobateres and Can Ponsich (Vallés-Penedés basin, Spain) is given and the following species of Carnivora described. *Indarctos vireti*, validated as the most primitive *Indarctos* known. *Ursavus brevirhinus* and *U. primaevus* as associated but distinct species. *Protursus simpsoni* n.g., n.sp. as an early member of the Ursinae. *Amphicyon* cf. *major* and Canidae indet.

Authors' addresses: M. Crusafont Pairó, Instituto Provincial de Paleontología, Sabadell, Spain; B. Kurtén, Department of Geology and Paleontology, University of Helsingfors, SF-00170 Helsingfors 17, Finland.

Contents

| | | | |
|---|----|--|----|
| Introduction | 3 | Protursus Crusafont & Kurtén, n.g. | 22 |
| List of species | 4 | Protursus simpsoni Crusafont & Kurtén, | |
| Systematic descriptions | 5 | n. sp. | 22 |
| <i>Indarctos vireti</i> Villalta & Crusafont .. | 5 | <i>Amphicyon</i> cf. <i>major</i> De Blainville | 24 |
| <i>Ursavus brevirhinus</i> (Hofmann) | 15 | Canidae indet. | 27 |
| <i>Ursavus primaevus</i> (Gaillard) | 16 | References | 28 |
| Notes on the history of <i>Ursavus</i> | 18 | Appendix: Abbreviations | 29 |

INTRODUCTION

The fossils to be described here come from the early Vallesian beds at Can Llobateres and Can Ponsich in the Vallés-Penedés basin (Spain). Both localities are situated in the immediate neighbourhood of the city of Sabadell; still another fossiliferous exposure of the same age is found at nearby Rio Ripoll. Can Llobateres is now richer in mammalian species than any other locality from the "Pontian", *sensu lato*, in all of Eurasia. Can Ponsich is the type site of the Vallesian Land-Mammal Stage.

The name Vallesian was introduced by CRUSAFONT (1950) for the lower levels of the "Pontian", characterized by the presence of a primitive *Hipparion*, giraffids of the genus *Palaeotragus*, and various relicts surviving from the preceding Vindobonian stage. Its stratigraphic position, then, is between the terminal Vindobonian as exemplified by La Grive Saint-Alban, and the upper or "typical" Pontian of Pikermi, the Pikerimian (CRUSAFONT 1950) or Turolian (CRUSAFONT 1965a). In the Vallés-Penedés basin, the late Vindobonian is represented by the fossiliferous exposure of the railway cut at Sant Quirze, while the Turolian is found at Piera; both sites have yielded large mammalian faunas. THALER (1966), in his suggested zonation of the continental Tertiary in Europe, makes an essentially similar arrangement, his "Sabadell Zone" corresponding to the Vallesian, and his "Teruel Zone" to the Turolian.

The Vallesian is an important phase in the evolution of the mammalian faunas: a process of modernization with the appearance of various new species and genera, with a datum line provided by the immigration of *Hipparion* occur-

ring about 12.5 m.y. BP (see VAN COUVERING, 1972). Although *Hipparion* and other forms of Oriental origin enter the Vallés-Penedés at this stage, the continuation of ecological conditions essentially similar to those of the Vindobonian resulted in a phase of endemism, the Vallesian phase of CRUSAFONT (1958a). Vindobonian relicts are numerous in the lower beds but gradually become more scarce as we ascend through the Vallesian beds, which have a maximum thickness of about 400 m.

The two localities discussed here are in the lower Vallesian. The site at Can Llobateres was discovered in 1926, but its Vallesian age was recognized in 1951 (CRUSAFONT & TRUYOLS, 1951). Can Ponsich, first discovered in 1946 and described by CRUSAFONT & TRUYOLS (1947) has yielded the type section of the Vallesian. It has a direct stratigraphic relationship with the underlying upper Vindobonian beds of Sant Quirze.

The Vallesian beds of the Vallés-Penedés rank with the Siwaliks as the main pongid-bearing strata in Eurasia (CRUSAFONT & HÜRZELER 1961; SIMONS & PILBEAM 1965; CRUSAFONT 1972a). A grant from the Wenner-Gren Foundation for Anthropological Research, as well as the acquisition of the site by a large chemical firm, have greatly furthered the work at this locality. We gratefully acknowledge the support thus received.

Studies of the faunas of Can Llobateres and Can Ponsich may be found in the papers already referred to; in addition see CRUSAFONT (1965b, 1972), CRUSAFONT & CASANOVAS (1973), CRUSAFONT & HÜRZELER (1969), CRUSAFONT & PETTER (1969), GOLPE (1971), HARTEN-

BERGER (1965, 1966), PETTER (1963, 1967).

The present paper is a study of the ursids and other bear-like forms (alter-

natively classified as Canidae, Ursidae, and Amphicyonidae) from Can Llobateres and Can Ponsich.

LIST OF SPECIES

An interim list of the species recognized to date at Can Llobateres and Can Ponsich is presented herewith. A comparison with the list given for the former locality in CRUSAFONT (1964) will indicate the rate at which the studies have been progressing.

| | Can Lloba- teres | Can Ponsich | | Can Lloba- teres | Can Ponsich |
|---|------------------------|----------------|---|------------------------|----------------|
| Insectivora | | | H. sp. | + | — |
| Postpalerinaceus vireti Crus. & Vill. 1947 | + | + | Cf. Spermophilus bredai (Meyer 1848) | — | + |
| Lantanotherium sanmigueli Vill. & Crus. 1944 | + | + | Citellus sp. | — | + |
| Galerix socialis Meyer 1865 | + | + | Miopetaurista aff. grimmi Black | + | — |
| Heterosorex sansaniensis Gaill. 1915 | + | + | Cryptopterus crusafonti Mein 1970 | + | + |
| Miosorex grivensis Viret & Zapfe 1951 | — | + | Monosaulax minutus (Meyer 1838) | + | + |
| Crusafontina endemica Gibert in litt. | + | — | Steneofiber jaegeri Kaup 1832 | + | — |
| Talpa minuta Blainv. 1839—64 | + | + | S. depereti Mayet 1908 | + | — |
| Plesiodimylus chantrei Gaill. 1899 | + | + | Progonomys aff. cathalai Schaub 1938 | + | — |
| Primates | | | Cricetodon sansaniensis Lartet 1851 | — | + |
| Dryopithecus piveteaui Crus. & Hürz. 1962 | + | + | C. (Hispanomys) decedens Schaub 1925 | — | + |
| Hispanopithecus laietanus Crus. & Vill. 1946 | + | + | Megacricetodon aff. minor (Lartet 1851) | + | + |
| Rahonapithecus sabadellensis Crus. & Hürz. 1962 | + | — | M. debruijni Freudenthal 1968 | — | + |
| Lagomorpha | | | M. aff. gregarius (Schaub 1925) | — | + |
| Prolagus oeningensis Meyer | + | + | Ruscinomys thaleri Hart. 1965 | + | + |
| Rodentia | | | Rotundomys sabadellensis (Hart. 1965) | + | — |
| Titanomys fontanesi Dep. | + | — | R. hartenbergeri Freud. 1967 | — | + |
| Pentaglis sp. | + | — | Anomalomys cf. gaillardi Viret & Schaub 1946 | + | — |
| Muscardinus (Muscardinus) crusafonti Hart. 1966 | + | — | Cotimus leemanni Hart. 1965 | + | — |
| M. (Eomuscardinus) vallesensis Hart. 1966 | + | — | Leptodontomys catalunicus (Hart. 1966) | + | — |
| Glirulus aff. lissiensis Hug. & Mein 1965 | + | — | Keramidomys pertesunatoi Hart. 1966 | + | — |
| Heteroxerus cf. rubricati Crus. & Vill. 1955 | + | — | Carnivora | | |
| H. grivensis (Major 1893) | — | + | Amphicyon cf. major Blainv. 1841 | + | + |
| H. hurzeleri Stehl. & Schaub 1951 | — | + | Indarctos vireti Vill. & Crus. 1943 | + | + |
| | | | Ursavus primaevus Gaillard 1899 | + | — |
| | | | U. brevihinus Hoffmann 1877 | + | — |
| | | | Protursus simpsoni Crus. & Kurtén n.g. n.sp. | + | — |
| | | | Ischyricteis (Ischyricteis) petterii Crus. 1972 | + | — |
| | | | Plesiogulo sp. | + | — |

| | Can Lloba- teres | Can Ponsich | | Can Lloba- teres | Can Ponsich |
|--|------------------------|----------------|---|------------------------|----------------|
| Circumustela dechasauxi Petter 1967 | + | — | Jourdan 1861 | + | + |
| Marcetia santigae Petter 1967 | + | — | D. giganteum Kaup 1829 | + | — |
| Martes aff. andersoni Schlosser 1924 | — | + | Perissodactyla | | |
| M. mellibulla Petter 1963 | + | — | Hipparion catalaunicum | | |
| M. munki Roger 1900 | + | — | Pirlot 1956 | + | + |
| Taxodon cf. sansaniensis | | | Macrotherium grande Lartet 1837 | + | + |
| Lartet 1851 | + | — | Tapirus priscus Kaup 1832 | + | + |
| Sabadellictis crusafonti Petter 1963 | + | — | Aceratherium incisivum Kaup 1834 | + | + |
| Trocharion albanense Major 1903 | + | — | ?Chilotherium sp. | + | + |
| Promephitis pristinidens Petter 1963 | + | — | Dicerorhinus sansaniensis (Lartet 1851) | + | + |
| Mesomephitis medius Petter 1967 | + | — | D. sp. | + | — |
| Paralutra sp. | + | — | Artiodactyla | | |
| Limnonyx sinerizi Crus. 1950 | — | + | Hyotherium soemmeringi Meyer 1834 | + | — |
| Semigenetta mutata (Filhol 1883) | + | — | H. palaeochoerus (Kaup 1833) | — | + |
| Progenetta crassa (Dep. 1892) | + | — | H. sp. | + | — |
| P. gaillardi Major 1903 | — | + | Parachleuastochoerus crusafonti Golpe 1971 | + | + |
| P. montadai (Vill. & Crus 1943) | — | + | Listriodon splendens Meyer 1846 | + | — |
| Metarctos batalleri Viret 1933 | + | — | Conohyus simorreensis (Lartet 1851) | — | + |
| Machairodus aphanistus Kaup 1833 | + | + | Dorcatherium jourdani Filhol 1883 | — | + |
| Grivasmilus jourdani (Filhol 1883) | + | + | D. sp. | + | — |
| Proboscidea | | | Euprox dicranocerus (Kaup 1835) | + | — |
| "Mastodon" sp. | — | + | E. furcatus (Hensel 1859) | — | + |
| Gomphotherium angustidens (Cuvier 1806) | + | — | Micromeryx flourensianus Lartet 1851 | + | + |
| Tetralophodon longirostris (Kaup 1835) | + | — | Capreolus sp. | + | + |
| Deinotherium laevium | | | Miotragocerus chantrei Dep. 1887 | — | + |
| | | | M. sp. | + | — |

SYSTEMATIC DESCRIPTIONS

Indarctos vireti Villalta & Crusafont

Indarctos vireti VILLALTA & CRUSAFONT 1943:54.
Agriotherium insignis pontiensis VILLALTA &
CRUSAFONT 1945:94.

Indarctos arctoides vireti, THENIUS 1959:284.

Material. VP 646—647, crushed skull and right and left rami of mandible. VP 633, parts of second skull with left mandibular ramus. VP 640, left M₂. VP 641—642, left and right M₁. VP 651—652, two left C_s. VP 655—656, right and left Ci. VP 668, left MC 2. VP 683—684, left and right MC 3 (probably same individual as VP 668). VP 669, left MC 4 fragment. VP 670, left MT 2 fragment. VP 665, right humerus. VP 666, right astragalus. VP 667, two left un-

ciform bones. No number, left and right M₃, two left MC 2, left Ci, two caudal vertebrae. All from Can Llobateres.

Diagnosis

A lightly built *Indarctos* with comparatively long jaws and uncrowded premolars; second and third premolars two-rooted, relatively large, elongate and premolariform with high, keeled crowns; molars on average somewhat smaller than in *I. arctoides*.

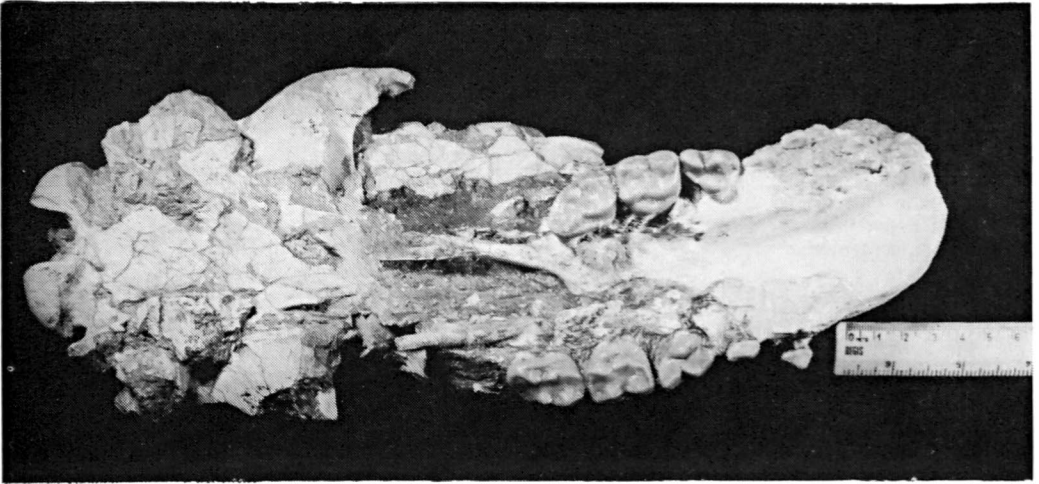


FIG. 1. *Indarctos vireti*, VP 646, skull, Can Llobateres.

Taxonomic history

The species *Indarctos vireti* was based by VILLALTA & CRUSAFONT (1943) on a right mandible fragment (Coll. Villalta) with the crowns of M_1 and M_2 , from the Vallesian of Can Purull at Viladecaballs in the Vallés-Penedés basin; its stratigraphic position is considerably higher in the stage than that of Can Llobateres. Somewhat later another part of the same jaw, with P_4 , was discovered (VILLALTA & CRUSAFONT 1945). At the same time another mandible from the same locality was described under the name *Agriotherium insigne* var. *pontiense*. The species *A. insigne* is, of course, a well-known Ruscinian guide fossil; in actual fact the specimen does belong to *I. vireti*. The error is presumably due to an ancient break in the fossil, which passes through the crown of M_1 and distorts its shape, giving it a certain resemblance to the agriothere carnassial. The specimen is a right mandible (in the Museum at Sabadell) with M_1 , M_2 and the roots of P_4 .

Brief descriptions of both species, on the basis of the same material, were reiterated in the survey by CRUSAFONT & VILLALTA (1951). *Agriotherium* was fin-

ally dropped from the faunal lists of the Vallesian by CRUSAFONT & TRUYOLS (1960).

The species *I. vireti* was originally characterized as follows (VILLALTA & CRUSAFONT 1943:54): *Indarctos* vecino del *I. arctoides* Depéret, del Pontiense de Montredon, aunque de talla claramente inferior, con tuberculosa (M_2) más alargada en relación con el M_1 comparativamente a la especie francesa. Metacónido de M_1 más soldado con la punta principal.

TOBIEN (1955) remarked on the similarity of what was then known of *I. vireti* and the species *I. arctoides* which is characteristic of the Pontian in western Europe. THENIUS (1959) concluded that there was no valid distinction between the two and regarded the Vallesian form as a subspecies of *I. arctoides*.

The larger material now at hand from Can Llobateres disproves this contention. *Indarctos vireti* turns out to be a more primitive species than any other in the genus, as befits its early date.

Description

The lower canines are ursiform but

somewhat more recurved than usual in bears. The internal keel is strongly developed and situated more internally than in *Ursus*; near the enamel basis the keel curves backward in a characteristic way. There is an incurvation of the enamel base in front of the keel, instead of right at its base. The posterior edge is rounded.

The upper canines have a well developed anterointernal ridge, but it is not quite as sharp as in C_i . At the enamel base it terminates in a convexity of the enamel border, as in *Felis*, for instance, rather than an incurvation. There is an incurvation in front, however.

Both the upper and lower canines show a distinct sexual dimorphism (see below).

P_1 is preserved only in the jaw VP 633. It has one root and looks rather like its homologue in *Tremarctos*. The outline is an elongate oval. The crown is flattened, with a posterior and posterointernal cingulum. The point of the main cusp is

in the anterior half of the tooth in this as in the other premolars. The ridge on the posterior slope of the tooth is well developed and widens backward; on the anterior slope it is faint and slightly curved, convexity to the lingual side.

P_2 and P_3 have two roots and thus differ from *I. arctoides* and *I. atticus*. Their outline in occlusal view is elongate and tending to the rhomboid. The main cusps are high and pointed, as for instance in P_4 of *Ursus americanus*. There is no accessory cusp. A cingulum encircles the tooth but it is weakly developed except along the posterointernal part. The front and hind slopes are keeled, but the edges are not particularly sharp.

These teeth represent a more primitive condition than that seen in other species of *Indarctos*. In *I. arctoides*, P_3 is two-rooted and may have resembled its homologue in *I. vireti* (unfortunately only the alveolus is known in the Pfaffstetten jaw described by THENIUS (1959)), but

TABLE 1. Measurements of lower canines and premolars of *Indarctos*.

| | | | C_i | | P_1 | P_2 | | P_3 | | P_4 | | H |
|------------------------------|----------------------|---------|-------|------|-------|-------|-----|--------|-----|-------|------|------|
| | | | L | B | L | L | B | L | B | L | B | |
| <i>Indarctos vireti</i> | | | | | | | | | | | | |
| Can Llobateres | VP 647 | { dext. | 18.5 | 13.0 | — | 10.8 | 6.7 | 13.5 | 8.0 | 16.9 | 9.4 | 9.5 |
| " | VP 633 | { sin. | 19.2 | 13.2 | — | 11.1 | 6.7 | 13.5 | 8.0 | 16.7 | 9.5 | 9.4 |
| " | VP 656 | sin. | — | 16½ | 10.4 | 9.9 | 6.5 | 12.2 | 7.7 | 16.3 | 8.9 | — |
| " | VP 655 | dext. | 22.7 | 15.3 | — | — | — | — | — | — | — | — |
| " | VP 654 | dext. | 21.8 | 16.6 | — | — | — | — | — | — | — | — |
| " | VP 654 | dext. | 24.3 | 16.5 | — | — | — | — | — | — | — | — |
| | No number | sin. | 20.1 | 12.8 | — | — | — | — | — | — | — | — |
| Can Purull, type | | dext. | — | — | — | — | — | — | — | 14.7 | 8.5 | 8.1 |
| <i>Indarctos arctoides</i> | | | | | | | | | | | | |
| Montredon, type Mtn 14 | sin. | | — | — | — | — | — | — | — | 16½ | 12.0 | 10.2 |
| Pfaffstetten | (After THENIUS) | | 18.4 | 13.8 | (8.5) | 9.7 | 6.1 | (11.0) | — | 15.8 | 9.6 | — |
| <i>Indarctos atticus</i> | | | | | | | | | | | | |
| Samos | (After HELBIG) | | — | — | — | — | — | 11.8 | 8.9 | 21.0 | 12.8 | 13.7 |
| Maragha | (After DE MECQUENEM) | | — | — | 10 | 9 | 7 | 13 | 9½ | 23 | 14 | — |
| <i>Indarctos anthracitis</i> | | | | | | | | | | | | |
| Monte Bamboli, cast | | dext. | — | — | — | — | — | 9.2 | 6.1 | 19 | 10.5 | — |

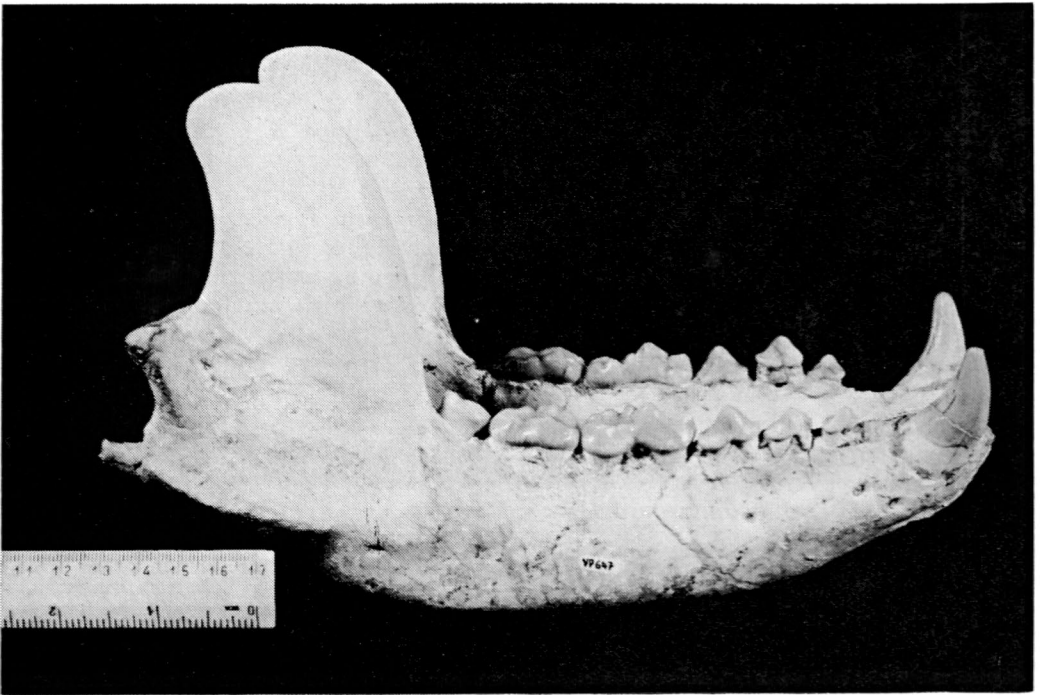


FIG. 2. *Indarctos vireti*, VP 647, mandible, Can Llobateres.

P₂, separated from P₃ by a long diastema, is one-rooted and much reduced. In *I. atticus*, P₃ is also one-rooted.

P¹ resembles P₁ rather closely, and similarly P² and P³ resemble P₂ and P₃; but their anterior keel is more deflected inwards, as usual in upper premolars. Again the large size and homodonty of the second and third premolars is a primitive condition. P¹ has one root, P² and P³ have two.

P₄ is somewhat larger than P₂-P₃ but otherwise rather similar, even to the absence of accessory cusps. The homodonty of the series P₂-P₄ is more primitive than the condition in any other species of the genus.

P⁴ is quite large. The protocone is well developed and set off from the blade. There is a tendency to protocone duplication, the anterior part being the smaller. Such a tendency is not uncommon in *I. arctoides* and *I. atticus*. There is no

parastyle, and indeed this element is uncommon in *Indarctos*, though present in *I. atticus* from Conclud. The paracone has a blunt edge fore and aft, and there is a ridge running from its apex to the front end of the protocone. The metacone forms a broad, blunt carnassial blade. In outline the tooth shows a deep notch in front of the protocone, but none behind it, where there is a well developed internal cingulum. The external cingulum is weak and only present in the metacone region, in contrast with *I. arctoides*, where it is well developed.

M₁ has a simply built trigonid, in which all the three cusps are low-crowned and single. The entoconid on the talonid is duplicated, with a smaller posterior part. There is no hypoconulid bordering the talonid basin at the back. The hypoconid is single, but there is a small cusp between the protoconid and the hypoconid, similar to that seen in

tremarctines (see KURTÉN 1966). At the same point, that is to say at the external junction between the talonid and the trigonid, there is a weak cingulum. The enamel surface of the tooth is smooth without wrinkling.

M¹ has a five-cornered outline, the inner wall being produced into an obtuse angle by the large cingulum. There are also external and posterior cingula. The paracone is the highest external cusp. The inner cusps are confluent and form a ridge with a somewhat individualized but obtuse and small hypocone. Between the inner ridge and the cingulum, the enamel is transversely wrinkled in a characteristic ursid manner. The middle field, on the other hand, is almost smooth, except for a few grooves.

M₂ has the front part somewhat broader than the hind. The main cusps are the protoconid and metaconid, which are connected by a transversal ridge with a notch in the middle, just as in *Arctodus*. The front part is basined and bounded in front by a semicircular wall

without a distinct paraconid. The talonid forms a larger basin, from the centre of which there radiate a number of small grooves to the notches between the principal cusps of the surrounding wall, the hypoconid and the double entoconid (of which the posterior part is the smaller, as in M₁). There is no posterior talonid cusp.

M² has a large paracone. The metacone is small, and the protocone is ridge-like, continuing into the small hypocone. There are no talon cusps apart from the last-mentioned, but there is a weak ridge encircling the talon field, which is almost smooth except for a few small wrinkles. There are more wrinkles between the inner ridge and the cingulum, as in M¹. The outer cingulum is large in VP 646, smaller in VP 633. The talon appears fairly long; perhaps this impression is determined in part by the relatively small transverse dimensions of the cheek teeth.

M₃ is nearly circular or ovoid. This is the only tooth with a system of enamel

TABLE 2. Measurements of lower molars of *Indarctos*.

| | | M ₁ | | Lt | M ₂ | | M ₃ | | | |
|------------------------------|-------------------|----------------|------|------|----------------|------|----------------|------|------|------|
| | | L | Ba | Bp | Lt | L | Ba | Bp | L | B |
| <i>Indarctos vireti</i> | | | | | | | | | | |
| Can Llobateres | | | | | | | | | | |
| " | VP 647 | dext. | 30.0 | 11.3 | 14.7 | 21.2 | 23.7 | 16.2 | 14.8 | 12.7 |
| " | | sin. | 30.2 | 11.4 | 14.9 | 21.0 | 23.6 | 16.2 | 14.8 | — |
| " | VP 633 | sin. | 32.7 | 12.8 | 16.8 | — | 25.0 | 17.2 | 16.0 | 12.4 |
| " | VP 640—641 | sin. | — | 12.9 | — | — | 26.1 | 18.0 | 16.1 | 17.2 |
| " | VP 642 | dext. | a32½ | — | — | — | — | — | — | 17.1 |
| Can Purull, type | | dext. | 30.8 | 12.2 | 15.1 | 21.4 | 22 | 15.6 | 13.4 | — |
| " | <i>pontiensis</i> | dext. | a34½ | 13.8 | 17.3 | — | 25.6 | 17.7 | 16.2 | — |
| <i>Indarctos arctoides</i> | | | | | | | | | | |
| Montredon, type Mtn 14 | | dext. | 35.7 | 14.8 | 18.3 | — | 25.2 | 19.0 | 17.2 | — |
| Pfaffstetten (After THENIUS) | | | 30.8 | — | 15.8 | — | 24.1 | 16.5 | — | — |
| Westhofen (After TOBIEN) | | | 32.6 | — | 17.3 | — | 25.2 | 17.4 | — | — |
| <i>Indarctos atticus</i> | | | | | | | | | | |
| Samos (After HELBING) | | | 41.6 | — | 22.2 | — | 32.4 | 23.3 | — | 21.5 |
| Maragha (After DE MECQUENEM) | | | 44 | 17 | 22 | — | 32 | 23 | 22 | — |
| Concud | | sin. | 42.4 | 17.8 | 22.2 | — | — | — | — | — |
| <i>Indarctos anthracitis</i> | | | | | | | | | | |
| Monte Bamboli, cast | | sin. | 33.2 | 13.5 | 16.7 | 24.0 | 23.7 | 16.5 | 15.5 | 13.5 |

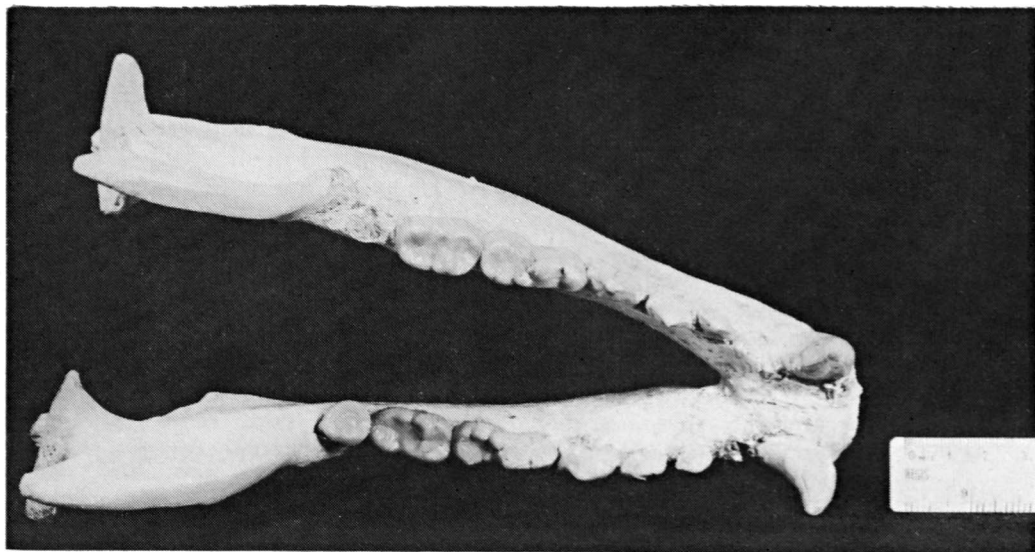


FIG. 3. *Indarctos vireti*, same specimen as fig. 2.

wrinkles on the occlusal surface similar to that in more advanced ursids. The middle field is surrounded by a slightly raised wall without any distinct cusps, only the protoconid forms a weak swelling, bounded posteriorly by a notch. A faint ridge runs from the protoconid to the centre of the field.

The only preserved skull, VP 646, is so crushed and distorted that little information on its original configuration can be obtained. The basicranial region resembles that in *I. atticus* described by THENIUS (1949a) but is much less shortened. The facial part of the skull is relatively much longer than in *I. atticus*.

The mandibles are better preserved. As in other *Indarctos*, the premasseteric fossa is absent. The lower border is strongly convex, and the ramus tapers forward. These are characters generally found in the genus, and likewise the position of the mental foramen below P_1 is typical. The mandibles are however noticeably slimmer and more elongate than in most *Indarctos*, especially *I. atticus*, and the teeth are small in relation to the length of the ramus.

Dimensions of the skull and teeth are given in table 5. It may be noted that the presumably female specimen VP 646—647 is only slightly shorter than the adult Samos II individual described by THENIUS (1959), though its teeth are much smaller. The presumed male, VP 265, probably exceeded the Samos form in skull and mandible length. Despite the small size of the teeth, it would seem that the head of *I. vireti* was about as long as that of *I. atticus*. In consequence, there is no crowding of the tooth row, so that the premolars stand in a straight line.

On the other hand, the head was certainly narrower in *I. vireti* than in *I. atticus*, and the animal was more slender-jawed, doubtless a primitive character. This tendency to lightness in build is also found in the postcranial skeleton.

Measurements of the limb bones of *I. vireti* from Can Llobateres are compared in Table 6 with data on *I. atticus* from Concud; on the large short-faced bear of the North American Pleistocene, *Arctodus simus*, from Rancho La Brea (after MERRIAM & STOCK 1925); and on

TABLE 3. Measurements of upper canines and premolars of *Indarctos*.

| | | | C ^s | | P ¹ | | P ² | | P ³ | | P ⁴ | | H |
|----------------------------|-----------------|-------|----------------|------|----------------|------|----------------|------|----------------|------|----------------|------|---|
| | | | L | B | L | B | L | B | L | B | L | B | |
| <i>Indarctos vireti</i> | | | | | | | | | | | | | |
| Can Llobateres | VP 633 | dext. | 22.7 | 16.0 | 10.0 | 10.2 | 6.2 | 11.9 | 6.8 | 23.7 | 17.7 | — | |
| " | VP 646 | | 19.5 | 13.5 | — | 11.8 | 6.2 | 12.4 | 6.7 | 21.8 | 17.4 | 11.7 | |
| " | VP 651 | sin. | 25.6 | 17.1 | — | — | — | — | — | — | — | — | |
| " | VP 652 | sin. | — | 16.1 | — | — | — | — | — | — | — | — | |
| <i>Indarctos arctoides</i> | | | | | | | | | | | | | |
| Montredon | (After HELBING) | | — | — | — | — | — | — | — | 27.4 | 21.0 | — | |
| Orignac | (After HELBING) | | — | — | — | — | — | — | — | 24.6 | — | — | |
| <i>Indarctos atticus</i> | | | | | | | | | | | | | |
| Samos | (After HELBING) | | — | — | 7.1 | 7.8 | — (9.5) | — | 29.1 | 24.3 | 18.5 | | |
| Samos II | (After THENIUS) | | 24.4 | 17.8 | (7.2) | 9.5 | 7.0 | 11.3 | 7.9 | 29.5 | 22.5 | — | |
| Concud | | | — | — | — | — | — | 12.0 | — | — | — | — | |

a specimen of the modern American black bear, *Ursus americanus*, from Florida (see KURTÉN 1966).

The humerus from Can Llobateres belongs to a young individual and lacks the proximal epiphysse. From its small size and its age it could well belong to the same individual as VP 646—647. This may also be true for some other bones.

The specimen is of about the same length as that of a large black bear. It is much smaller than the humerus of *Arctodus* but resembles the latter more than it does *Ursus*. As in the short-faced bear, the supinator ridge is weaker than in *Ursus* but the deltoid ridge is more developed than in *Arctodus*. The entepicondylar foramen is larger than in *Arctodus*, and the medial epicondyle is more

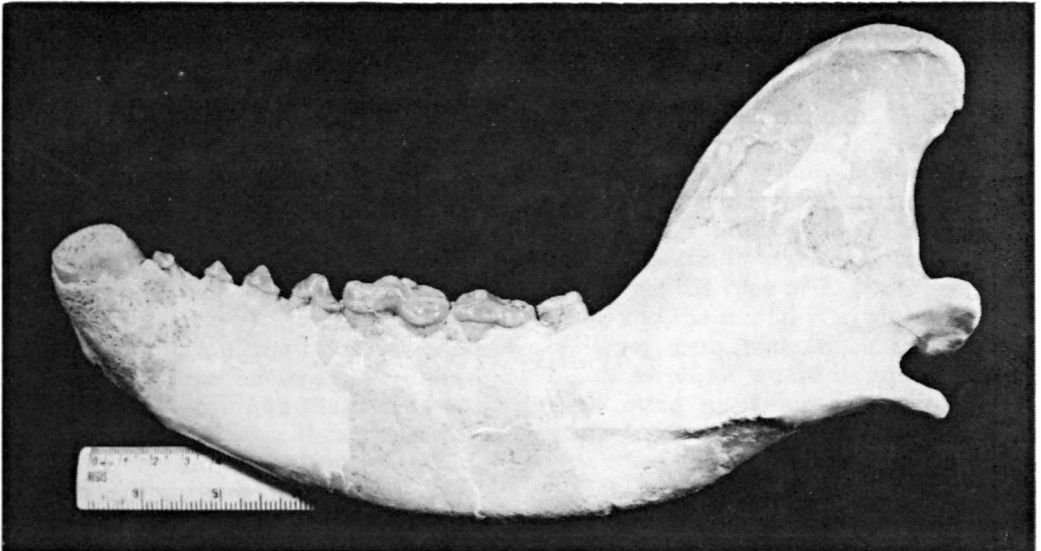
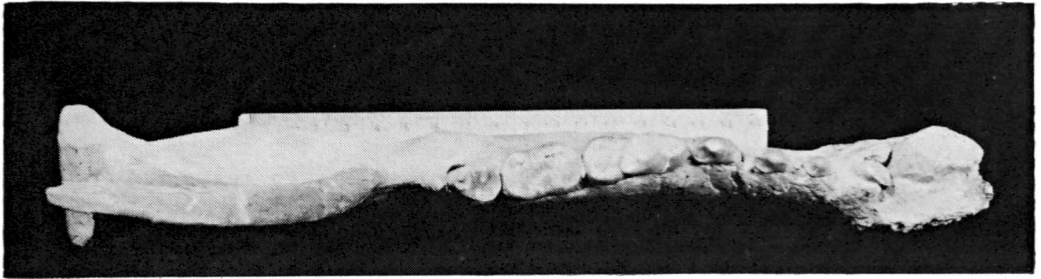


FIG. 4. *Indarctos vireti*, VP 633, mandible. Can Llobateres. Part restored in plaster.

FIG 5. *Indarctos vireti*, same specimen as fig. 4.

prominent. In the distal articulation the capitulum is less clearly set off from the trochlea than in *Arctodus*.

The only carpal bone represented is the unciform, which is somewhat closer in proportions to *Ursus* than to *Arctodus*, as the homologous bone in the latter is much extended proximo-distally.

Four metacarpal bones are preserved. The two MC 2 may represent male and female individuals respectively; an additional specimen is broken. The shorter MC 2 measures some 24.1 per cent of the length of the humerus, which is more than in *Ursus* (20.9) or *Arctodus* (19.5) and indicates that the hand was more elongate in *Indarctos* than in the later ursids.

The fragmentary MC 3 is rather hea-

vily built and presumably comes from a male. This is probably also true for the MC 4. If the latter belonged to the same individual as the large MC 2, the difference between the lengths of the two bones would amount to 6.4 per cent of the MC 2 length. Corresponding figures are 9.7 for *Arctodus* and 13.3 for *U. americanus*. It may perhaps be suggested that the outer fingers in *I. vireti* were less enlarged, relatively to the inner, than in the Pleistocene and recent forms; as a corollary it would apparently follow that the typical toe-in position of the bears had not yet evolved in the Vallesian form. The length of the metacarpals may suggest that this animal was not as fully plantigrade as modern bears.

The astragalus is represented by one

TABLE 4. Measurements of upper molars of *Indarctos*.

| | | | M ¹ | | | | | M ² | | |
|----------------------------|--------|--------------------|----------------|------|------|------|-----|----------------|------|------|
| | | | Ba | L | Bp | Hp | Hm | Ba | L | Bm |
| <i>Indarctos vireti</i> | | | | | | | | | | |
| Can Llobateres | VP 633 | dext. | 24.5 | 19.5 | 20.6 | — | — | 27.9 | 19.0 | 17.2 |
| " | VP 646 | | 22.4 | 19.6 | 21.0 | 9½ | 9.8 | 27.3 | 19.7 | 17.8 |
| <i>Indarctos arctoides</i> | | | | | | | | | | |
| Montredon | Mtn 17 | sin. | 24 | 22.2 | 22.2 | — | — | 29.3 | 20.5 | 18.8 |
| " | | sin. ¹ | 27.0 | 22.5 | 24.0 | — | — | 31.0 | 24.0 | — |
| Orignac | | dext. ¹ | 24.6 | — | 22.0 | — | — | 28.2 | 22.0 | — |
| <i>Indarctos atticus</i> | | | | | | | | | | |
| Samos ¹ | | | 29.0 | 26.0 | 28.5 | 15.2 | — | 34 | 26 | — |
| Samos II ² | | | 28.3 | — | 26.2 | — | — | 30.0 | 26.5 | — |

¹ After HELBING.² After THENIUS.

TABLE 5. Measurements of skull and mandible of *Indarctos*.

| | <i>I. vireti</i> | | <i>I. arctoides</i> | | <i>I. atticus</i> | <i>I. anthracitis</i> | |
|---------------------------------------|------------------|--------|---------------------|---------------------|--------------------|-----------------------|--------------|
| | VP 646-7 | VP 633 | Type | Pfaff. ¹ | Samos ² | Samos ³ | Mte. Bamboli |
| Skull | | | | | | | |
| Basal length | 300 | — | — | — | e310? | e325 | — |
| Palatal length | 150 | — | — | — | e151 | e162 | — |
| Width over condyles | 65.0 | — | — | — | — | e74 | — |
| Mandible | | | | | | | |
| Length, C to condyle | 218 | a265 | — | — | e246 | e243 | — |
| Height, coronoid process | — | e115 | — | — | e98 | e111 | — |
| Depth under P ₄ | 43 | a53 | a41 | 44.0 | — | 54.0 | 46 |
| Depth under M ₂ | 48 | 60 | 46 | 49.5 | — | 61.0 | 46 |
| Length M ₁ —M ₃ | 67 | 72 | a65 | — | — | — | 68 |

¹ Pfaffstetten, after THENIUS.

² Samos I, juvenile, after HELBING.

³ Samos II, adult, after THENIUS.

specimen, which may be compared with the corresponding bone in *I. atticus* from Concud, in *Arctodus*, and in the black bear. Of all these the Can Llobateres bone is by far the least bear-like, with a longer and more constricted neck than the others. The *Indarctos* bone from Concud shows a more advanced bear type, although its neck is still somewhat longer than in *Ursus*. Both forms of *Indarctos* have large sustentacular facets of identical shape, but the ectal facet is more reduced in *I. atticus*.

The graceful build of the Can Llobateres astragalus again emphasizes the slenderness of the *I. vireti* skeleton and its heritage from more nearly digitigrade ancestors.

MT 2 is the only metatarsal bone preserved. It is rather long and powerful, exceeding the largest MC 2 by 9.0 per cent of the length of the latter bone. In *Arctodus* the corresponding figure is only 4.7 per cent, while in the black bear the metatarsal is shorter than the metacarpal. Again, this is obviously a trait retained from more fast-running ancestors.

The specimens of MT 2 from Concud are about as long as the *I. vireti* bone,

but they are plumper and heavier. They are much shortened relative to the Concud MC 2, so that the relationship in *I. atticus* resembled that of modern bears more closely than *I. vireti*.

Sexual dimorphism

There is an apparent sex dimorphism in the size of the jaws and teeth (Tables 1, 3, 5) and also in the postcranial bones. VP 633 is probably a male, while the skull and mandible VP 646—647 is probably a female. The isolated canines VP 651—656 are quite large and probably male, while the specimen without a number is probably female. At Can Purull, too, both sexes are probably represented, the type of *I. vireti* being female, and the second jaw, with markedly larger teeth, male. Such a degree of sex dimorphism would be equivalent to that found in larger members of the genus *Ursus* (KURTÉN 1955).

Phyletic position

Indarctos vireti stands out as the most

primitive known species of the genus. In the dentition, the premolars are less reduced than in other *Indarctos*, and the head and jaws are slimmer and more lightly built. The limb bones indicate a lightness and fleetness of foot very different from the orthodox bear image. It may well have been a more active,

predaceous carnivore than the modern bears in general.

In an evolutionary perspective, *I. vireti* retains many characters from the ancestors of the bears. Its closest relative is evidently *I. arctoides* of the later Pontian, which most probably was a direct descendant of the Vallesian spe-

TABLE 6. Measurements of limb bones in *Indarctos* and other Ursidae.

| | <i>Indarctos</i> | | | | | <i>Arctodus</i> | <i>Ursus</i> <i>americanus</i> |
|--------------------|------------------|------------|--------|-------------------|--------------------|-----------------|-----------------------------------|
| | Can | Llobateres | Concud | Rancho La Brea | UF 5639 Florida | | |
| Humerus | | | | | | | |
| Length | e290— | — | — | — | — | 497 | 304 |
| Shaft width | 24.3 | — | — | — | — | 43.5 | 29.6 |
| Distal width | 75.4 | — | — | — | — | 126.8 | 84 |
| Dist. artic. width | 50.6 | — | — | — | — | 97 | 55½ |
| Unciform | | | | | | | |
| Dist. anteropost. | 27.9 | 25.2 | — | — | — | 38.5 | 21.3 |
| Dist. transverse | 21.2 | 22.3 | — | — | — | 39.7 | 19.0 |
| Depth | 24.5 | 24.6 | — | — | — | 50.8 | 24.2 |
| MC II | | | | | | | |
| Length | 70 | 78 | — | 115 | 118 | 96.8 | 63.7 |
| Prox. anteropost. | 27.8 | 25.4 | 24.0 | 29.3 | 28.8 | 30 | 19.2 |
| Shaft width | 12.0 | 12.8 | 13.8 | 14.0 | 14.0 | 13.4 | 10.9 |
| Distal width | 20.0 | 19.5 | — | 22.9 | — | — | 17.3 |
| MC III | | | | | | | |
| Length | — | — | — | — | — | 104 | 68.8 |
| Prox. anteropost. | 25.5 | — | — | — | — | 31.6 | 21.5 |
| Shaft width | 14.4 | — | — | — | — | 14 | 11.1 |
| MC IV | | | | | | | |
| Length | e83 | — | — | — | — | 106.2 | 72.2 |
| Prox. anteropost. | 24.5 | — | — | — | — | 31 | 20.0 |
| Shaft width | 15.7 | — | — | — | — | 15.8 | 11.8 |
| Astragalus | | | | | | | |
| Width | 36 | — | — | 43.1 | — | 86.2 | 42.0 |
| Length | 45.2 | — | — | 48.8 | — | 79 | 39.4 |
| Width, trochlea | 29.0 | — | — | 32.0 | — | — | 31.4 |
| Width, head | 25 | — | — | 32.4 | — | — | 25.3 |
| Width, sust. facet | 17.7 | — | — | 20.8 | — | — | 16.8 |
| Width, ectal facet | 14.0 | — | — | 7.8 | — | — | 14.7 |
| MT II | | | | | | | |
| Length | e85 | — | — | 87 | 86 | 101.3 | 58.8 |
| Prox. anteropost. | 28 | — | — | 31.0 | 30.5 | 36.8 | 18.3 |
| Shaft width | 14.5 | — | — | 15.0 | 17.8 | 16.3 | 10.7 |

cies. The position of the Italian form *I. anthracitis* (= *lawillardii*) is at present uncertain; it may be a precociously specialized form. *Indarctos atticus* of the Turolian, on the other hand, is more advanced with larger cheek teeth, more reduced premolars, heavy and powerful jaws, and ursine limb proportions. This species, too, may well have arisen from *I. vireti*.

Ursavus brevihinus (Hofmann)

For synonymy see THENIUS (1949b).

Material. Teeth of two individuals (Can Llobateres): Specimen A, left and right P¹ and P⁴, left M¹ and M², right M¹ fragment, left and right C₁, P₃, P₄, M₁—M₂, left M₃; specimen B, left P⁴, M¹, M², M₁; left and right C₃.

Description

For dimensions see tables 7—9.

The lower canines are less flattened in cross section than in *Ursus*, and more pointed and higher crowned. The posterior edge is sharp, and there is a prominent crest along the lingual side from the tip to the cingulum at the enamel base. The upper canines are also sharply pointed and have a comparatively broad base. Their posterior crest is very sharp, while the anterior ridge, which arises from the basal cingulum, is less developed than in the lower canines.

The anterior premolars are dorsoventrally flattened, one-rooted unicuspid with a longitudinal ridge. P₄, which has two roots, has a distinct posterior cusp in addition to the main cone; both lie on the same longitudinal ridge. The enamel of this tooth tends to wrinkle on the inner cingulum.

P⁴ is comparatively large, and the size difference between specimens A and B is marked. Presumably A, which tends to larger dimensions in all the teeth, is a male, while B is a female. The protocone of P⁴ shifts backward in the evolution of the Ursidae; in the present

form it lies just anterior to the notch between paracone and metastyle. The protocone lobe is rather small, and the actual cusp lies in the posterior part of the lobe; it is low and sharply pointed.

M₁ has a trigonid which retains much of the canid carnassial facies with a high protoconid, a rather large paraconid and a small, simple metaconid lying somewhat posterior to the protoconid. The talonid is a simple, basined structure, much broader than the trigonid, with a large hypoconid and a low, ridge-like, bipartite entoconid. The enamel is smooth; there is a small external cingulum.

M₂ is smaller than M₁. The anterior lobe is broader than the posterior. The protoconid and metaconid, which form the summit of the crown, lie beside each other and are connected by a transverse ridge, which divides the middle field into a small anterior and a large posterior basin. Notches in the outer and inner walls separate the trigonid and talonid. Of the talonid cusps, only the entoconid is individualized. The middle field is nearly smooth.

The single M₃ is somewhat damaged but clearly had an ovoid outline and an almost flat, slightly wrinkled surface surrounded by a rim without any individual cusps.

M¹ is broadly quadrangular with a large paracone, a smaller metacone and two inner cusps showing up along the inner ridge. There is no distinct parastyle, but the anteroexternal corner of the crown protrudes distinctly. The inner cingulum is large, the outer small; the enamel is mostly smooth but has a slight tendency to wrinkling in the valleys and along the cingular border.

M² is not unlike a miniature replica of its homologue in *Indarctos*. It has a large paracone with a longitudinal ridge and smooth outer wall; it is separated from the metacone by a deep notch. The metacone is smaller but of the same type. An oblique ridge extends from the metacone to the inner (protocone) ridge, separating

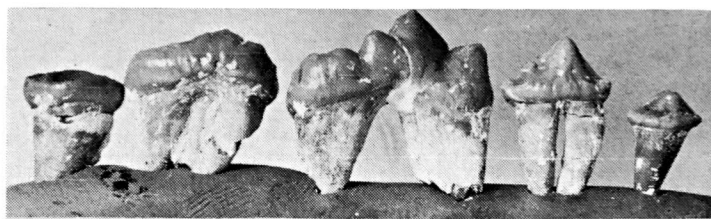


FIG. 6. *Ursavus brevirhinus*, left lower cheek teeth, Can Llobateres specimen A. 1 1/2 nat. size.



FIG. 7. *Ursavus brevirhinus*, same specimen as fig. 6. 1 1/2 nat. size.

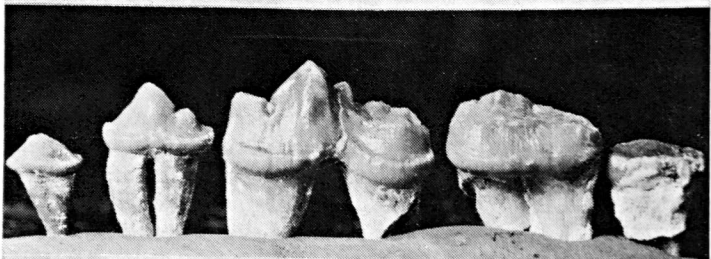


FIG. 8. *Ursavus brevirhinus*, same specimen as figs. 6—7. 1 1/2 nat. size.

the talon from the trigon. The protocone itself is only developed as a lingual flexure in the inner ridge. The middle field is only faintly wrinkled, and the flat talon, which slopes gently outward, is quite smooth except for the low bordering rim and the small protuberance of the internal cusp. A small cingulum borders the paracone and metacone; the inner cingulum is somewhat larger.

Ursavus primaevus (Gaillard)

For synonymy see THENIUS (1949b).

Material. Right and left M^2 (the former described and figured by CRUSAFONT 1959), Can Llobateres. Right lower jaw with M_1 — M_3 , Can Ponsich.

Description

M_1 resembles that of *U. brevirhinus*

but is more elongated, clearly lower crowned, and with a relatively longer paraconid. As in *U. brevirhinus*, the talonid carries one outer and two inner cusps. The talonid basin forms a straight fore-and-aft furrow which is continued up to the hind edge of the protoconid, which thus has a vertical excavation of this face of the cusp.

M_2 is much larger than in *U. brevirhinus* and its talonid shows a greater development of the cusps. There are two well separated inner cusps and one outer cusp in this part of the tooth. The transverse ridge between protoconid and metaconid is again present, and is notched in the middle. As in *U. brevirhinus* it separates the anterior and posterior basins, both of which are well developed.

M_3 is also larger than in *U. brevirhinus* and forms a basin rimmed by a slightly raised border on which only the protoconid has a certain individuality.

TABLE 8. Measurements of canines and precarnassial premolars in *Ursavus*.

| | P ¹ | | Ci | | P ₃ | | L | P ₄ | | H |
|--------------------------------|----------------|-----|----|-----|----------------|-----|-----|----------------|-----|---|
| | L | B | L | B | L | B | | L | B | |
| <i>Ursavus brevirobinus</i> | | | | | | | | | | |
| Can Llobateres, A | 6.9 | 4.8 | — | 7.6 | 6.2 | 4.3 | 9.2 | 5.4 | 5.4 | |
| Steyregg, type (After THENIUS) | — | — | — | — | 6.6 | 3.6 | 8.0 | 3.9 | — | |
| <i>Ursavus primaevus</i> | | | | | | | | | | |
| Oppeln | — | — | — | — | — | — | 9.6 | 5.1 | — | |
| „ | — | — | — | — | — | — | 9.4 | 4.9 | — | |

minent, but there is no outer cusp, and the talon slopes outward as in *U. brevirobinus*. The middle field is intensely wrinkled, mostly in the transverse direction, while the talon has a system of radiating wrinkles in its posteroexternal part. There is a distinct cingulum at the base of the paracone, and a large lingual cingulum extends from the protocone to the talon.

The mandibular ramus is markedly curved in shape, probably indicating that the condyle was raised well above the occlusal plane of the cheek teeth.

The masseteric fossa extends forward to a point below the front end of M₃. The depth of the ramus below M₂ is 24.8 and below M₃ 24.0 mm., measured on the internal side. The width of the ramus beneath M₂ is 10.3 mm.

The size of the teeth compares closely with those from La Grive (see Tables 7, 9).

Notes on the history of *Ursavus*

Vallesian members of the genus *Ursavus*

TABLE 9. Measurements of lower molars of *Ursavus*.

| | L | M ₁ | | Lt | L | M ₂ | | M ₃ | | |
|-----------------------------|------|----------------|------|------|------|----------------|------|----------------|---|--|
| | | B | | | | Ba | Bp | L | B | |
| <i>Ursavus brevirobinus</i> | | | | | | | | | | |
| Can Llobateres, A | 17.6 | 8.6 | 11.6 | 13.1 | 9.1 | 8.4 | 8.6 | — | | |
| „ B | 15.0 | 7.5 | 9.9 | — | — | — | — | — | | |
| Steyregg, type ¹ | 16.2 | 7.2 | — | 11.8 | 7.4 | — | — | — | | |
| Göriach ¹ | — | — | — | 11.7 | 8.4 | — | — | — | | |
| „ | — | — | — | 11.8 | 8.7 | — | 6.8 | 6.5 | | |
| <i>Ursavus primaevus</i> | | | | | | | | | | |
| Can Ponsich | 21.2 | 9.5 | 14.7 | 15.9 | 9.9 | 9.2 | 9.7 | 8.5 | | |
| La Grive | 20.6 | 10.4 | 14.0 | 14.8 | — | — | 10.8 | 8.3 | | |
| „ | — | — | — | 15.1 | 9.2 | 8.8 | — | — | | |
| Deinothere Sands | 20.4 | 10.1 | — | — | — | — | — | — | | |
| Oppeln | 19.2 | 10.1 | — | 14.4 | 9.6 | 9.4 | — | — | | |
| „ | 19.4 | 10.0 | — | 14.2 | 9.6 | 9.5 | — | — | | |
| <i>Ursavus depereti</i> | | | | | | | | | | |
| Luzinay | — | 11.4 | — | 17.6 | 10.8 | 11.2 | — | — | | |
| Melchingen ² | 23.5 | 12.5 | — | 17.3 | 11.8 | 10.6 | — | — | | |

¹ After THENIUS.

² After FRICK.

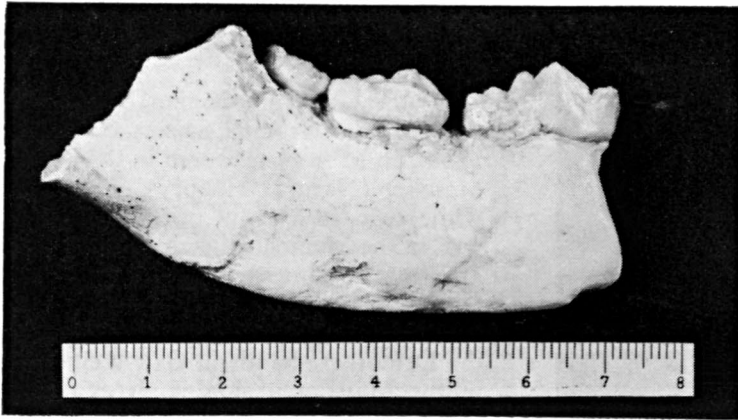


FIG. 13. *Ursavus primaevus*, right mandible, Can Ponsich. 1/1 nat. size.

have hitherto been little known. It now appears that both the typical Vindobonian species *U. brevirohinus* and *U. primaevus* survived into Vallesian times, in common with many other Vindobonian holdovers.

To facilitate comparison, metric data on various ursavi have been collected in tables 7—9.

By far the largest local sample of a single *Ursavus* species available at present is that of *U. elmensis* Stehlin from the early Burdigalian fissure filling at Wintershof-West (DEHM 1950). This is also the most primitive species of the genus, and so is a useful standard of comparison. The material was studied

by one of us (Kurtén) in the Museum of the University, Munich.

The next larger species, *U. brevirohinus*, has been found at several localities of Vindobonian age. Original measurements were taken by Kurtén on material from Kieferstadt and Steinheim am Albuch. The Kieferstadt specimen (KOKEN 1888; SCHLOSSER 1899) is a cast of a right maxilla in the Basel Museum (NHMB A.S. 88); the Steinheim specimen, also a cast of a right maxilla, is in the same museum (NHMB Sth. 751). The latter was regarded as a subspecies of *U. primaevus* by DEPERÉT & GOMEZ (1928) but we regard it as *U. brevirohinus*. In addition, measurements of the

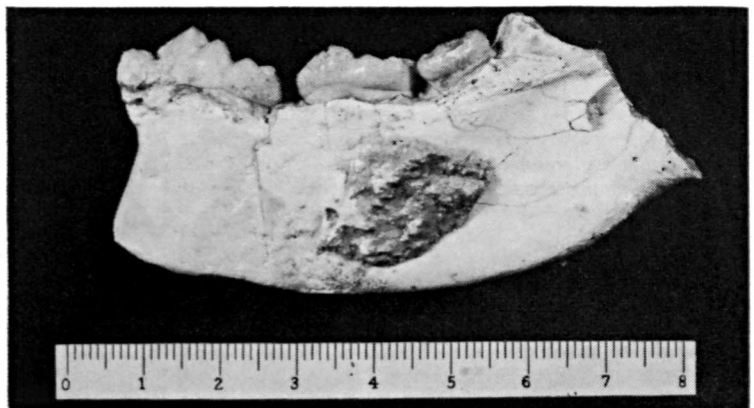


FIG. 14. *Ursavus primaevus*, same specimen as fig. 13. 1/1 nat. size.

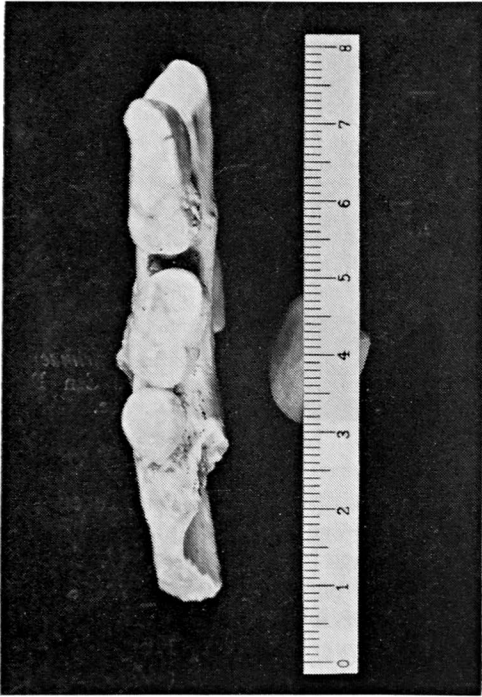


FIG. 15. *Ursavus primaevus*, same specimen as figs. 13—14. 1/1 nat. size.

type (from Steyregg) and of specimens from Göriach have been provided by THENIUS (1949b).

Of the late Vindobonian *U. primaevus* from La Grive (DEPÉRET & GOMEZ 1928), an M^2 was measured in the British Museum (Natural History), BM 5318, while casts of various other teeth were seen in the Munich collection. Here were also measured casts of the specimens from Oppeln (Neudorf) described by WEGNER (1913). A lower carnassial from the Deinothere Sands in Gau Weinheim, in the Museum of Mainz, is evidently also *U. primaevus*. WEITZEL & TOBIEN (1952) referred the Deinothere Sands *Ursavus* to *U. depereti*, but they are distinctly inferior in size to that species and agree well with *U. primaevus*. Since the Can Llobateres and Can Ponsich material proves that this species survived into post-Vindobonian (Vallesian) times, there is no reason to refer the Weinheim material differently.

Ursavus depereti Schlosser, the Turolian species, is represented by the lower

TABLE 10. Measurements of the dentition of *Ursavus elmensis*, Wintershof-West.

| | N | O.R. | M | S.D. | V |
|----------------------|----|-----------|------------|------|-----|
| P^4 , length | 5 | 9.5—11.5 | 10.52±0.33 | 0.74 | 7.0 |
| width | 5 | 6.3— 7.4 | 6.94±0.20 | 0.45 | 6.5 |
| height (external) | 5 | 5.7— 6.4 | 6.14±0.13 | 0.29 | 4.7 |
| M^1 , length | 16 | 9.9—12.3 | 10.80±0.14 | 0.56 | 5.2 |
| width | 15 | 8.8—11.5 | 10.39±0.16 | 0.61 | 5.9 |
| height of paracone | 13 | 4.5— 5.2 | 4.82±0.06 | 0.22 | 4.3 |
| height of metacone | 13 | 4.1— 4.8 | 4.49±0.07 | 0.24 | 5.3 |
| M^2 , length | 4 | 9.2—10.0 | 9.50±0.18 | — | — |
| width | 4 | 8.3— 8.8 | 8.60±0.12 | — | — |
| height of paracone | 4 | 3.4— 3.8 | 3.55±0.09 | — | — |
| P_4 , length | 4 | 8.0— 8.6 | 8.32±0.14 | — | — |
| width | 4 | 3.5— 4.0 | 3.85±0.12 | — | — |
| height (external) | 4 | 4.5— 5.1 | 4.80±0.17 | — | — |
| M_1 , length | 13 | 12.6—14.3 | 13.63±0.19 | 0.69 | 5.1 |
| width | 13 | 5.3— 6.7 | 6.22±0.11 | 0.41 | 6.6 |
| length of trigonid | 10 | 8.2— 9.7 | 9.02±0.20 | 0.64 | 7.1 |
| height of protoconid | 9 | 5.7— 6.6 | 6.30±0.11 | 0.32 | 5.1 |
| height of hypoconid | 11 | 3.4— 4.4 | 3.86±0.08 | 0.28 | 7.3 |
| M_2 , length | 10 | 9.7—11.2 | 10.38±0.16 | 0.50 | 4.8 |
| anterior width | 9 | 5.9— 6.7 | 6.40±0.12 | 0.36 | 5.6 |
| posterior width | 10 | 5.6— 6.3 | 6.04±0.08 | 0.26 | 4.4 |
| height of protoconid | 6 | 3.6— 3.9 | 3.72±0.06 | 0.15 | 4.0 |
| height of hypoconid | 5 | 3.1— 3.3 | 3.20±0.03 | 0.07 | 2.2 |
| height of metaconid | 6 | 3.5— 4.0 | 3.78±0.08 | 0.19 | 5.1 |
| M_3 , length | 3 | 5.3— 6.9 | 6.20±0.47 | — | — |
| width | 3 | 4.2— 5.4 | 4.87±0.35 | — | — |

TABLE 11. Average lengths of cheek teeth in samples of *Ursavus* expressed as percentages of means for *U. elmensis*.

| | | P ⁴ | M ¹ | M ² | P ₄ | M ₁ | M ₂ | M ₃ |
|-------------|-----------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| Burdigalian | <i>U. elmensis</i> | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| Vindobonian | <i>U. brevirhinus</i> | 108 | 119 | 140 | 96 | 119 | 113 | 110 |
| | <i>U. primaevus</i> | 137 | 135 | 170 | 114 | 145 | 141 | 174 |
| Vallesian | <i>U. brevirhinus</i> | 114 | 113 | 136 | 111 | 120 | 126 | 139 |
| | <i>U. primaevus</i> | — | — | 181 | — | 153 | 153 | 156 |
| Turolian | <i>U. ehrenbergi</i> | 138 | 153 | 205 | — | — | — | — |
| | <i>U. depereti</i> | 195 | 180 | 235 | — | 172 | 167 | — |
| | <i>U. sp.</i> | 123 | — | — | — | — | — | — |

teeth from Luzinay (DEPÉRET & GOMEZ 1928), while the Melchingen data are from FRICK (1926). The upper dentition is represented by the Soblay material in Lyon (VIRET & MAZENOT 1949); here is also found the smaller *Ursavus* sp. figured by VIRET (1949).

The Turolian species *U. ehrenbergi* (Brunner) is only known from a skull fragment with the upper dentition, described anew by THENIUS (1947).

We do not follow STROMER (1928, 1940) and THENIUS (1949b) in uniting the two species *U. brevirhinus* and *U. primaevus*. The combined variation in these would greatly exceed that in other species of *Ursavus*, and the two evidently represent quite distinct foci, in size as well as morphology. The separation of the two species is evident in the lengths and widths of M¹ and M² (see Table 7). Important morphological differences were noted in the description of the

Spanish material. It is now evident that the two species existed side by side in Europe during a long period of time, which constitutes definitive proof of specific distinction.

A measure of the evolution and differentiation in *Ursavus* can be obtained by expressing the lengths of the cheek teeth in local and temporal samples as a percentage of the corresponding mean values for the Burdigalian *U. elmensis* from Wintershof-West (see Table 10). The data are summarized in Table 11. In the Vindobonian, the two species *U. brevirhinus* and *U. primaevus* are distinct but not very strongly separated. Both are larger than *U. elmensis* and have changed somewhat in relative proportions; for instance, P⁴ is relatively small in both, and M² is elongated. So is M₃, but only in *U. primaevus*.

In the Vallesian, the situation is basically similar, but both species are

TABLE 12. Average size index for cheek tooth lengths in samples of *Ursavus*, compared with *U. elmensis*.

| Species | Locality | | Age | Size |
|-----------------------|-----------------|-------|-------------|-------|
| <i>U. depereti</i> | Various | | Turolian | 188.5 |
| <i>U. ehrenbergi</i> | Euboea | | Turolian | 162.8 |
| <i>U. sp.</i> | Soblay | | Turolian | 123 |
| <i>U. primaevus</i> | Can Llobateres | | Vallesian | 161.5 |
| <i>U. primaevus</i> | La Grive | Upper | Vindobonian | 152.6 |
| <i>U. primaevus</i> | Oppeln | Lower | Vindobonian | 135.3 |
| <i>U. brevirhinus</i> | Can Llobateres | | Vallesian | 118.3 |
| <i>U. brevirhinus</i> | Various | | Vindobonian | 115.7 |
| <i>U. elmensis</i> | Wintershof-West | | Burdigalian | 100 |

TABLE 13. Measurements of M₂ in early Ursinae.

| | <i>Protursus simpsoni</i> | <i>Ursus</i> (Ruscinian) | | Perpignan | Paris |
|--------------------|---------------------------|--------------------------|---------------|-----------|-------|
| | | Weze | Baroth-Köpecz | Lyon | |
| Length | 11.8 | ca. 18½ | 18.4 | 20.5 | 20.7 |
| Width, anterior | 6.9 | 11.2 | 11.2 | 12.2 | 12.8 |
| Width, posterior | 6.0 | — | 11.0 | 12.0 | 13.2 |
| Height, protoconid | 3.7 | 7.6 | 7.3 | — | 7.5 |
| Height, hypoconid | 2.6 | — | 6.0 | — | 7.1 |

slightly larger. *Ursavus brevirhinus* now shows elongation of M₃ and the two species differ a little more in size.

In the Turolian of Soblay, Luzinay, Melchingen and Euboea a new situation is found. An *Ursavus* of *brevirhinus* type still survives (the *U.* sp. of Soblay), but the *primaevus* type seems to have vanished, replaced by two still larger species, *U. ehrenbergi* and *U. depereti*. The former shows progressive characters in the reduction of P⁴ and elongation of M² relative to M¹, while *U. depereti* is more conservative in relative proportions, though well distinguished by its large size.

Information on phyletic growth may be summarized by averaging out the percentages for individual teeth (Table 12). It is suggested that *U. primaevus* and *U. brevirhinus* arose by branching from *U. elmensis*. Both species flourished in the Vindobonian and Vallesian, increasing slightly in size. *Ursavus brevirhinus* may have given rise to the *U.* sp. of Soblay. The two large species, *U. ehrenbergi* and *U. depereti*, both of which show a tendency to lophodonty in the upper molars, may have been derived from *U. primaevus*. This character, as well as the size and complication of P⁴ in *U. depereti*, makes it unlikely that that species was ancestral to later ursids (VIRET 1949). THENIUS (1947) considered that *U. ehrenbergi* may have been close to the *Ursus* line. Comparison of dental morphology would however seem to favour a derivation of ursine

bears from some form more closely related to the *U. brevirhinus* branch.

If so, however, the derivation probably dates well back into pre-Vallesian times; for, as will be shown below, a more *Ursus*-like form was already in existence in the Vallesian.

Protursus Crusafont & Kurtén, new genus

Type species. *Protursus simpsoni*, new species.

Diagnosis. Small Ursidae in the *Ursavus* size range but with talonid of M₂ more elongate, clearly narrower than trigonid, and tapering posterad; talonid with five distinct cusps, of which two external, one posterior, and two internal, and a flat middle field; trigonid with the three original cusps plus a fourth, anteroexternal cusp, together enclosing a transverse basin.

Age. Vallesian.

Protursus simpsoni

Crusafont & Kurtén, new species

Type. Left M₂ (Figs. 16—17).

Derivatio nominis. We take pleasure in naming this species for George Gaylord Simpson, leader in contemporary paleomammalogy.

Diagnosis. Sole known species of genus; for dimensions of type see Table 13.

Age and locality. Vallesian, Can Llobateres, Spain.

Description

The crown is completely preserved and unworn, except for a wear facet on the summit of the metaconid. The anterior root is broken; it was fairly large and expanded transversely. The posterior root is expanded anteroposteriorly but compressed laterally, and tapers to a point.

The outline of the tooth is elongate and somewhat irregular. Its maximum width is at the middle of the trigonid, from where it tapers posterodorsally, but its long axis is distinctly curved, so that the outer wall is concave and the inner convex. The front end is rounded. There is no cingulum.

The cusp pattern is generally bear-like. The protoconid and metaconid, which are at the same level, are the largest cusps. The protoconid carries a sharp anteroposterior keel, while the metaconid is more faintly keeled; its summit is obliterated by wear in this specimen. A transverse ridge from the protoconid to the metaconid is interrupted by the deep valley between the cusps. The valley connects with the transverse valley in front of the protoconid, which in turn is bounded in front by the low, transverse paraconid. The paraconid is separated from the metaconid by a notch and from the anteroexternal cusp by another. The last-mentioned cusp lies at the anteroexternal corner of the tooth and so completes the enclosure of the valley, while in *Ursus* there is usually an outlet in this region. The trigonid thus carries four distinct cusps.

The talonid is elongate, with low relief. Externally there are two well-defined cusps, of which the anterior corresponds to the main hypoconid of *Ursavus*, while the posterior may correspond to the element usually termed a hypoconid in *Ursus*. The hind edge of the tooth carries a blunt hypoconulid. On the inner rim there are again two

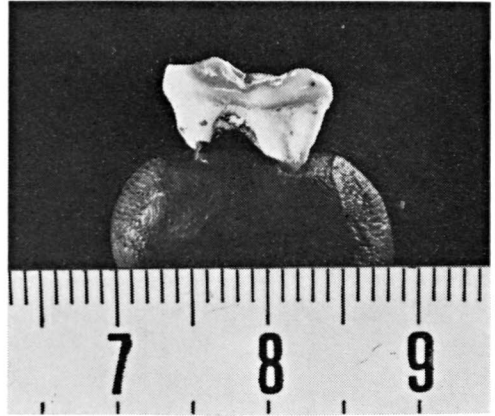


FIG. 16. *Protursus simpsoni*, type, left M₂, Can Llobateres. 2/1 nat. size.

distinct, faintly defined cusps. The middle field or talonid basin is practically featureless.

Comparison

In comparison with *Ursavus* this tooth appears progressive because of the relatively weak development of the two main cusps (protoconid and metaconid), the great elongation of the talonid, and the large size of the posterior talonid cusps. The well-developed posterior "hypoconid" and "entoconid" are only represented in *Ursavus* by small accessory elements, while in progressive *Ursus* they are the major talonid cusps. The condition in *Protursus*, in which the anterior and posterior cusps are subequal, is thus intermediate.

When compared with a Ruscinian specimen of *Ursus* (a jaw from Perpignan in the Natural History Museum, Paris), *Protursus* appears more primitive. The talonid is still quite narrow, while in the Ruscinian specimen it is actually broader than the trigonid (but in other Ruscinian *Ursus* the talonid may be narrower than the trigonid: see Table 13). The posterior "hypoconid" is quite dominant in the Rusci-



FIG. 17. *Protursus simpsoni*, same specimen as fig. 16. 2/1 nat. size.

nian form, and the anterior or original hypoconid may be represented by a small section of the outer rim just behind the protoconid, bounded by two small notches. On the other hand, the two entoconid elements are still of about the same size in the Ruscinian bear, just as in *Protursus*. The trigonid of the Ruscinian form is more reduced in front, and the anteroexternal cusp, which is presented in *Protursus*, has been lost. (It is however retained in *Helarctos*.)

The twist of the tooth axis, which is so pronounced in the *Protursus* specimen, cannot be matched in *Ursavus* or *Ursus*.

The length of the specimen is the same as in *Ursavus brevirohinus*, but it is considerably narrower and probably came from a somewhat smaller animal, perhaps about the size of *U. elmensis* (in which the width is about the same). It is less than two-thirds the size of the Ruscinian *Ursus* M₂ (Table 13).

Phyletic position

Protursus, being more advanced than *Ursavus* and more primitive than *Ursus*, may represent a step in the sequence leading from the former genus to the

latter. Its temporal position is correct for a link of this kind. It is much younger than the earliest known *Ursavus*, which dates from the Burdigalian, and may thus be derived from an early form of that genus. This would allow all of the Vindobonian, and perhaps part of the Burdigalian, for its evolution. Again it is distinctly older than any true *Ursus* or any of the tremarctine bears. Both of these groups make their appearance in the Ruscinian-Hemphillian, so that there is all of the intervening Turolian to account for the evolution of higher ursids.

Such inferences, however tempting, must yet remain provisional, for the evidence obtained from a single tooth can hardly justify very far-reaching conclusions. The peculiar twist of the tooth axis may, for instance, indicate that the Can Llobateres species was off the main line of ursine evolution. Should this be so, perhaps another species of *Protursus* was the true ancestor of *Ursus*. It is therefore necessary to await the discovery of additional material. Meanwhile, the new genus *Protursus* may be provisionally referred to the subfamily Ursinae as its earliest and most primitive representative.

Amphicyon cf. *major* De Blainville

Material. Left and right M₂, left C_i, right humerus, Can Llobateres. Left C_i, Can Ponsich.

Description

The second molars from Can Llobateres, which are only slightly worn, resemble entirely the specimens from Sansan described and figured by GINSBURG (1961: pl. II fig. 1, pl. IV fig. 1). The dimensions of the two specimens are 23.0×17.2 (right) and 23.6×17.1 (left). Sansan lengths are 24.5 and 25.0 mm.

The lower canines differ from those

in *Indarctos* in several characters. The root is flatter and shorter, there is no internal cingulum and the inner ridge is stronger, more nearly straight and closer to the midline of the tooth; the crown curves sharply outward. The same characters are seen in the Sansan material.

The canine from Can Llobateres, which is much worn, measures 21.5×15.0 at the base of the enamel. The corresponding data for the Can Ponsich tooth are 19.5×13.2 . The latter tooth is unworn, but the tip is broken. The morphological resemblance is so complete that we tentatively record the species from Can Ponsich on the basis of

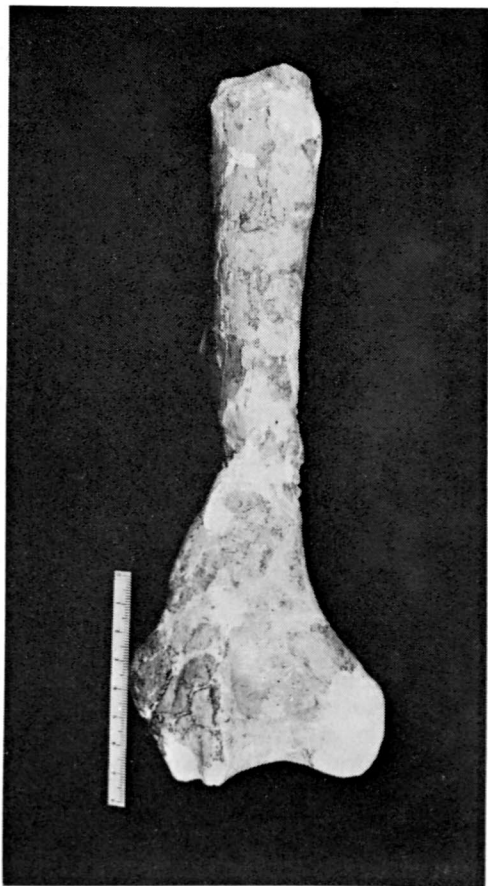


FIG. 18. Cf. *Amphicyon*, right humerus, Can 3/8 nat. size.

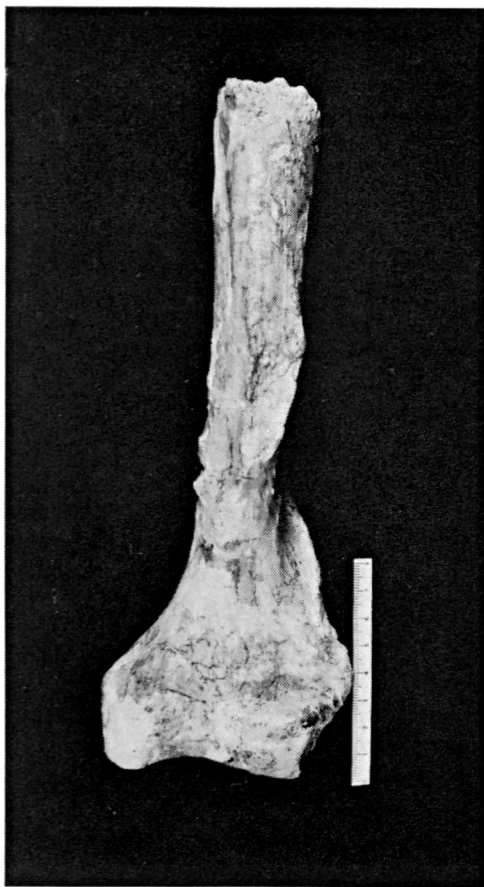


FIG. 19. Cf. *Amphicyon*, same specimen as fig. 18. Ca. 3/8 nat. size.

this canine, but it is also possible that the canine belongs to the other canid to be described below.

Dimensions of C_i from Sansan cited by GINSBURG are again slightly larger (lengths 23.4 and 26 mm.).

Can Llobateres has also yielded a humerus which may belong to the same species as the teeth. The proximal end is damaged so that only about three-fourths of the bone is left; the preserved part is about 250 mm. long. The least transverse width of the shaft is 28.0, while the greatest distal width is approximately 90 mm.

The size of this bone, which exceeds

that in *I. vireti*, shows that it belonged to a large carnivore, while its morphological characters preclude reference to the other great predator of this locality, *Machairodus aphanistus* Kaup. Since this humerus is of the paraursoid type (as defined in VILLALTA & CRUSAFONT 1943) it would seem natural to refer it to the *Amphicyon*. However, its characters differ considerably from those found in the Sansan *A. major* as described by GINSBURG (1961: fig. 9, pl. XVII fig. 1, pl. XVIII fig. 1).

According to the figures and description, the olecranon fossa in *A. major* is small, elongate, deep and triangular in shape. In our specimen it is larger, rather shallow, short and broad: its shape is that of an equilateral triangle rather than the isosceles triangle on a narrow base in the Sansan form. It is of course possible that the intra- or interspecific variation in the genus may suffice to accommodate both variants, for this character in our specimen is quite similar to that in a humerus of *A. cf. lemanensis* Pomel described and figured by HÜRZELER (1945). Oddly enough, the humerus of *Hemicyon sansaniensis* figured in the same paper by Hürzeler shows a fossa of the same type as that in *A. major* described by GINSBURG. GINSBURG (1961) does not ascribe any postcranial material from Sansan to *Hemicyon*.

The following alternative explanations of this situation are suggested:

(1) The variation within *Amphicyon* accommodates both types of humeri, in which case the humerus from Can Llobateres may belong to the same species as the teeth.

(2) The humerus from Can Llobateres is *Hemicyon*, while the teeth are *Amphicyon*; in this case the determinations in HÜRZELER's study should be exchanged.

(3) The humerus from Sansan ascribed by Ginsburg to *Amphicyon* is in reality *Hemicyon*, in which case, again, the humerus from Can Llobateres would be *Amphicyon* like the teeth.

We favour alternatives (2) and (3) but are unable to choose between them.

The deltoid ridge is powerfully developed in the Can Llobateres humerus, and runs down to the lower third of the bone; in this respect the resemblance to *A. major* (as figured by GINSBURG) is great. On the other hand, marked differences are seen in the supinator ridge. Its alar portion is relatively shorter than in the Sansan form, with a notable development of the part corresponding to the extensor carpi; while the area of origination of the extensor communis digitorum on the external side forms a marked projection not visible in the Sansan humeri.

The part corresponding to the entepicondylar ridge is poorly preserved, and the foramen cannot be studied. The distal articulation is horizontal and cylindrical in shape, as normally in ursids and paraursoid dogs. The surface for the insertion of the m. coracobrachialis, although not completely preserved, seems relatively large.

The size of this specimen is only slightly inferior to that in the humeri from Sansan, for which GINSBURG gives the length of 333 mm.; it agrees fairly well with the size of *A. crassidens* described and figured by HELBING (1929).

TABLE 14. Measurements of canid calcaneus from Can Ponsich.

| | |
|--|----------|
| Greatest length from tuber to cuboid facet | 93.2 mm. |
| Greatest depth | 39.8 |
| Greatest width at level of posterior astragalar facet | 39.2 |
| Distance from upper border of anterior facet to cuboid facet | 49.8 |
| Least width of tuber calci | 16.3 |
| Depth of tuber calci | 28.3 |

TABLE 15. Measurements of caudal vertebrate.

| | Canidae indet. Can Ponsich | <i>Indarctos vireti</i> Can Llobateres | |
|-----------------------|-------------------------------|---|------|
| Length | 52.5 | 39.4 | 45.6 |
| Least width at middle | 15.3 | 10.0 | 8.0 |
| Least depth at middle | 14.2 | 8.3 | 7.2 |

Unfortunately Helbing's figure does not show the olecranon fossa.

Since the characters of this bone do not agree well with the material from Sansan, there remains some uncertainty as to its taxonomic status and indeed as to that of the dental material. For this reason, our reference to the genus and species *Amphicyon major* must remain tentative.

Canidae indet.

Material. Right calcaneus, caudal vertebra, distal end of metapodium, all from Can Ponsich.

Description

In addition to the canid C_i tentatively attributed to *Amphicyon major*, a few postcranial bones of a large canid have been unearthed at Can Ponsich. The most significant specimen is the right calcaneus, which is certainly not *A. major* and probably not amphicyonine at all; it is entirely different from the Sansan material (GINSBURG 1961) and from the *A. major* calcaneus found at Buñol (CRUSAFONT & TRUYOLS 1957).

The bone is long and slender in proportions, with a narrow and elongate sustentacular part quite different from that in *Amphicyon*. The groove for the tendon of the flexor digitorum is deep and well developed, as in primitive canids generally, while *Amphicyon* is bear-like in this respect. The posterior end of the tuber calci is compressed, not expanded as in *A. major*, and the insertion on the plantar side for the ab-

ductor of the fifth digit is weakly developed, in contrast with *Amphicyon*.

The cuboid facet is triangular in shape but much narrower and deeper than in *A. major*. The posterior articular facet for the astragalus has a shorter radius of curvature than in *A. major*. The groove for the insertion of the accessorius of the m. perforans on the inner face is well marked, but does not extend back to the tuber calci as in the Sansan form. The anterior astragalar facet is much longer than in *Amphicyon*, and its extension reaches the border of the cuboid facet, as in the hemicyonines.

The bone thus differs greatly from the type seen in *A. major* and *A. crassidens* as well as the ursids; the great length from the anterior astragalar facet to the cuboid facet is especially noteworthy. The combination of characters in the specimen indicates that its possessor was digitigrade rather than plantigrade as the amphicyonids. There are various incompletely known large ca-

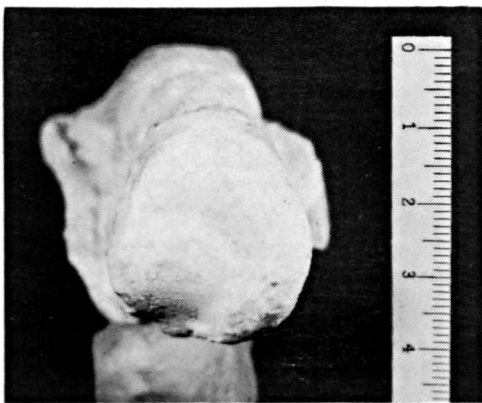


FIG. 20. Canidae indet., right calcaneus, Can Ponsich. Ca. 9/10 nat. size.

nids from the Vindobonian and Pontian that might fill the bill, for instance *Agnotherium* or some other member of the Thaumastocyoninae (HÜRZELER 1940).

The dimensions of the calcaneus are listed in table 14.

The caudal vertebra evidently comes from an animal of about the same size as the calcaneum. It is much larger than the specimens of *I. vireti* from Can Llobateres (Table 15). The distal fragment of metapodial also belonged to a carnivore of this size; its greatest transverse diameter is 22.2 mm.

References

- CRUSAFONT, M. 1950: La cuestión del llamado Meóico español. — *Arrahona* 1950 (1): 1—10. Sabadell.
- 1958a: Endemism and Paneuropeism in Spanish fossil mammalian faunas, with special regard to the Miocene. — *Comment. Biol. Soc. Sci. Fennica* 18:1—31.
- 1958b: Nuevo hallazgo del pongido vallesiense *Hispanopithecus*. — *Biol. Inform. AEPV* 13—14:37—44.
- 1959: Primer hallazgo en España del género *Ursavus* (Carnivora, Ursidae). — *Notas y Com. Inst. Geol. Min. España* 55: 137—144.
- 1964: La biota de Can Llobateres (Sabadell) y su significación biológica. — *Curs. y Conf. Inst. Lucas Mallada* 9:177—179.
- 1965a: Observations à un travail de M. Freudenthal et P. Y. Sondaar sur des nouveaux gisements à Hipparion d'Espagne. — *Proc. Kon. Akad. Wet. Amsterdam, B* 68 (3):121—126.
- 1965b: El desarrollo de los caninos en algunos driopitécidos del vallesiense de Catalunya. — *Notas Com. Inst. Geol. Min. España* 80:179—192.
- 1972a: Los Primates fósiles de España. — *Enciclopedia Mundo*. Barcelona.
- 1972b: Les *Ischyrictis* de la transition Vindobonien-Vallesien. — *Palaeovertebrata* 5:253—260.
- CRUSAFONT, M. & CASANOVAS, L. 1973: *Mammalia Tertiaria Hispaniae*. — *Foss. Catal. I. Animalia* 121:1—198.
- CRUSAFONT, M. & HÜRZELER, J. 1961: Les pongidés fossiles d'Espagne. — *C. R. Acad. Sci. Paris* 252:919—920.
- 1969: Catálogo comentado de los Póngidos fósiles de España. — *Acta Geol. Hispanica* 4:44—48.
- CRUSAFONT, M. & PETER, G. 1969: Contribution à l'étude des Hyaenidae. La sous-famille des Ictitheriinae. — *Ann. Paléont.* 55:89—128.
- CRUSAFONT, M. & TRUYOLS, J. 1947: Sobre el descubrimiento de un nuevo yacimiento del Meóico en el Vallés. — *Bol. Inst. Geol. Min. España* 60:71—107.
- 1951: Hallazgo del *Plesiodimylus chantrei* Gaill. en el Meóico del Vallés. — *Notas Com. Inst. Geol. Min. España* 22:3—30.
- 1957: Descubrimiento del primer yacimiento de mamíferos miocénicos de la cuenca valenciana. — *Notas Com. Inst. Geol. Min. España* 48:1—20.
- 1960: Sobre la caracterización del Vallesiense. — *Notas Com. Inst. Geol. Min. España* 60:109—126.
- CRUSAFONT, M. & VILLALTA, J. F. 1951: Los nuevos mamíferos del neógeno de España. — *Notas Com. Inst. Geol. Min. España* 22:1—25.
- DEHM, R. 1950: Die Raubtiere aus dem Mittel-Miozän (Burdigalium) von Wintershof-West bei Eichstätt in Bayern. — *Abh. Bayerischen Akad. Wiss., Math.-Nat. Kl., (N.F.)* 58:1—141.
- DEPÉRET, Ch. & GOMEZ, F. 1928: Sur l'*Indarctos arctoides* et la phylogénie des ursidés. — *Bull. Soc. Géol. France*, (4) 28:149—160.
- FRICK, C. 1926: The Hemicyoninae and an American Tertiary bear. — *Bull. Amer. Mus. Nat. Hist.* 56(1):1—119.
- GINSBURG, L. 1961: La faune des carnivores miocènes de Sansan (Gers). — *Mém. Mus. Nat. Hist. Nat., n.s.* C9:1—190.
- GOLPE, J. M. 1971: Suiformes del Terciario español y sus yacimientos. — *Paleont. y Evol.* 2:1—197.
- HARTÉNBERGER, J. L. 1965: Les Cricetidae de Can Llobateres (Néogène d'Espagne). — *Bull. Soc. Géol. France* (7)7:487—498.
- 1966: Les rongeurs du Vallésien (Miocène supérieur) de Can Llobateres (Sabadell, Espagne): Gliridae et Eomyidae. — *Bull. Soc. Géol. France* (7)8:596—604.
- HELBING, H. 1929: Zur Osteologie von *Amphicyon crassidens* Pomel. — *Verh. Naturf. Ges. Basel* 40:280—294.
- HÜRZELER, J. 1940: Über felinoide Caniden des europäischen Miozäns. — *Verh. Schweiz. Naturf. Ges.* 1940:150—151.
- 1945: Zur Kenntniss des Extremitätenskelettes einiger oligocaener und miocaener Carnivoren Europas. — *Ecl. Geol. Helv.* 38:635—655.
- KOKEN, E. 1888: Ueber die miocänen Säugethier-Reste von Kieferstädtl in Oberschlesien und über *Hyaenarctos minutus* Schlosser MS. — *Sitzber. Ges. Naturf. Fr. Berlin* 1888:44—49.
- KURTÉN, B. 1955: Sex dimorphism and size trends in the cave bear, *Ursus spelaeus*

- Rosenmüller and Heinroth. — Acta Zool. Fennica 90:1—48.
- > 1966: Pleistocene bears of North America. 1. Genus *Tremarctos*, spectacled bears. — Acta Zool. Fennica 115:1—120.
- MERRIAM, J. C. & STOCK, C. 1925: Relationships and structure of the short-faced bear, *Arctotherium*, from the Pleistocene of California. — Carnegie Inst. Washington Publ. 347:1—35.
- PETTER, G. 1963: Contribution a l'étude des mustélidés des bassins néogènes du Vallès-Pénédès et de Calatayud-Teruel. — Mém. Soc. Géol. France n.s. 42(97):1—44.
- > 1967: Mustélidés nouveaux du Vallésien de Catalogne. — Ann. Paléont. 53:93—114.
- SCHLOSSER, M. 1899: Über die Bären und bärenähnlichen Formen des europäischen Tertiärs. — Palaeontographica 46:95—147.
- SIMONS, E. L. & PILBEAM, D. R. 1965: Preliminary revision of the Dryopithecinae (Pongidae, Anthropeidea). — Folia primat. 3: 81—152.
- STROMER, E. 1928: Wirbeltiere im obermiozänen Flinz Münchens. — Abh. Bayer. Akad. Wiss. 32(1):1—71.
- > 1940: Die jungtertiäre Fauna des Flinz und des Schweiss-Sandes von München. Nachträge und Berichtigungen. — Abh. Bayer. Akad. Wiss. n.s. 48:1—102.
- THALER, L. 1966: Les rongeurs fossiles du Bas-Languedoc dans leur rapports avec l'histoire des faunes et la stratigraphie du tertiaire d'Europe. — Mém. Mus. Nat. Hist. Nat. n.s. C 17:1—295.
- THENIUS, E. 1947: *Ursavus ehrenbergi* aus dem Pont von Euböa (Griechenland). — Sitzber. Akad. Wiss. Wien 156:225—249.
- > 1949a: Über die Gehörregion von *Indarctos* (Ursidae, Mamm.). — Sitzber. Akad. Wiss. Wien 158:647—653.
- > 1949b: Die Carnivoren von Göriach (Steiermark). Beiträge zur Kenntnis der Säugetierreste des steirischen Tertiärs IV. — Sitzber. Akad. Wiss. Wien 158:695—762.
- > 1959: *Indarctos arctoides* (Carnivora, Mammalia) aus dem Pliozän Österreichs nebst einer Revision der Gattung. — N. Jahrb. Geol. Pal., Abh. 108:270—295.
- TOBIEN, H. 1955: Neue und wenig bekannte Carnivoren aus den unterpliozänen Dinotheriensanden Rhein Hessens. — Notizbl. Hess. Landesamt. Bodenforsch. Wiesbaden 83:7—31.
- VAN COUVERING, J. A. 1972: Radiometric calibration of the European Neogene. — In: BISHOP, W. W. & MILLER, J. A. (ed.): Calibration of hominoid evolution: 247—271. Edinburgh.
- VILLALTA, J. F. & CRUSAFONT, M. 1943: *Indarctos vireti*, nova sp. un nuevo úrsido del grupo de los hemiciónidos del Mioceno superior del Vallés-Penedés. — Consejo Sup. Invest. Cien. Madrid 1943:45—62.
- > 1945: Nuevas aportaciones al conocimiento de los carnívoros potiensés del Vallés-Penedés. — Miscellánea Almera, Publ. Inst. Geol. Barcelona 7:81—124.
- VIRET, J. 1949: Observations complémentaires sur quelques mammifères fossiles de Soblay. — Ecl. Geol. Helv. 42:469—476.
- VIRET, J. & MAZENOT, G. 1949: Nouveaux restes de mammifères dans le gisement de lignite pontien de Soblay (Ain). — Ann. Paléont. 34:1—42.
- WEGNER, R. N. 1913: Tertiär und umgelagerte Kreide bei Oppeln (Oberschlesien). — Palaeontographica 40:175—274.
- WEITZEL, K. & TOBIEN, H. 1952: *Indarctos* und *Ursavus* (Carnivora, Mamm.) aus den unterpliozänen Dinotheriensanden Rhein Hessens. — Notizbl. Hess. Landesamt. Bodenforsch. Wiesbaden 6(3):7—14.

Appendix: Abbreviations

The following abbreviations appear in the tables of measurements:

L length, B breadth, H height, a anterior, p

posterior, Lt trigonid length, Hp paracone height, Hm metacone height. All cusp heights measured from enamel base to summit.

126. ANN-MARIE FORSTÉN: Variation in and between three populations of *Mesobippus bairdii* Leidy from the Big Badlands, South Dakota. 16 pp. (1970).
127. BENGT WESTERLING: Rumen ciliate fauna of semi-domestic reindeer (*Rangifer tarandus* L.) in Finland: composition, volume and some seasonal variations. 76 pp. (1970).
128. WOLFRAM NOODT: Zur Ökologie der Copepoda Harpacticoidea des Küstengebietes von Tvärminne (Finnland). 35 S. (1970).
129. R. B. ANGUS: A revision of the beetles of the genus *Helophorus* F. (Coleoptera: Hydrophilidae). Subgenera *Orphelophorus* d'Orchymont, *Gephelophorus* Sharp and *Meghelophorus* Kuwert. 62 pp. (1970).
130. ELAINE ANDERSON: Quaternary evolution of the Genus *Martes* (Carnivora, Mustelidae). 132 pp. (1970).
131. BJÖRN KURTÉN: The Neogene wolverine *Plesiogulo* and the origin of *Gulo* (Carnivora, Mammalia). 22 pp. (1970).
132. C.-H. von BONSDORFF, T. FORSSTEN, M.K.S. GUSTAFSSON and B.-J. WIKGREN: Cellular composition of plerocercoids of *Diphyllobothrium dendriticum* (Cestoda). 25 pp. (1971).
133. RAINER ROSENGREN: Route fidelity, visual memory and recruitment behaviour in foraging wood ants of the genus *Formica* (Hymenoptera, Formicidae). 106 pp. (1971).
134. GÖRAN GYLLENBERG and A. J. P. GORE: Some preliminary models for the energy flow of a *Chorthippus parallelus* (Zett.) (Orthoptera) population. 25 pp. (1972).
135. BRIT GODSKE BJÖRKLUND: The rotifer fauna of rock-pools in the Tvärminne archipelago, Southern Finland. 30 pp. (1972).
136. MARTIN MEINANDER: A revision of the family Coniopterygidae (Planipennia). 357 pp. (1972).
137. ANN-MARIE FORSTÉN: Size and shape evolution in the cheek teeth of fossil horses. 31 pp. (1973).
138. M. K. S. GUSTAFSSON: The histology of the neck region of plerocercoids of *Triaenophorus nodulosus* (Cestoda, Pseudophyllidea). 16 pp. (1973).
139. H. SILFVERBERG: A revision of the genus *Prosmidia* Weise (Coleoptera, Chrysomelidae). 54 pp. (1973).
140. BJÖRN KURTÉN: A history of Coyote-Like Dogs (Canidae, Mammalia). 38 pp. (1974).
141. KARI VEPSÄLÄINEN: The life cycles and wing lengths of Finnish Gerris Fabr. species (Heteroptera, Gerridae). 73 pp. (1974).
142. GÖRAN BYLUND: The taxonomic significance of embryonic hooks in four European *Diphyllobothrium* species (Cestoda, Diphyllobothriidae). 22 pp. (1975).
143. RAUNO LINNAVUORI: Revision of the Cicadellidae (Homoptera) of the Ethiopian Region III. Deltocephalinae, Hecalini. 37 pp. (1975).
144. MIGUEL CRUSAFONT PAIRÓ and BJÖRN KURTÉN: Bears and Bear-Dogs from the Vallesian of the Vallés-Penedés Basin, Spain. 29 pp. (1976).

Helsingin Yliopiston
Metsäkirjasto

Exchange — Austausch — Echange
SOCIETAS PRO FAUNA ET FLORA FENNICA
Snellmaninkatu 9—11 Snellmansgatan
00170 Helsinki 17 Helsingfors

For sale — Verkauf — En vent
Akateeminen Kirjakauppa — Akademiska Bokhandeln
00100 Helsinki 10 Helsingfors

ISBN 951-661-013-7
ISSN 0001—7299
PRINTACO