The Hemicyoninæ and an American Tertiary Bear

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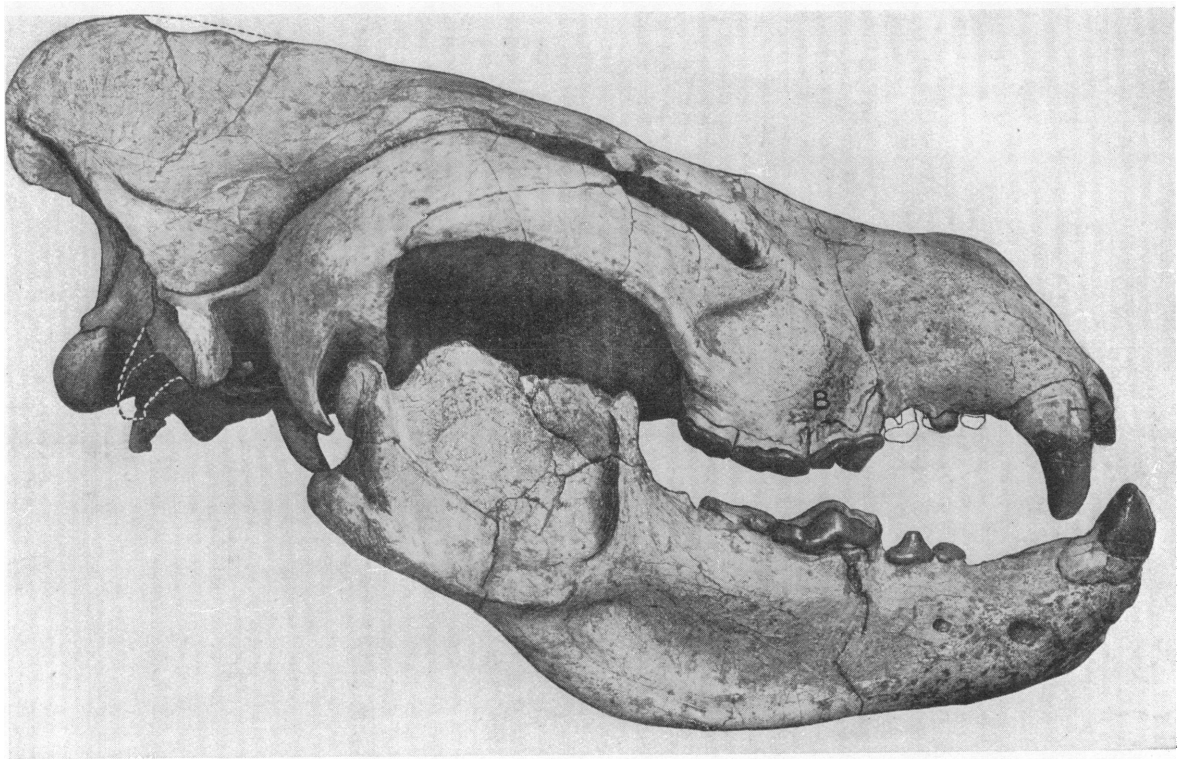

Frontispiece. *Hemicyon* (*Canis*) *ursinus* (Cope), skull and jaws of neotype, from Santa Fé Miocene, New Mexico, Amer. Mus. No. 21101. × 3/7. (See p. 38.)

INTRODUCTION

The present paper deals primarily with the extinct genera, *Hemicyon*, *Dinocyon*, *Hyænarctos*, and *Ursavus*. These four genera, hitherto distributed among the Canidæ and Ursidæ, are here referred, upon the presence of certain characters of mandible and teeth, to a morphological group, the Hemicyoninæ. A number of new or little-known species are described, the published species are revised, and the affinities of the group and of its several genera are discussed on the basis of a restudy of the classic material in certain European museums and upon rich new evidence secured during the course of the writer's researches in the Pliocene and Miocene of California, and the Miocene of New Mexico and Colorado. The closing sections of the paper, as a means of throwing this morphological group into stronger relief, are devoted to a discussion of true bear, its unexpected discovery in the American Lower Pliocene (*Plionarctos edensis*, new genus and species), and its reported occurrences in the Tertiary deposits of Europe. Our finding *Hyænarctos* in the Pliocene of California, our quite unexpected discovery of remains of *Hemicyon* in the Miocene of California, and our securing of a nearly complete skeleton (Frontispiece) of the latter genus from the Miocene of New Mexico have occurred in rapid succession. That *Hemicyon* as well as *Hyænarctos* was represented in the Western Hemisphere is believed to be one of the most interesting revelations of recent palæontological research. The following studies and results are presented as a step toward the solution of certain phylogenies, interesting in themselves and all-important in their bearing on broader palæontological and geological problems, such as the history and correlation of the respective faunas and determination of coeval strata of the Western and Eastern Hemispheres.

The unfortunate confusion that exists in the literature in regard to *Hemicyon* and *Ursavus* and the material variously referred to each, to *Dinocyon*, to *Amphicyon*, and to *Pseudocyon*,[1] and to a less degree to the forms of *Hyænarctos*, has been due largely to the generally fragmental nature of the fossil data and to the non-recognition of the coexistence in the same formations of the widely differing genera *Hemicyon* and *Amphicyon*. In this regard, one of the new species of *Hemicyon* described in the sequel is of particular import in calling attention to the presence of *Hemicyon* in the fauna of La Grive St. Alban with *Ursavus* and the genotypic species of *Dinocyon*. The latter genus, which at best is but

[1] *Pseudocyon* Filhol, synonymous with *Amphicyon* Lartet. (See note under *Hemicyon sansaniensis* Lartet, p. 51.)

little understood, has been unrecognized as yet in American deposits. *Hyænarctos* was widely distributed in the Pliocene, fragmentary remains being known from the horizons of America, Europe, and Asia. *Amphicyon* was coexistent with *Hemicyon* in the Miocene of America as in that of Europe, and perhaps present with *Hyænarctos* in the Pliocene of Asia and of America. At the moment, *Hemicyon* is the only one of the four genera that is represented either by associated upper and lower dentitions or by skull and associated skeletal elements. *Hyænarctos* is known only by the partial skull of the type and unassociated fragments of the upper and lower series.

The study of the material variously referred to *Hemicyon*, *Ursavus*, *Dinocyon*, *Hyænarctos*, *Amphicyon*, and "*Pseudocyon*," has called my attention to certain peculiar characters of the dentition and mandible,[1] which seem to be of unusual taxonomic value, in that they are present in *Hemicyon*, *Ursavus*, *Dinocyon*, and *Hyænarctos* alone of all known *megalocreodontic*[2] Carnivora. The new evidence thus indicates the desirability, for the matter of present convenience at least, of considering the genera, *Hemicyon*, *Ursavus*, *Dinocyon*, and *Hyænarctos*, as a morphologic group.[3] I call this group, as above noted, the Hemicyoninæ. To what

[1]The diagnostic value of mandibular characters, as well as those of the teeth, has been well substantiated in the case of certain of the Mammalia (mastodon and man). Osborn, H. F., 1916, 'Men of the Old Stone Age,' p. 100.

[2]Lydekker (1883, Pal. Indica, Ser. 2, X, pp. 179, 205), following a modification of a system adopted by Huxley in his classification of the dogs, notes that certain of the Mustelinæ and Melinæ may be divided according as the p^4 is smaller than the m^1, i.e., meionocreodonts, or larger than m^1, i. e., megalocreodonts.

[3]I employ "morphologic group" as a collective term for this particular assemblage of forms, the members of which though united by certain common characters are perhaps rather widely separated by others. I use this term to avoid the words "family" and "subfamily," and the implication of an idea of real relationship that the use of these Linnæan divisions might imply under present current usage. I would limit to the "subfamily" such restricted assemblages as are there referred by Miller and Pocock. To my mind the best evidence now is that such subgroups were already well differentiated from one another at an early date. Matthew (1924, Bull. Amer. Mus. Nat. Hist., L, p. 122) divides the Tertiary canids into two phyla which he derives from two White River ancestors, the small-bullæd *Daphænus* and the large-bullæd *Nothocyon*. Oligocene-Miocene representatives of canid forms are as common in our collections as representatives of early mustelids, procyonids, and ursoids are rare or absent. Certain dentitions from the mid-Pliocene of the Siwaliks, which in tooth form are typical of the recent genera *Lutra* and *Mellivora*, but which are too specialized to have themselves been ancestral to the genera of today, afford evidence of the probable presence, in the Pliocene or even at an earlier date, of dentitions typical in both form and formula of the recent genera. Until proven otherwise, an hypothetical derivation of subgroups separable by conformable characters must, in the writer's opinion, admit of as equally distinct an ancestry for each as that shown by Doctor Matthew for the canids. It should thus, amid the "Mustelidæ," distinguish the line of the large-bullæd-*megalocreodontic-Mustela* and *Mellivora* from that of the flat-bullæd-*Lutra-Conepatus* forms, and of the large-bullæd-*meionocreodontic-Meles* from the flat-bullæd-*Arctonyx*.

The morphological group, Hemicyoninæ, is certainly not as homogeneous an assemblage of forms as the "subfamily" of recent authors—per example, the Melinæ or Mustelinæ. The Hemicyoninæ, however, might well be covered by the older conception of the "subfamily," which included under the same term "Melinæ" (in unnatural association) the very widely differing genera *Meles*, *Arctonyx*, *Taxidæ*, and *Mellivora*. Or again, certain of the members of the Hemicyoninæ may have been even so far removed from one another, in all else but a somewhat parallel specialization of mandible and teeth, that the most loosely drawn conception of the term "family" might alone suffice. I refer here to the "conjoint Ursidæ" of Lydekker, in which he provisionally included (1883, p. 203) both the bears and the dogs, believing both to have been descended from one not too remote stem.

Matthew (as noted above) recognizes in the case of the dog the existence of two separate phyla that stretched far back into the Oligocene. In the writer's opinion, *Helarctos*, *Ursus*, and *Tremarctos* were probably as mutually distinct from as full early a date; and the ancestors of *Tremarctos* and of certain of the widely differing Miocene-Pliocene Hemicyoninæ acquired (either independently or by common inheritance) from yet more remote sources the tendency or tendencies that have since resulted in the below-noted unusual and somewhat similar mandibular adaptation in two forms so widely separated by dental and cranial characters.

extent these presumably somewhat interdependent specializations of the mandible, of the upper, and of the lower teeth represent parallel specializations on the part of otherwise differing or not too closely related forms, or of forms representative of distinct phyla, must await a fuller understanding of the osteology of these genera, which is as yet utterly unknown except in the case of *Hemicyon*. It must be noted, however, that the group, in whatever way considered, is not as homogeneous an assemblage as is the Amphicyoninæ, the Caninæ, or the Procyoninæ and Melinæ of recent authors,[1] the Ursinæ, or the Tremarctinæ.

Hyænarctos has heretofore been regarded as an ursid, and *Hemicyon* and *Dinocyon* have usually been classified as canids.[2] The skulls of *Hemicyon* and *Hyænarctos* (as seen in *Hemicyon ursinus* and *Hyænarctos sivalensis*) apparently have many characters in common, and resemble more the short-faced section of the contemporaneous amphicyons than any more recent form. The bulla differs from that of *Amphicyon*, but is situated anteriorly and more as in *Amphicyon* than in any recent genus.[3] In nowise bear-like are the unique development of the posterior cranium, the arrangement of the basi-cranial area, the *megalocreodontic* carnassials, the proportions of the limbs and of the tarsus, and the condition of the axis and vertebral column. Nor do the characters of the base of the skull, of the mandible, of the teeth, and of the skeleton, permit the placing of *Hemicyon* with the Caninæ. In the adaptation of the mandible, the Hemicyoninæ differ from the *megalocreodontic* Amphicyoninæ and Caninæ as the *meionocreodontic* arctotheres and *Tremarctos* differ from the true bears. The skull, limb, and foot characters (at least as seen in *Hemicyon*) are likewise too widely different from those of *meionocreodontic Tremarctos* to permit of the two being placed in the same group, though they do remarkably parallel one another in the "undivided" metaconid of m_1, and in the strikingly similar adaptation of the mandibular fossa, which are among the more important characters that separate *Tremarctos*

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[1]Hollister, 1916, Proc. U. S. Nat. Mus., XLIX, p. 143. Miller, G. S., Jr., 1924, Bull. U. S. Nat. Mus. No. 128, pp. 107, 114, etc. Pocock, 1921, Proc. Zool. Soc. London, p. 389.

[2]See Flower and Lydekker (1891, 'An Introduction to the Study of the Mammals, Living and Extinct,' p. 556), ". . . *Dinocyon* . . . , so far as its teeth are concerned, connects *Amphicyon* with the ursoid genus *Hyænarctos* so closely as to render it absolutely impossible to indicate any characters of family importance by which they can be distinguished.". Weber (1904, "Die Säugetiere," p. 535) places *Hemicyon* and *Hyænarctos* in the Ursidæ, and derives the Ursidæ from *Amphicyon* (p. 538). Zittel (1923, 'Grundzüge der Paläontologie,' pp. 469, 471) places *Hemicyon* and *Dinocyon* in the Cynodontinæ; *Hyænarctos* and *Ursavus* in the Ursinæ. Doctor Boule (1919, 'Les Grottes de Grimaldi,' I, p. 254) places *Hemicyon* and *Hyænarctos* in the ancestral line of *Ursus*, deriving *Ursavus* from *Hemicyon*, and *Hyænarctos* and *Ursus* from *Ursavus*.

[3]The amount of inflation of the bulla even within certain species is subject to considerable variation. For example, while the bulla in mature *Ursus* is typically unswollen and thus widely differing from the condition in *Canis*, in immature *Ursus* and *Tremarctos* it is considerably swollen and lacks the typical ossified meatus of the aged condition, and even in mature *Helarctos* tends to be moderately swollen. External flattening of the bulla in the bear is thus to a certain degree a condition of age. The degree of application of the post-glenoid and paroccipital processes about the bulla is evidently largely dependent upon the size of the latter.

from the true bear. (The non-anterior position of the deuterocone of the otherwise widely differing p^4, and the non-inflation of the differently situated bulla of *Tremarctos*, may scarcely be taken as similarities.)

The evident correlation of the mandibular adaptation with the development of the maxilla and teeth is discussed on a later page. The exact purpose is unknown. I have noted the appearance of a suggestive trace of such a fossa in certain specimens of the common raccoon. In the latter, strangely enough, the proportions and arrangement of the tarsus, the proportions of the limbs, and the general characters of the axis and of the vertebral column are much like those of the similar parts in *Hemicyon*, and noticeably differ from those in the cat, the dog, the bear, and the wolverene, etc. Moreover, it may be noted that when the upper teeth of *Procyon*, which, though characteristically different, are structurally readily comparable to the molars of *Hemicyon* (see Figs. 1A–1B), are hypothetically converted to the *Hemicyon* type, the result at each stage of such conversion is further and further from the bear type. Thus in the case of the p^4, the conversion to the hemicyonid condition being *megalocreodontic*, and that to the ursid-tremarctid condition being *meionocreodontic*, the lines of development in each case would necessarily follow opposite directions, and would not tend to cross. We might then say that the teeth of *Hemicyon* are more specialized than those of *Procyon*, and that the teeth of *Ursus* are either more primitive than those of *Procyon* or are specialized in a quite contrary direction.[1]

Interestingly enough, certain characters present in *Hemicyon* and lacking in the recent neotropical genus *Procyon* are present or to an extent suggested in the oriental genus *Ælurus*, as the alisphenoid canal, the depressed and less posteriorly produced palate, the greatly restricted bulla, and the slightly more prominent sagittal crest. A well-known study by Matthew[2] has shown the procyonid characters of the dog-like toothed White River form, *Phlaocyon*. This parallels to an impressive degree the recent genus *Bassaris*, but differs from it, among other characters, in the larger bullæ, in the condition of m_1, the reduction of the first digit of the pes, and in the presence of other (and perhaps to a certain

[1]A similar but less marked differentiation in development is noted in the Melinæ (as usually grouped) in the comparison of *Mellivora* with *Arctonyx* and *Meles*. In *Mellivora* the present megalocreodontic state of p^4 evidently was attained by enlargement (evenly continued, intermittent, or with retrogression, but with the same net result for enlargement). In *Meles*, the present meionocreodontic state of p^4 seemingly has been attained by a steadfast lack of progression or by enlargement followed by reduction. It might then well be considered that in *Mellivora* there has been a fixed plan for enlargement, and in *Meles* for non-enlargement. The condition of the p^4 in *Ursus* differs as markedly from that in *Canis* (or in *Procyon*) as does that in *Mellivora* from that in *Meles*. Further, in the milk dentition the dp^3 of *Ursus* is a simple two-rooted cone, versus the typical three-rooted carnassiform tooth of *Canis*, *Procyon*, and *Meles*.

[2]Matthew, W. D., 1899, Bull. Amer. Mus. Nat. Hist., XII, p. 131, Fig. 10 and Pl. VI.

degree primitive) characters which are also present in the genus *Hemicyon*. These are: the straightness and length of the facial profile, the breadth of the muzzle in relation to the frontal area, the restriction of the cranium relative to the face, the straighter posterior production of the occiput, and the retention of the alisphenoid canal and of m_3. It must be noted that the various species of *Bassaris* itself are variable to quite a considerable extent in the development of the p^4 and its deuterocone tubercles, the sectorial quality of the trigonid of m_1, the presence or absence of accessory tubercles in p_4, the size of the bulla, and the presence or non-development of the sagittal crest. However, the occurrence in the Oligocene of a form so closely approaching *Bassaris* may well be interpreted as emphatic evidence of the probable presence in the same epoch of forms as fully developed in the direction of *Procyon*, of *Ælurus*, of *Hemicyon*, and of *Ursus*. I do not wish to imply that *Hemicyon* ever lay as near to the Miocene or Oligocene ancestors of *Procyon*, *Bassaris*, *Ælurus*, or *Æluropus* as these greatly differing forms of today do to one another. A desire to transcribe the unknown in terms of the known and to visualize phylogenies may too frequently result in the attempt to interpret the extinct creatures of the past in terms of the surviving mammals of today; such is that interpretation of the present creature which argues that, being neither of the cat nor dog, it must perforce be of the bear tribe.

Our discovery of remains of typical ursine dentitions in the Lower Pliocene of Eden, California, as noted below, in association with those of a giant *Hyænarctos*, in calling attention to the heretofore unrecognized antiquity of the *meionocreodontic* bear form in America, tends to substantiate its reported but still questioned presence in the Tertiary of Europe, and at the same time further evidences the improbability of its hyænarctid descent. In the closing pages of this paper I describe and discuss these unique Eden remains and the recorded occurrences of Tertiary bear in Europe.

Except for the possibility that a fragmentary specimen from the Sables d'Orleans represents an Oligocene member of the Hemicyoninæ, the pre-Miocene representatives of the group are quite unknown. The Pliocene occurrence of *Hyænarctos*, Miocene occurrence of *Hemicyon*, and the general similarity of *Hemicyon* to the typical section of *Hyænarctos*, intimate that the latter and *Hemicyon* may have sprung from some not too distant common ancestor. Likewise, the stronger similarity, excluding the difference in size, existing between *Ursavus* of the Sansan Miocene and *Indarctos* of the Indian Pliocene suggests that the ancestry

of the latter may have in the Miocene passed near one of the species grouped under the former. The antiquity of individual forms, however, the disadvantage of a too close grouping of species represented by readily differentiable dentitions, and the danger of too quickly considering one form derivable from another, ever become more apparent.

The genus *Hemicyon* is at present known from two localities in the Upper Miocene of the Western Hemisphere, and from six localities in the Eastern Hemisphere which, though of probable equivalent age, are correlated by European writers with the mid-Miocene. *Ursavus* species of variable characters are reported, from some eight European localities likewise of apparent mid-Miocene facies. The reference to the same group of the peculiar (?) *U. pawniensis* of the American Upper Miocene as noted below is extremely doubtful. The seventeen species now loosely collected under *Hyænarctos* represent widely separate areas variably correlated with the mid-Miocene to Pliocene.[1] The type localities of the more typical section of the genus, which alone represent even a wider distribution than known *Hemicyon*, have been broadly correlated with phases of the Pliocene (overlooking the difference between the time scales of European and American writers). In three of these widely separated faunistic assemblages, those of the Eden, the Montpellier, and the Red or Coralline[2] Crag, there are found, in unexpected association with the respective *megalocreodontic* hyænarctid forms, *meionocreodontic* bear forms. Material representative of the second, "bear-like" molared, and at present less known section, includes two Indian and an Oregon species. These, like the remaining Indian forms, are from the Dhok Pathan zone, and are considered by Pilgrim[3] as of Pikermi age, and earlier than *H. sivalensis* of the typical section. It is noteworthy that the perhaps most specialized of all hyænarctid forms, that from Monte Bamboli,[4] should be found in a supposedly mid-Miocene assemblage correlated with the Stätzling stage, as it interprets a very specialized form as having been contemporaneous with the Stätzling *Hemicyon*. This examples the inadequacy of existing data on these extinct genera, as what may well be considered the least specialized of all known forms of *Hyænarctos* comes from the Upper Miocene of Maragha.

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[1]The reported Pleistocene age of a Chinese reference is unsubstantiated.

[2]Ray Lankester (1924, NATURAL HISTORY, XXIV, p. 655) contends that the terrestrial remains of the Red Crag were derived from the earlier Coralline Crag deposits and that the Red Crag itself should be assigned to the Pleistocene. J. Reid Moir (*loc. cit.*, p. 640) discusses the occurrence of Eolithic flint implements in the detritus bed lying at the base of the Red Crag.

[3]Pilgrim, G., 1913, Rec. Geol. Surv. India, XLIII, p. 278, *et seq.*

[4]Depéret, Charles, 1907, Proc. Seventh Int. Zool. Congress, Boston, p. 305 ("St. Gaudens stage of mid-Miocene").

The value of *Hemicyon* and *Hyænarctos* as time fossils must in the last analysis be dependent on a much fuller knowledge of the history of both. In other words, this must await the knowledge as to whether *Hemicyon* occurred alone in the Miocene, as our scant data now evidence, or existed fully developed at an earlier period, as we might well suppose; whether *Hemicyon* actually became extinct throughout its range previous to the appearance of *Hyænarctos;* and, in addition, whether typical *Hyænarctos* itself did not predate the Pliocene period. *Amphicyon* species, it must be noted, were to our best evidence present as such through the Miocene to the Lower Pliocene. The study that will alone lead to a truer understanding of the relationships of the European and American *Hemicyon-Hyænarctos* faunas and to a resulting more exact correlation of the Eastern and Western Tertiary is dependent upon the securing of additional fossil data, the reward of active and extensive work in the field.

Strange indeed it is that these great megalocreodont creatures should have so completely disappeared. Lydekker[1] interestingly suggests that ". . . it is not impossible that the more carnivorous nature of many of these forms, which is almost certainly indicated by the size and form of the carnassial, may have brought them into closer competition with the larger feline carnivores, and that not being such fleet animals they had not such good chances of obtaining their prey, and thus died out; while the meionocreodont forms, which, with the exception of the peculiarly situated polar bear, are not extensively carnivorous, have still remained, and hold their place among modern felines, without entering into direct competition with them." These megalocreodont forms, however, represent but one of the many recognized, and probable myriad of unrecognized, evanishments of wonderfully differentiated groups—further exampled among mammals by the chalicotheres, the uintatheres, the oreodonts, and in the case of the American continent by the once common and now vanished camels, horses, and rhinoceroses. But, in the writer's opinion, more remarkable than the disappearance of all these forms is the survival of the forms of today—remnants of the hazards and catastrophies of orogenetic movements, of changes of climate and food supply, of the depredations of pestilence, and of hostile hosts. Fossil specimens once supposed to belong to existing genera, when better known may well be found to be different and generically distinct; for the chance of recovering a direct progenitor of a particular form, through vagaries of habitat and

[1]Lydekker, 1883, Pal. Indica, p. 206.

paucity of the fossil record, is always remote. None the less, the antiquity of forms is ever becoming more apparent through the increase of fossil evidence, which witnesses the coexistence of species resembling those of recent time with genera now long extinct, as exampled by the bear-like and *Equus*-like species occurring with *Hyænarctos* and typical *Pliohippus* in the Eden Pliocene of California. The occurrence of human remains even with those of extinct Pleistocene mammals is perhaps yet to be definitely substantiated, but must not the lineage of higher forms in general have been as remote as that of the bear, the dog, the camel, and the horse, which were already highly developed in the Lower Pliocene. As Gaudry[1] has so well said, "Les progrès de la paléontologie ont pour résultat de faire découvrir une plus grande ancienneté des différents êtres . . . "

I take particular pleasure in acknowledging the courtesy of Dr. Smith Woodward of the British Museum, of Director Marcellin Boule of the Muséum d'Histoire Naturelle, Paris, and of Dr. Claude Gaillard of the Muséum des Sciences Naturelles, Lyon, in granting me access to the classic material in their respective institutions, and of Dr. Gunter, of the Florida Geological Survey, for the loan of the Florida molar. I would further express my debt to the work of the various authorities so frequently referred to throughout the text, and especially to the valued criticism of my friend Dr. W. D. Matthew. Finally, I would record my appreciation of the efforts of Mr. Rak and those field workers elsewhere named which have made these studies possible. The drawings, except where otherwise noted, were made under my personal supervision by Miss H. Deberard. The new material was prepared by Messrs. Charles Christman and Charles Falkenbach.

HEMICYONINÆ

CHARACTERS

Mandible with premasseteric fossa; tooth crowns moderate to low. Carnassials large and blades well developed; molars large, m^3 absent.

Premolars relatively small; $p\frac{1}{1}$ single-rooted; and $p\frac{2}{2}$ tending to be single-rooted to lost in *Hyænarctos*.

p^4, anteroposterior diameter equaling or slightly exceeding that of m^1, deuterocone at posterior base paracone and supported on separate root.

m^1, anteroposterior diameter slightly less (*Hemicyon ursinus*), to considerably exceeding (*Indarctos* and *Ursavus*) transverse diameter; inner ridge forming a moderate to strong wedge.

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[1]After Gaillard, C., 1899, Arch. Mus. Hist. Nat., Lyon, VII, p. 48.

m^2, heel absent (*Hemicyon* and *H. sivalensis*), or considerably developed (*Indarctos* and *Ursavus*).

m_1, protoconid situate median (*Hemicyon*), to anteromedian (*Hyænarctos* and *Ursavus*), blades developed, talonid forming a basin (except in *Dinocyon*), metaconid single (undivided) and noticeably posterior.

m_2, anteroposterior diameter less than that of m_1, protoconid-metaconid ridge distant from anterior tooth edge, talonid relatively short and narrowed posteriorly.

m_3 round and single-rooted (*I. punjabiensis*) to elongate and occasionally double-rooted (*H. ursinus*).

Peculiar skull and skeletal characters, as evidenced by the *Hemicyon ursinus* neotype (see p. 38).

The Amphicyoninæ-Caninæ and the Arctotheriinæ-Tremarctinæ thus differ from the Hemicyoninæ markedly as follows:

(A) In the *megalocreodontic* Amphicyoninæ and Caninæ the premasseteric fossa is absent, the crowns of the carnassials are high, and the blades strongly developed, the deuterocone of the p^4 is situate broadly antero-inwardly, and in m^1 the transverse diameter exceeds the anteroposterior diameter.

Also in the Amphicyoninæ:

m^1 is greatly extended transversely, and its protocone is strong and "crescentic."

m_1–m_2, the hypoconid is unusually prominent, and the inner cusps of the talonid are rudimentary to absent. (The external auditory meati and mastoid process are prominent, the bulla evidently moderately large.)

And in the Caninæ:

m^1 protocone tends to be anteromedian, the posterior tooth border to be concave.

m^2 is relatively reduced.

m_1 talonid is typically small and bicuspid. (The auditory bullæ are strongly inflated.)

(B) In the *meionocreodontic* arctotheres and *Tremarctos*, true carnassials are not developed, the p^4 is relatively minute, the deuterocone is posterior and the deuterocone root tends to be fused with the main posterior root (though in certain arctotheres it has been found to be partially separate); the premasseteric fossa suggests that of the hemicyonids, but it distinctly differs in form (Figs. 55A and E); the upper molars are moderately broad to typically narrow and elongate (in this to a certain degree suggesting the upper molars of *Indarctos* and *Ursavus*).

In tooth characters the members of the new group thus differ as much from the amphicyonids and canids, which they parallel in the *megalocreodont* character of the carnassials, as they do from the *meionocreodont* arctotheres and *Tremarctos*, which they parallel in the presence of a premasseteric fossa in the mandible, and the undivided metaconid of m_1. In the development of the basicranial area of the skull, *Hemicyon* is itself widely distinct from the dog and the bear, as it is from *Amphicyon*, which it, however, parallels to a certain extent in the general develop-

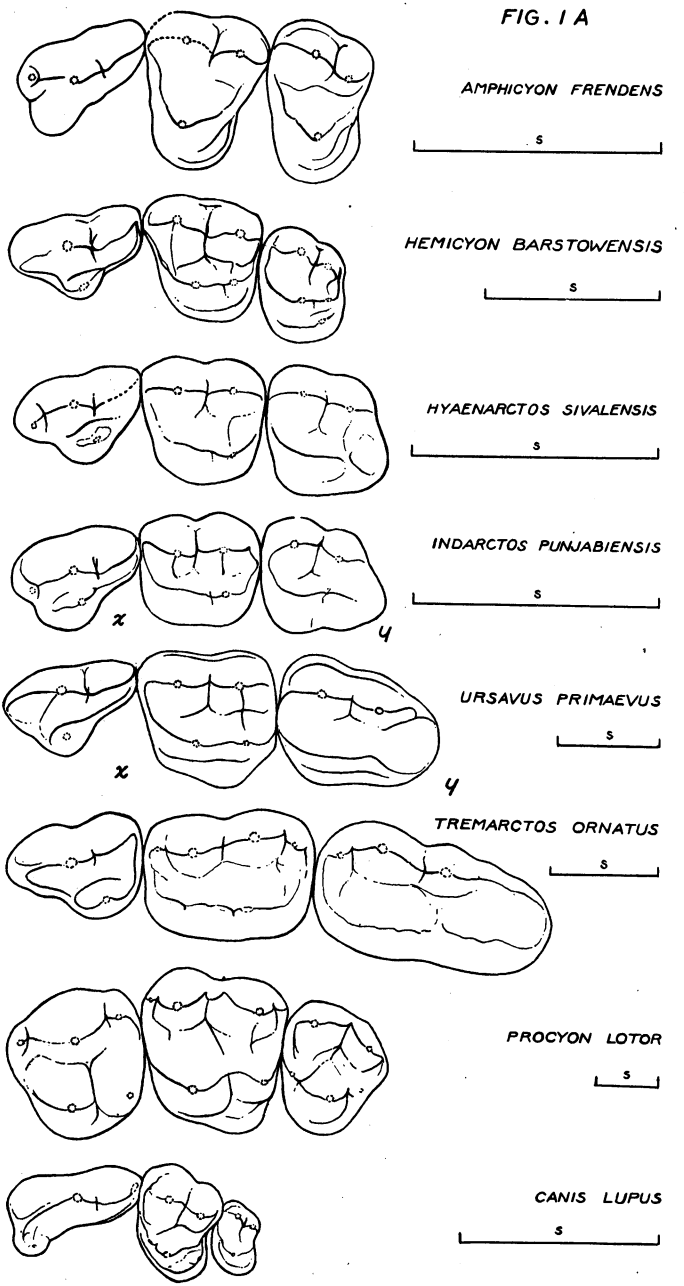


Fig. 1A. Comparative outline drawings of upper cheek-teeth of the type specimens of *Amphicyon frendens* Matthew; *Hemicyon barstowensis*, new species; *Hyænarctos sivalensis* Lydekker; *Indarctos punjabiensis* Lydekker (m^2 referred); *Ursavus primævus* Gaillard (m^2 referred); and specimens of *Tremarctos ornatus*, *Procyon lotor*, and *Canis lupus*. The anteroposterior diameter of p^4 (indicated by line "s") in each case has been brought to unity.

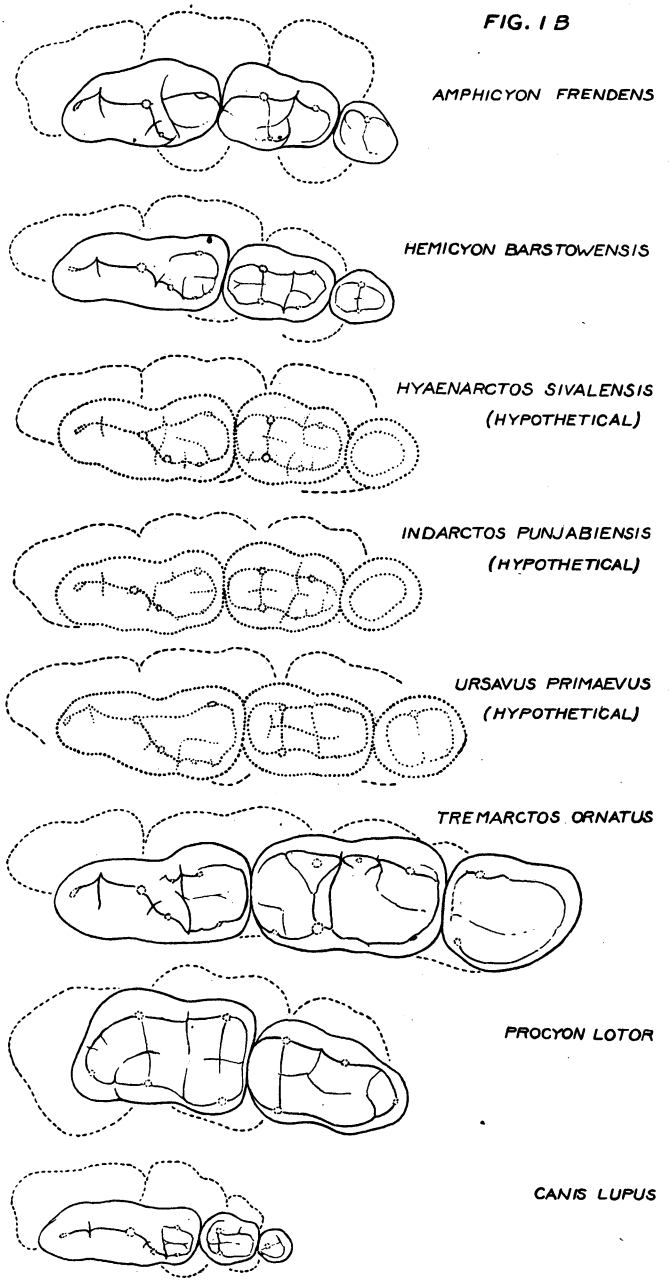


Fig. 1B. Comparative outline drawings of lower cheek-teeth (superimposed over Fig. 1A to show teeth occlusion). The teeth of the type specimens (solid outline) of *Amphicyon frendens* Matthew, *Hemicyon barstowensis*, new species; and of hypothetical *Hyænarctos sivalensis*, *Indarctos punjabiensis* and *Ursavus primævus* (dotted); of recent *Tremarctos*, *Procyon* and *Canis* (solid). Scale as in Fig. 1A.

ment of the cranium, location of the bullæ, etc. The characters of the vertebræ, limbs, and tarsus are likewise widely different from those of the dog and bear.

The adjacent diagrams (Figs. 1A–B) depict in outline the crowns of the upper and lower carnassials and molars of certain of the Hemicyoninæ, together with *Amphicyon*, *Tremarctos*, *Procyon*, and *Canis*. Each series has been scaled to the p^4, which has been brought to unit anteroposterior diameter (that of *U. primævus*, see actual diameter at "s"), the figured tooth thus being greatly enlarged over the actual in *Tremarctos*, and much-reduced in *Amphicyon*. A very homologous development of the tooth-crowns is manifest in *Hemicyon*, *Hyænarctos* and *Ursavus*, as contrasted with *Canis*, *Amphicyon*, *Procyon*, and *Ursus*. These four latter genera visibly represent four very diverse dental types. The first was already well established in the Oligocene; the other types presumably existed at as early a date, though that of the bear has not yet been recognized previous to the Lower Pliocene.

It is observed: (A) that the p^4 is of shearing structure in *Ursavus*, *Hemicyon*, *Amphicyon*, and *Canis*, of broad crushing form in *Procyon*, and weak non-carnassial type in the bear; (B) that the upper molars (compared to the unit-sized p^4) represent six or more peculiar specializations, being (1) rather symmetrically developed, as in *Hemicyon* and typical *Hyænarctos;* or (2) somewhat more anteroposteriorly elongate, as in *Ursavus* and *Indarctos;* or (3) disproportionately elongate, as in the bear (notable even in *Tremarctos*, where the m^2 is short compared to Eden Pliocene bear, and much shorter compared to *U. americanus*); or (4) relatively transversely extended, as seen (4A) in *Canis* (molar small, and proportionately narrower than in *Cynodictis*), (4B) in *Amphicyon* (molars large but inwardly constricted), or (4C) in *Procyon* (molars massive); and (C) that the molars of the upper jaw are paralleled by m_2 of the lower, the second lower molar of *Canis* and *Tremarctos* representing two opposite extremes.

The tooth characters of the hemicyonid genera relative to *megalocreodontic* dog and *meionocreodontic* bear are recapitulated in the following:

Key

Megalocreodontic Species

p^4, anteroposterior diameter equaling that of m^1, deuterocone anteromedian to anterior; dp^3 carnassiform and three-rooted (in canids, amphicyonids, procyonids, etc., and presumably the same in hemicyonids).

1. Hemicyoninæ. Premasseteric fossa present, p^4 deuterocone tending to be median, m_1 anteroposterior diameter considerably exceeding that of m_2,

m_1 metaconid single, m^1 tending to quadrilateral, m^2 to be wide transversely, m^3 absent, m_1 talonid cusps tending to enclose a broad and posteriorly open basin, except in *Dinocyon*. (As seen in *Hemicyon*, unique characters of skull and tarsus, humerus with entepicondylar foramen, etc.)

A. Medium-sized Miocene forms—*Hemicyon*. Premolars $\frac{1-3}{1-4}$ small; p^4 parastyle absent to rudimentary, deuterocone more anteromedian; m^{1-2} paracone larger than metacone, inner ridge directed antero-inwardly and formed (hypothetical) of protocone plus "fused" metaconule and hypocone; post-cingulum cusplet is prominent; m_3 elongate.

B. Huge to moderate-sized Miocene forms—*Dinocyon thenardi* and (?) related forms; p^4 unknown; molars more elongate transversely (m_{1-2} somewhat tending to approach the form of these teeth in *Amphicyon*), inner ridge m^{1-2} weak.

C. Small-sized Miocene forms—*Ursavus*. Premolars unreduced; p^4 parastyle absent; m^{1-2} moderately elongate, main cusps reduced, inner ridge prominent and lying medianly between inner border and line of main cusps, paracone bolder than metacone, m^2 with variably developed talon; m_3 round.

D. Huge-sized Pliocene forms—*Hyænarctos*. Premolars reduced (jaws shortened); p^4 parastyle strong, deuterocone more posteromedian; m^{1-2} paracone taller than metacone, but slightly less massive, inner ridge directed antero-externally and formed of protocone plus "fused" hypocone and post-cingulum cusplet (undeveloped metaconule), antero-inward face of ridge prominent; m_3 round to elongate.

D_1 Upper molars wide transversely; m^2 without developed talon; m_2 relatively short—*Hyænarctos* group proper.

D_2 Upper molars elongated, narrow transversely, m^2 with developed talon; m_2 relatively long—*Indarctos* subgroup.

D_3 Upper molars less wide transversely, inner ridge bold, lingual border rounded, m^2 peculiarly narrowed posteriorly—*Lydekkerion* (*H. palæindicus*), new subgroup.

2. Cyoninæ–Amphicyoninæ–Caninæ. No premasseteric fossa; p^4 deuterocone anterior, molars tending to be triangular, crowns high; m^2 typically reduced.

A_1 m_1 hypoconid strong, sectorial, inner cusps of talonid greatly reduced.

Molars large and greatly extended transversely, protocone strongly "crescentic," bullæ anterior (probably moderate in size): Long-faced forms; m^3 present—*Amphicyon*.
Short-faced forms; m^3 absent—*Pliocyon*.

A_2 m_1 hypoconid weak-sectorial; m_3 small to absent; m^1 toe unproduced; face broad—*Lycaon*, *Cyon*, *Icticyon*.

A_3 m_1 talonid relatively weak, typically bicuspid to variable, metaconid may be absent; m^1 with inner cingulum; m^3 absent; face elongate; bullæ large—*Tephrocyon-Tomarctus*, *Canis*, *Ælurodon*, *Hyænognathus*, etc.

Meionocreodontic Species

p^4, anteroposterior diameter much less than that of m^1, not carnassiform, deuterocone tending to be posterior; dp^3 quite unlike that in other Carnivora, being two-rooted and peg-like (in bears, and presumably the same in arctotheres); m_2 anteroposterior and transverse diameters tending to exceed those of m_1; m^2 with elongated talon, molar crowns tending to be flat and unworn surfaces "wrinkled";

1. Arctotheriinæ. Premasseteric fossa present; m_1 metaconid single (humerus with foramen), i. e., in these characters parallels the hemicyonids, but differs from them absolutely in the meionocreodont condition of the carnassials, etc.
   - A. Molars tending to be square—Arctotheres (excepting the *Arctotherium angustidens* type).
   - B. Molars elongate—*A. angustidens* and recent *Tremarctos*.
2. Ursinæ. No premasseteric fossa; m_1 metaconid doubled (no foramen in humerus).
   - A_1 m^1-m^2 shorter anteroposteriorly; inner cusps fused into weak ridge situated adjacent to inner border, canine base heavy, mandibular symphysis deep—*Helarctos*.
   - A_2 m^1-m^2 longer anteroposteriorly, inner cusps weak and not fused, canine base moderate, mandibular symphysis lighter—*Ursus*, etc.

HEMICYON Lartet

Frontispiece, and Figures 1–17

GENERAL DISCUSSION.—In the present section I describe a superb skull with associated mandible and skeleton from the Miocene of New Mexico, and two well represented forms from the California Miocene referable to the Lartet genus; call attention to the presence of *Hemicyon* (undescribed species) in the fauna of La Grive St. Alban; discuss the characters and relationships of the American and European material; and review the literature and synonymy. While, as stated above, *Amphicyon* and *Hyænarctos* have been obtained from the deposits of both the Eastern and Western Hemispheres, *Hemicyon* up to the present has been recognized from the Miocene horizons of Europe alone. I first noted the American occurrence of the genus during the course of an examination of a shipment of fossils collected by Mr. Joseph Rak in the Barstow Miocene[1] of California. This deposit has been long known through the important researches of Dr. John C. Merriam.[2] The study of the unexpected specimen and of later received remains of the same form from the same locality, bringing a clear understanding of the char-

[1]The recent work in the Barstow has been carried on by Mr. Joseph Rak for the writer as part of the latter's contribution towards the larger plan of Dr. John C. Merriam for the investigation and correlation of the deposits and the study of the life history of the extinct faunas of the Pacific Coast.

[2]Merriam, J. C., 1919, Univ. Cal. Pub. Dept. Geol., XI, No. 5, p. 476.

acter of the genus, subsequently resulted in my recognition of *Canis ursinus* Cope[1] of the Santa Fé marls, New Mexico,[2] as *Hemicyon*. The Cope specimen, it will be recalled, is the portion of a mandible with worn and broken teeth which has been variously referred to *Canis*, *Ælurodon*, and *Amphicyon*. I have had the privilege of examining the *Hemicyon* remains in the collections of the Muséum d'Histoire Naturelle, Paris, and the Muséum des Sciences Naturelles, Lyon, particularly the fine associated palate and mandible recovered at Sansan by Filhol. Our collection from the Barstow locality, which I have recently revisited, now includes remains representing two distinct species. Late in the season of 1924, in the hope of securing representative material of the Santa Fé form, we determined to send a Museum party into the historic New Mexican locality. The deposits of the Santa Fé area, at present so famed through archæological discoveries, had lain palæontologically untouched since Cope's hurried work of 1874. The occasion was opportune and the attempt well timed, for on the fifth day of their reconnaissance Messrs. Charles Falkenbach and G. G. Simpson, of our party, had the great good fortune to come upon the magnificent skull and skeleton noted above. Curiously enough this was the one and only specimen of *Hemicyon* found during some nine weeks in the field.[3] This splendid and unique trophy, which the storms and disintegration of another season might have utterly destroyed, has greatly increased our knowledge of this genus, the characters of the skull and skeleton of which have heretofore been unknown.

The recent recognition of *Hemicyon* in America illustrates the danger, in the present state of palæontological knowledge, of too greatly stressing the absence from any particular fauna of any particular species, as well as the great need of active and sustained field work in old as well as new localities. For only by the continued collection of the remains of the life of the past, as brought to the surface through the seasonal erosion of ancient accumulations of sand and clay, data available today and gone forever tomorrow, may we learn the history of nature's course in the production of the existing forms, of those that were in a broad sense ancestral to the faunas of today, and of those strange and unthought of forms that predominated in and vanished with the faunas of the past.

To summarize, the genus *Hemicyon* of Lartet is now known from six localities, two in the New and four in the Old World: Barstow, Cali-

[1]Cope, E. D., 1875, Proc. Acad. Nat. Sci., Phila., XXVII, p. 256.
[2]Cope, E. D., 1873, Third Ann. Rept. U. S. Geol. Surv. Terr., pp. 166–170; 1875, Ann. Rept. Chief of Engineers, Appendix LL, p. 64 *et seq.* Osborn, H. F., 1910, 'The Age of Mammals,' p. 298.
[3]The only additional *Hemicyon* specimen secured during the otherwise very successful field season of 1925 was a maxillary fragment, two much-worn molars.

fornia; Santa Fé, New Mexico; Stätzling; La Grive St. Alban; Sansan, and Göriach. Furthermore, the presence at Barstow of a smaller and larger species, and the evidence of the occurrence of a second and larger species at both Sansan and Göriach suggest the possible presence of additional species at the other localities. The relative ages of the several deposits are yet in doubt.

Merriam[1] considers that the nearest relationships of the Barstow fauna, outside of the Great Basin of California, are with the Santa Fé of New Mexico. He finds that several types which are among the most important forms of the Santa Fé beds are similar to species in the Barstow fauna, and that these include species of *Ælurodon*, *Merychippus*, *Procamelus*, and *Merycodus*. He notes that, as a considerable distance separates the Barstow geographically from the Santa Fé, some difference in fauna is to be expected; that it is also possible that the Santa Fé beds represent more than one horizon, or may include beds ranging into stages older or younger than the Barstow. He considers that in relation to the recognized mid-Miocene of the Mascall and Virgin Valley, to the Pliocene of the Rattlesnake and Thousand Creek, the Santa Fé and the Barstow faunas evidently fall within the Upper Miocene, which he correlates with the European stage of La Grive St. Alban of France.

According to the researches of Charles Depéret,[2] the Stätzling deposit represents a considerably later phase of the mid-Miocene than either Sansan or Göriach. This well recognized authority divides the European mid-Miocene (Vindobonian) into three stages:

An uppermost or Saint Gaudens stage, including Stätzling.

A middle or Simorre stage, including La Grive St. Alban.

A lowermost or Sansan stage, including Sansan and Göriach.

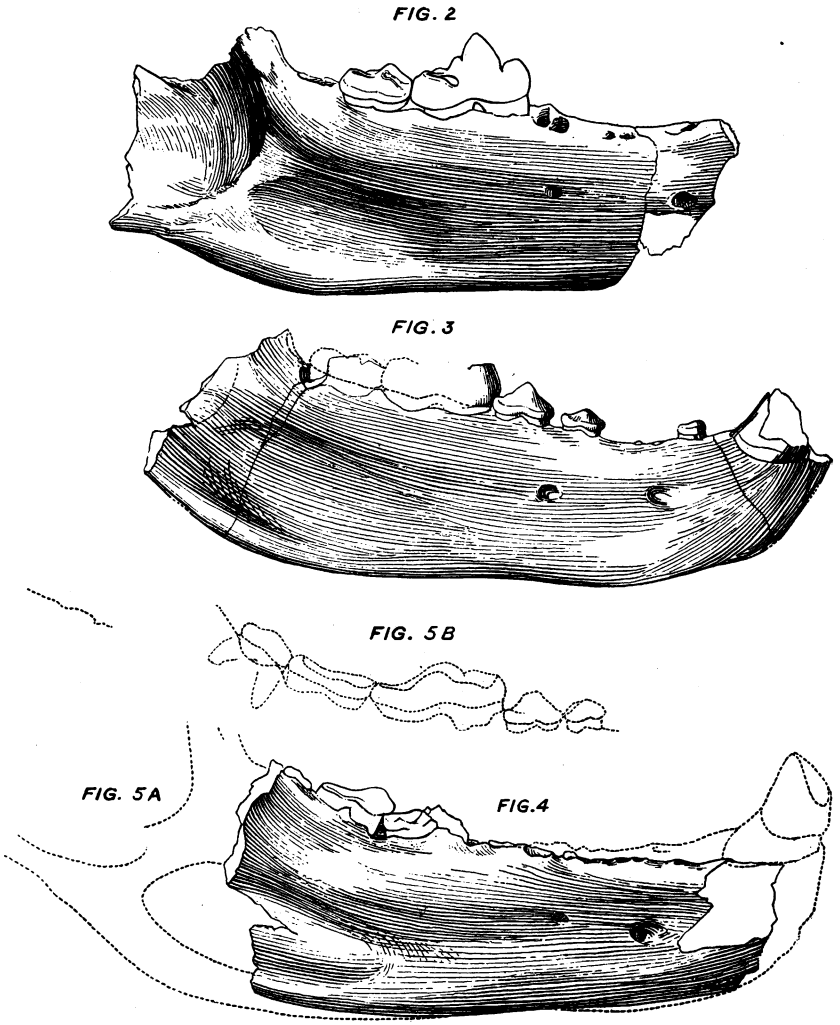
More recent collections from the two American horizons witness the existence of long-jawed trilophodont mastodon, of rhinoceros, and of browsing-horse (*Anchitherium*) forms in America as in Europe during these Miocene times. *Hemicyon*, we have seen, was common to both the American and European horizons. *Amphicyon* and pseudælurid-like genera, now definitely known from the Barstow as well as from the European horizons, we may expect to find at Santa Fé. While certain small to medium-sized *Tephrocyon-Tomarctus* species of the Santa Fé are suggestive of certain specimens from the Barstow, a large and long-jawed *Tephrocyon* of the Barstow is as yet unrecognized in the Santa Fé, as are the moderate (*Canis wheelerianus* Cope) to bear-sized and typi-

[1] *Op. cit.*, p. 453.
[2] Compte rendu heb. Acad. Sci. (Paris), 1906, CXLIII, p. 1122.

cally deep-jawed-broad-faced *Ælurodon* species of the Santa Fé unknown from the Barstow. Similarly the variable *Merychippus-Pliohippus* and camel forms of the two horizons, though in certain cases closely suggestive of one another, are apparently specifically distinct. The *Merycochœrus*, *Merycodus*, *Merychippus-Pliohippus*, and camel genera of the same American horizons, to the best of our evidence, were absent from the European horizons (though the camel at least was known in Asia). In other words, in Miocene time, as today, the faunal assemblages of the two continents, while distinct, are seen to have had certain common elements. Further, in the Miocene, as today (as illustrated by recent *Canis*, *Mustela*, *Felis*, etc.), these common elements of the faunas of the two continents were to a certain degree indistinguishable in skull and dentition.

Remains here referred to *Hemicyon* are considered consecutively in the order listed below, the material of each locality being interpreted as representing a geographical species. It has seemed preferable to hold the finds of each locality separate and, as such, pending a more definite interpretation of the respective faunas now variously correlated by different authorities with the Upper Miocene and phases of the mid-Miocene. These *Hemicyon* forms, unlike those at present included in the genus *Hyænarctos*, are all of a very uniform type. The differences that exist are mainly those of size, and to a much less extent of relative tooth proportion, development of cingula, etc. Two distinct species are known from the one level at Barstow, the occurrence recalling the presence of *Amphicyon major* and *A.* (*minor*) *sansaniensis* in the Sansan fauna, and the variable species of *Canis* present in recent faunas. The considerable size variation observed in material from the better-represented of the remaining localities, as noted above, implies the similar occurrence of large and medium-sized species. It may be presumed that an overlap in size occurs between such species, as between the widely distributed forms of recent *Canis*, which are not generally separable on tooth characters alone. The seven named species and the tentative Depéret form are as follows:

Hemicyon barstowensis, new species
Hemicyon californicus, new species
Hemicyon (*Canis*) *ursinus* (Cope)
Hemicyon sansaniensis Lartet, genotypic species
Hemicyon grivensis, new species
Hemicyon (*Dinocyon*) *göriachensis* (Toula in part)
Hemicyon stätzlingii (*H. sansaniensis* Lartet—Roger in part); and (?)*H. race minor* of Depéret, the affinities of which last are in doubt.



Hemicyon mandibles, showing premasseteric fossa, outer view. × ½.

Fig. 2. *Hemicyon sansaniensis* Lartet, from Sansan, lectotype, Mus. Hist. Nat., Paris, after Blainville, Pl. XIV, "*Amphicyon major*" (in part).

Fig. 3. *Hemicyon barstowensis*, new species, from Barstow Miocene, California; cotype, Amer. Mus. No. 20813. (See Fig. 12, lateral view.)

Figs. 4 and 5. *Hemicyon* (*Canis*) *ursinus* (Cope), from Santa Fé Miocene, New Mexico. 4. Type specimen, U. S. Nat. Mus., after Cope, Ann. Rept. Chief of Engineers, 1877, Pl. LXIX, Fig. 1.

Fig. 5A. Mandible of neotype superimposed in dotted line over the Cope type specimen; 5B, dotted elevation of teeth of neotype, Amer. Mus. No. 21101. (See Fig. 10, occlusal view.)

A comparative table of measurements of the material may be found on page 43.

HISTORY OF THE GENUS.—Lartet, in the note of 1851 (for references see under genotypic species, p. 48), in which he establishes the genus *Hemicyon*, makes no designation of type or mention of material: ". . . larger than the European wolf, and nearer the dog than *Amphicyon*, it seems to approach in certain details of its characteristic teeth certain species of the marten family, particularly the glutton." He had apparently first noticed the occurrence of this form at Sansan as early as 1837, and certainly had it in mind in 1838 when he mentions in a letter to Flourens ". . . fragments of a new large carnivore nearer the dog, it seems to me, than that already designated by the name *Amphicyon*." Pomel (1853) proposed the separation from *Amphicyon major* under *A. laurillardi* of the smaller Sansan "*Amphicyon*" specimens, but failed to note that the smaller material represented more than a single form. Blainville (1839–64 left top, Pl. XIV) figures under "*A. major*" (this paper Fig. 2) a mandible and first upper molar of *Hemicyon*, and figures with other material under "*Amphicyon minor*" (Pl. XVI) a fourth upper premolar of *Hemicyon*, remarking that the deuterocone of the particular specimen, instead of being quite anterior as in *Amphicyon* and the dogs or more posterior as in the bears, is median. Gervais (1848–52) transfers *Hemicyon* Lartet to *Hyænarctos* (*H. hemicyon*), noting that the characters of the former are homologous with those of *Hyænarctos sivalensis*. Gervais (1852, Pl. IV, Fig. 2), under *Hyænarctos hemicyon*, figures a maxillary specimen said to have been found by Laurillard at Sansan, which he considers to represent *Hemicyon sansaniensis* Lartet. Gervais (1859, Pl. LXXXI, Fig. 8) refigures and describes this maxillary fragment containing the molars and three roots of the fourth upper premolar as representing the Lartet form,[1] but states (in ambiguous footnote, p. 211) that Lartet is not certain that the specimen really belongs to his genus *Hemicyon*, and that it may have belonged to a species not known by Lartet at the time of his description. Gervais again notes the general resemblance of the specimen to *Hyænarctos sivalensis* and *Hyænarctos insignis*, and prefers to consider it as of the genus *Hyænarctos* (as *Hyænarctos hemicyon*) rather than as representing a separate genus *Hemicyon*. Gervais, however, errs in referring two molars from opposite sides of the jaw (Pl. LXXXI, Fig. 9), which he was advised of by Lartet, to

[1]This is the only maxillary specimen containing teeth in the Lartet collection now in the Muséum d'Histoire Naturelle, Paris, and was attributed by Filhol to Lartet.

this form (footnote). Filhol (1891, p. 153) notes that the genus *Hemicyon* should be maintained for certain material from Sansan and Göriach. Filhol, while he rightly criticises Gervais for having grouped with Lartet's mandibular and maxillary specimens the m^1 and m^2 of different proportions (Gervais, 1859, Pl. LXXXI, Fig. 9), errs in stating that Gervais founded his *Hyænarctos hemicyon* on the character of these two molars (see above). Unfortunately, moreover, Filhol bases his own main description on a mandible ("*H. sansaniensis* Lartet," 1891, Pl. VIII) which he acknowledges, in the latter part of the same description, through discovery in the meantime of an associated palate and mandible, could not belong to the Lartet species. He correctly remarks on the peculiar conformation of the external face of the latter mandible, the reduction of the m_3 (Text Fig. 2, p. 304), and the median position of the deuterocone of p^4. Lydekker (1883) considers it doubtful whether the maxillary and the two molar specimens figured by Gervais are the same as Lartet's *Hemicyon*. He believes it best, as he considers it fairly certain that they do not belong to *Hyænarctos*, and though he notes a slight difference between the two specimens, to refer them both to *Dinocyon*. Depéret (1892, p. 38), under misapprehension that the p^4 of the material from Göriach was wolf-like, disagrees with Filhol as to the reference of the Göriach species to *Hemicyon*, but admits that there exists a very great resemblance in the form of the premolars and molars between the Göriach species and *Hemicyon sansaniensis*. He, however, recognizes the resemblance of the small Sansan jaw and fragments, figured by Blainville (Pl. XIV, left top), to the Göriach species, notes Pomel's reference of this Blainville figured specimen to *A. laurillardi* Pomel, and wonders at Filhol's lack of mention of same. Depéret contends that, if Blainville is correct in referring the whole to the one form, that, following Schlosser, this should be referred to *Dinocyon* and take precedence as *Dinocyon laurillardi* Pomel, over *Dinocyon göriachensis* Toula. Schlosser (1887) remarks that *Hyænarctos hemicyon* undoubtedly belongs to *Dinocyon*, but he later (1899) agrees with Filhol that the genus *Hemicyon* Lartet is distinct from *Dinocyon*. While he considers the genus to be structurally transitional between *Amphicyon* and *Ursus*, he notes that any attempt at derivation of *Ursus* (*Ursavus*) by way of it is forbidden, because of the presence in the same deposit of the small form *Ursavus*, which he states stands itself incomparably nearer to *Ursus* than does *Hemicyon*. Schlosser (1902, Geol. Pal. Abhandl., p. 43) suggests that *Hemicyon* may have sprung from *Cephalogale*.

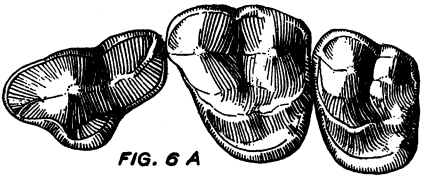


FIG. 6 A

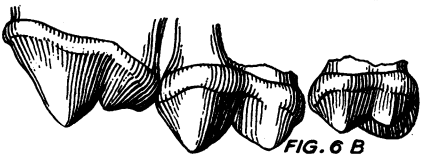


FIG. 6 B

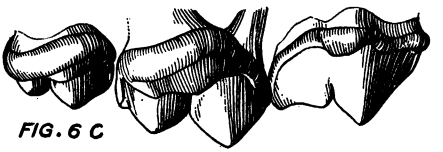


FIG. 6 C

FIG. 7

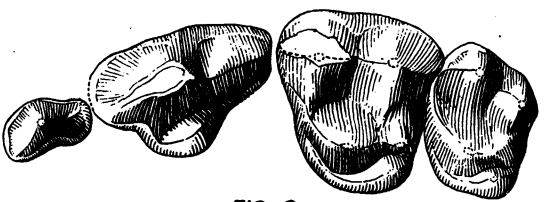


FIG. 8

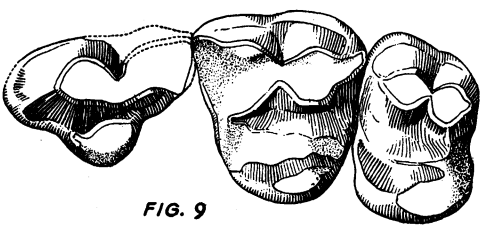


FIG. 9

Figs. 6–8. *Hemicyon barstowensis*, new species, from Barstow Miocene, California. Natural size.

Figs. 6A–C.—p^4–m^2 of type specimen, Amer. Mus. No. 20810. Occlusal, outer and (slightly distorted) inner views.

Fig. 7. p^4-m^2 of worn cotype, Amer. Mus. No. 20811. (Anteroposterior diameter m^2 slightly under actual.)

Fig. 8. p^3–m^2 of referred and larger cotype, Amer. Mus. No. 20816.

Fig. 9. *Hemicyon* (*Canis*) *ursinus* (Cope), p^4–m^2 of neotype, crown view, from Santa Fé Miocene, New Mexico, Amer. Mus. No. 21101. (Anteroposterior diameter m^2 slightly under actual).

Characters of *Hemicyon*[1]

Mandible with elongated premasseteric fossa and everted inferior border, sulcus moderately deep, horizontal ramus moderately long and deep, anterior mental foramina inferior to p_{1-2}.

Lower Dentition.—Premolars small, generally oval, and enveloped by cingula, accessory tubercles generally absent; p_1 with single root, separated from c_1; p_1, p_2 (lost in Santa Fé neotype), and p_3 adjacent but uncrowded (Figs. 10–12).

p_3, variable, elongate-oval in Sansan and Barstow forms (Figs. 11 and 12) to short triangular in Santa Fé neotype (Fig. 10).

p_4, moderately enlarged relative to p_3, broader posteriorly than anteriorly; and in large Barstow mandible (Fig. 12) with a slightly posterior-inner accessory tubercle.

m_1, protoconid median, moderately low; talonid moderately broad relative to anteriorly narrowed trigonid; inner tooth border swollen over base of metaconid and postero-accessory cusplet, and rounded posteriorly; postero-external border produced posteriorly; endoconid small; strong accessory cusplet posterior to metaconid, hypoconid prominent and extended in fore and aft ridge lying inward of tooth border. In *Amphicyon* the hypoconid is greatly enlarged and more median, the heel is shorter and metaconid farther forward. The tooth suggests that referred to *Lydekkerion palæindicus* rather than that to *Indarctos punjabiensis*, mainly differing in its proportionately higher crown and smaller talonid.

m_2, elongate, trigonid low, paraconid area developed in round elevated ridge, protoconid higher than metaconid and less anterior to metaconid than in *Canis*, slight accessory cusplet antero- and postero-adjacent to metaconid, outer tooth border strongly indented between protoconid and hypoconid, talonid reduced and postero-inner corner narrowed and much rounded. This tooth generally suggests that of *Indarctos punjabiensis*, which, however, differs in the prominence of the metaconid relative to the protoconid, that is even more marked in the short-proportioned m_2 of *L. palæindicus*. In *Amphicyon* the anterior external corner is prominent, the protoconid high, and the antero-inner cusp developed.

m_3, elongate, narrowed posteriorly, external border swollen opposite metaconid, cusps greatly reduced. The tooth is double-rooted in the Santa Fé neotype, single-rooted in Cope's type and in the Barstow specimens.

Upper Dentition.—Canines, large with heavy bases. (Figs. 6–9, and 13B.)

Incisors (upper) increasing in size outward, i^3 much enlarged.

p^1, separate from c^1; p^2, p^3 and p^4 adjacent but uncrowded; p^{1-3} low-crowned, oval-elongate as in mandible.

p_4, transverse diameter slight relative to molars; anteroposterior diameter slightly greater than anteroposterior diameter of m^1; parastyle usually indefinitely suggested, is moderately well developed in Sansan neotype; paracone-metacone shear relatively low, tooth surrounded by cingulum, external border tending flat with indentation opposite paracone-metacone division (in *Hemicyon sansaniensis*, in *H. göriachensis* indentation is slightly more anterior). Deuterocone anteromedian, appressed against base paracone and supported on separate root (less appressed in *H. sansaniensis* and *H. göriachensis*). (The deuterocone notch receives the paraconid-protoconid as in *Ursus*, versus the deuterocone lying anterior to paraconid in *Canis*.)

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[1]For peculiar skull, skeletal, and tarsal characters, see under *H. ursinus*, neotype, p. 38.

m^1, transverse diameter slightly greater in Santa Fé and approximately equal in Barstow form to anteroposterior diameter; outer cusps heavy; inner cusps (protocone and metaconule) tending to fuse into diagonally directed ridge, which lies nearer to the inner border than to the line of the main cusps, slopes posteriorly, and with the outer cusps bounds a forward-widening valley (posteriorly widening valley in *Hyænarctos*); metacone and metaconule tend to be connected by an incipient cross crest; inner posterior tooth corner with prominent cingulum cusplet.

m^2, anteroposterior diameter considerably shorter than that of m^1; transverse diameter nearly as long as that of m^1 in Santa Fé and considerably shorter than m^1 in the Barstow type; outer cusps moderately angulated, toe broader-proportioned and relatively further produced inward than in m^1; inner cingula well developed, forming prominent nub at posterior inner tooth corner; inner ridge weaker than in m^1. The tooth tends to be quadrate; superficially it more suggests the transversely elongated m^2 of *Amphicyon* than the more anteroposteriorly elongate tooth of *Hyænarctos*, in which the relative transverse narrowness of the teeth has seemingly resulted in the fusion of the hypocone and metaconule and non-development of the post-cingulum cusplet, and the reversion of direction of the "inner ridge."

The closing of the jaws in *Hemicyon* results in: the paraconid shear of m_1 biting into the notch between the deuterocone and paracone base of p^4 (this results in the gradual abrasion of the deuterocone); the anterior portion of the inner ridge of m^1 biting into the broad talonid of m_1, the posterior cingulum cusplet of m^1 overlapping the paraconid corner of m_2, and the cingulum cusplet of m^2 falling between m_2 and m_3. In *Canis* the paraconid shear falls clear of the anteriorly flung deuterocone. (Compare Fig. 1.)

Hemicyon barstowensis, new species

Figures 1A and 1B (in part), 3, 6, 7, 8, 11, 12, 12A (Measurements, page 35).

TYPE.—Left maxillary fragment with p^4–m^1 associated with portion right mandible with alveolus c, alveolus p_1, p_2–m_2, and portion left mandible m_1–m_3, collected by Mr. Joseph Rak, Barstow Miocene, Mohave Desert, California, Amer. Mus. No. 20810, Figs. 6 and 11. The whole of apparently similar proportions and state of wear, and as found in the same block believed to represent a single individual.

PARATYPES.—Left maxillary fragment with p^4–m^2. Teeth somewhat worn. Type locality, Amer. Mus. No. 20811, Fig. 7.

Portions of both maxillæ of large individual with p^3–m^2 of left, and p^3, alveolar base p^4, m^{1-2} of right side. Teeth moderately worn, outer border paracone m^1 broken. Type locality, Spring 1925. Amer. Mus. No. 20816, Fig. 8.

Right maxillary and mandibular fragments with m^1–m^2 and base p^4, and m_2–m_3 and p_4. Teeth much worn, slightly smaller than type, from type locality. Amer. Mus. No. 20814.

Left maxillary fragment m^1–m^2 (broken), larger than type. Type locality. Amer. Mus. No. 20812.

Right maxillary fragment with m^1–m^2. Type locality. Amer. Mus. No. 20818. p^4 right. Type locality. Amer. Mus. No. 20817.

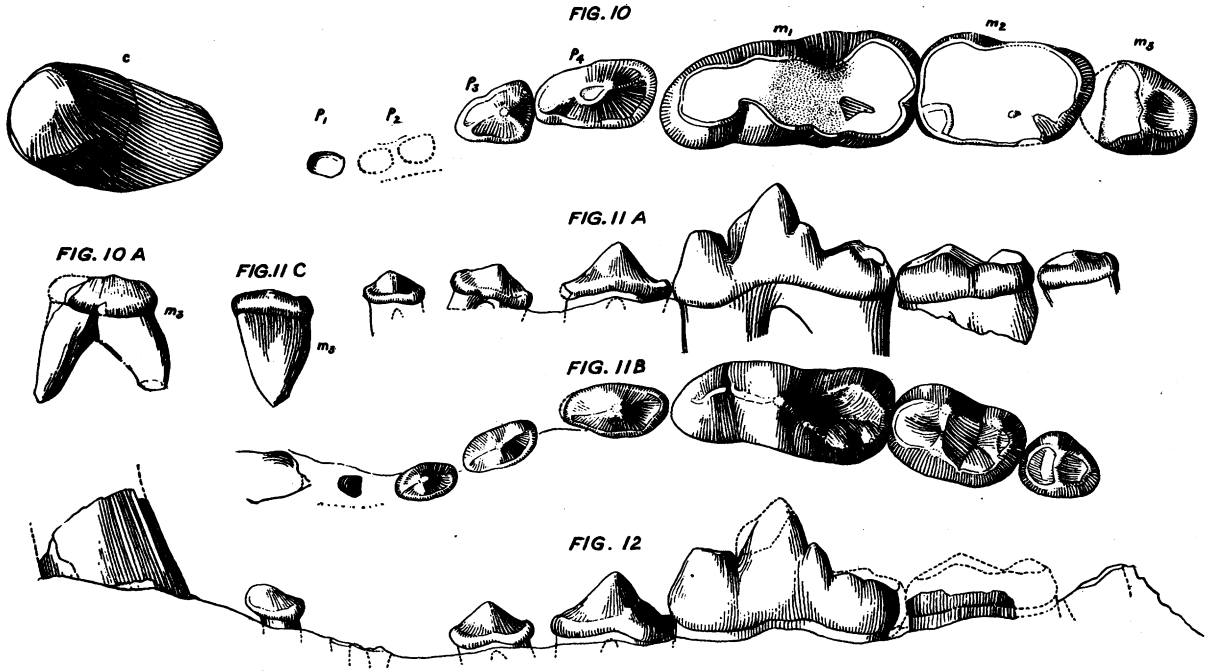

Fig. 10. *Hemicyon (Canis) ursinus* (Cope), neotype, c–m_3, occlusal view. Amer. Mus. No. 21101. 10A, m_3, lateral view, showing double root. Natural size.

Figs. 11–12 *Hemicyon barstowensis*, new species, from Barstow Miocene, California. Natural size.

Fig. 11A-B. p_2–m_3, type specimen (in part), Amer. Mus. No. 20810, inner view, and occlusal view; 11C, m_3, lateral view, showing single root.

Fig. 12. c–m_2 of large cotype, inner view, from type locality, Amer. Mus. No. 20813.

Right ramus of large-sized mandible with indication of alveolus third incisor, c base, p_1, p_2 alveolus (two-rooted), p_3–p_4, m_1 (broken), fragment of m_2, and indication of alveolus m_3. Teeth slightly worn. Horizontal ramus well preserved and showing deep premasseteric fossa. Type locality. Amer. Mus. No. 20813. Figs. 3 and 12.

Large m_1 left. Type locality. Amer. Mus. No. 20819.

Left mandible fragment with m_1 (broken), and m_2 (heel broken). Teeth considerably worn. Type locality. Amer. Mus. No. 20815.

Portion of skull including entire region posterior to postorbital processes; and mandible of same individual containing the alveoli and m_1-m_3 of left side, and canine alveolus, p_1, p_2 alveolus, and p_3-m_3 of right side. (Fig. 12A, in part). Amer. Mus. No. 20820. (Specimens secured after paper went to press.)

Anterior portion of skull containing canine (broken), p^1 alveolus, p^2-m^2 of left side, and p^2-m^2 (par. broken) of right side. (Fig. 12A, in part) Amer. Mus. No. 20821.

Portion of skull of immature individual (of equal size to Amer. Mus. No. 20820), sutures open, parietal frontal region full, sagittal crest unformed, and bulla represented alone by inner tympanic area. Amer. Mus. No. 20822.

Right ramus of mandible with p_2 and alveoli of remaining teeth. Amer. Mus. No. 20824.

Left ramus of mandible with p_4-m_2 (cracked) and etc. alveoli. Amer. Mus. No. 20825.

Also fragment of right m_1, and canine and incisor fragments. Amer. Mus. No. 20815A. All specimens collected by Mr. Joseph Rak in our so-called "*Hemicyon* stratum."

Discussion.—The characters of the teeth of the type specimen are listed on the preceding page under "*Hemicyon* characters." As above noted, the type locality has now yielded fragmentary *Hemicyon* dentitions representative of fourteen or more different individuals. The stratigraphy gives definite evidence that these individuals existed together and at one time with certain species of *Amphicyon* and *Tephrocyon*. The specimens vary to a certain degree in general appearance and in size. Eleven, inclusive of the type specimen, though somewhat smaller, are of very similar form and proportion to the known material from Sansan. Three of the specimens, including a large maxillary specimen (Fig. 8), large mandible (Figs. 3 and 12), and large m_1 (No. 20819), considerably exceed the former in size, and more nearly approximate the species *H. californicus*, but are smaller than the Filhol neotype, which in turn is considerably exceeded in size by the Santa Fé neotype [see figures and measurement table]. The slight difference in size within the two Barstow species is taken to represent individual variaton, such as is seen today in *Canis occidentalis*, or to at least as great a degree in *Hemicyon sansaniensis* (as noted by a comparison of the mandible of the Filhol neotype, Fig. 2, with the large single m_1 in the Mus. Hist. Nat. Paris Coll.), and as is exhibited in the Santa Fé species in comparison of the neotype and Cope type. The Barstow material further evidences a

variation in the form of the teeth. This is exampled in the p^4s in the constriction in the type specimen of the outer border opposite the paracone and the metacone division, versus the swollen condition of the same in a larger and heavier-proportioned specimen (No. 20816). (This difference between these two p^4s approaches that existing between those of *Hyænarctos sivalensis* and *H. insignis*, or *H. gregori*. None of the p^4s exhibits an incipient parastyle as does one of the Sansan specimens.) The m^1s have the hypocone variably developed. The most interesting variation, however, is noted in the size of m^2 relative to m^1, as seen in comparison of the two maxillæ (Figs. 7 and 8). Finally, the Barstow material indicates the considerable change in the contour of the teeth that takes place with wear. Thus a comparison of the worn m^2 and m^1 of specimen No. 20812 with the unworn type teeth, in the angulation and the narrowness of the lingual portion of m^1, and in the relative proportions of the main cusps, as in the apparent large relative size of m^2, might suggest at first glance the presence of still another species.

The premasseteric fossa is very slightly indicated in the broken type specimen, but is well shown in the specimen of Fig. 3. The portions of the maxilla preserved in specimen No. 20820 (Fig. 13A) exhibit the depression at the malar root, the broad zygoma, the forwardly placed infraorbital foramen, and adaptation of the inferior border of the orbit characteristic of the maxillary region of the Santa Fé skull.

The posterior portions of two skulls, received after this paper had gone to press, give first knowledge of the proportions of the post-facial area of *H. barstowensis* and other relatively small species (as contrasted with *H. ursinus*), both in early maturity and in the young. While the basic characters of the mature skull are seen to be similar to those of the much larger species, the general aspect of the full-grown Barstow specimen, through the absence of characters dependent on huge size and advanced age, is markedly different. Thus, the Barstow specimen quite lacks the remarkable development of the sagittal crest, constriction of the post-frontal-parietal and supra-cranial region, and deep fossæ for muscular attachment so characteristic of the former skull. That the characters of the Santa Fé are a resultant of size and age is further shown in the specimen of the post-cranial region of an immature individual, No. 20822, in which the sutures are still open, the cranium is full and unconstricted, the sagittal crest is entirely absent, the basi-occipital is relatively narrow, and the inner portion of the tympanic bone alone represents the ear (the bony external auditory meatus and bulla presumably not having been ossified; in the mature Barstow specimen the

small bullæ are seen to be slightly more inflated than in the aged Santa Fé.)

Compared to *H. (Canis) ursinus* (Cope), from the Santa Fé, N. Mex.

Comparison is difficult because of the poorly preserved condition of the teeth of the Cope type (Fig. 4), and the worn state of those of the Santa Fé neotype (Figs. 5 and 10):

(a) Much smaller size (the second Barstow species, *H. californicus*, in size more nearly approaching the Santa Fé neotype).

(b) p^4 and m^1 of similar proportions though much smaller.

(c) m^2 less enlarged relative to m^1 (? individual variation).

(d) m^3 single-rooted (as apparently the condition in Cope's type mandible), versus strangely double-rooted in the Santa Fé neotype.

(e) p_3–p_4 proportionately much lighter and lower-crowned, p_3 oval, versus short and triangular.

Compared to *H. sansaniensis* Lartet, from the mid-Miocene of Sansan, France (Fig. 2).

(a) Somewhat smaller average size, the type specimen being considerably smaller than, but the large referred specimens more nearly approximating the Sansan in size.

(b) p^4, deuterocone less bold and more appressed, and prominent parastyle-cingulum of the Filhol neotype absent; tooth, however, closely resembles a large referred p^4 from Sansan in which the deuterocone is somewhat similarly appressed and the anterior "parastyle" development of the cingulum is likewise absent.

(c) m^1, inner ridge slightly stronger.

(d) m_1 and m_2, talonid somewhat longer and narrower proportioned; m_1, tooth border at base hypoconid more prominent; m_2, metaconid much less prominent than protoconid.

(e) m_3, agrees very closely with the only slightly larger m_3 of Filhol's neotype.[1] [An m_3 of quite a different type, figured by Blainville, adjoining the small mandible (left top Pl. XIV), which I have taken as the type of *Hemicyon sansaniensis*, evidently pertains to *Amphicyon* and not to *Hemicyon*.]

Compared to *Hemicyon (Dinocyon) göriachensis* Toula (in part), from Göriach (Fig. 16 of referred mandible).

(a) The Barstow type specimen is smaller than the Göriach type, but the large referred Barstow material must have represented individuals that were fully as large as that of the Göriach type.

(b) p^4 is as broadly proportioned in referred specimen No. 20818; the cingulum of the inner and slight cingulum of the outer tooth border is less noticeable in *H. göriachensis*, but presumably only on account of stage of wear.

(c) m's are transversely less broadly proportioned, in that they are less produced inwardly than in *H. göriachensis*.

(d) m^2 is notably smaller relative to the m^1.

(e) m_1, accessory cusplet postero-adjacent to metaconid is larger versus smaller than endoconid (Toula, 1884, Pl. VIII, Figs. 12–13, referred p_4-m_2).

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[1]Filhol, 1891, 'Mamm. Sansan,' text figure, p. 304.

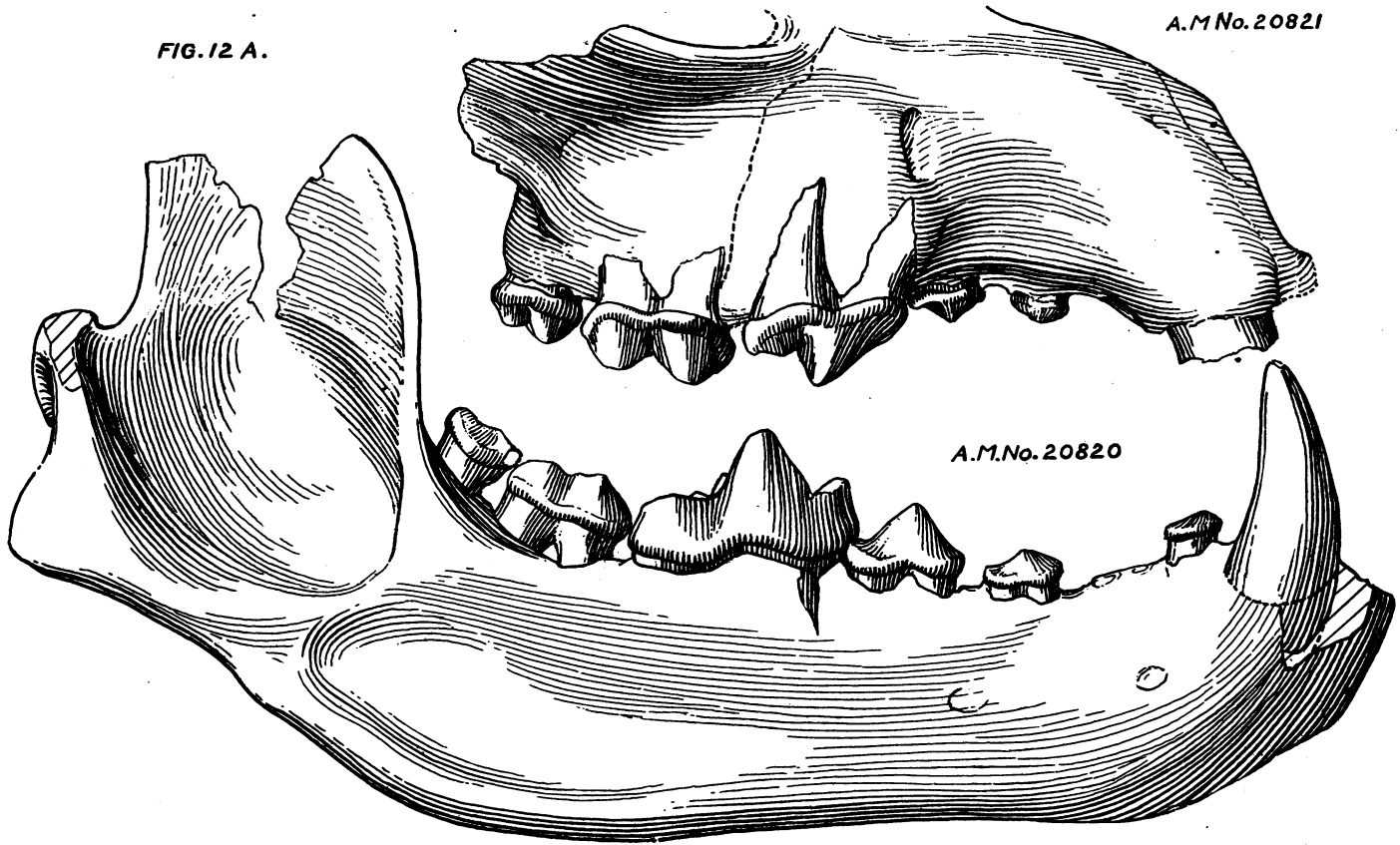
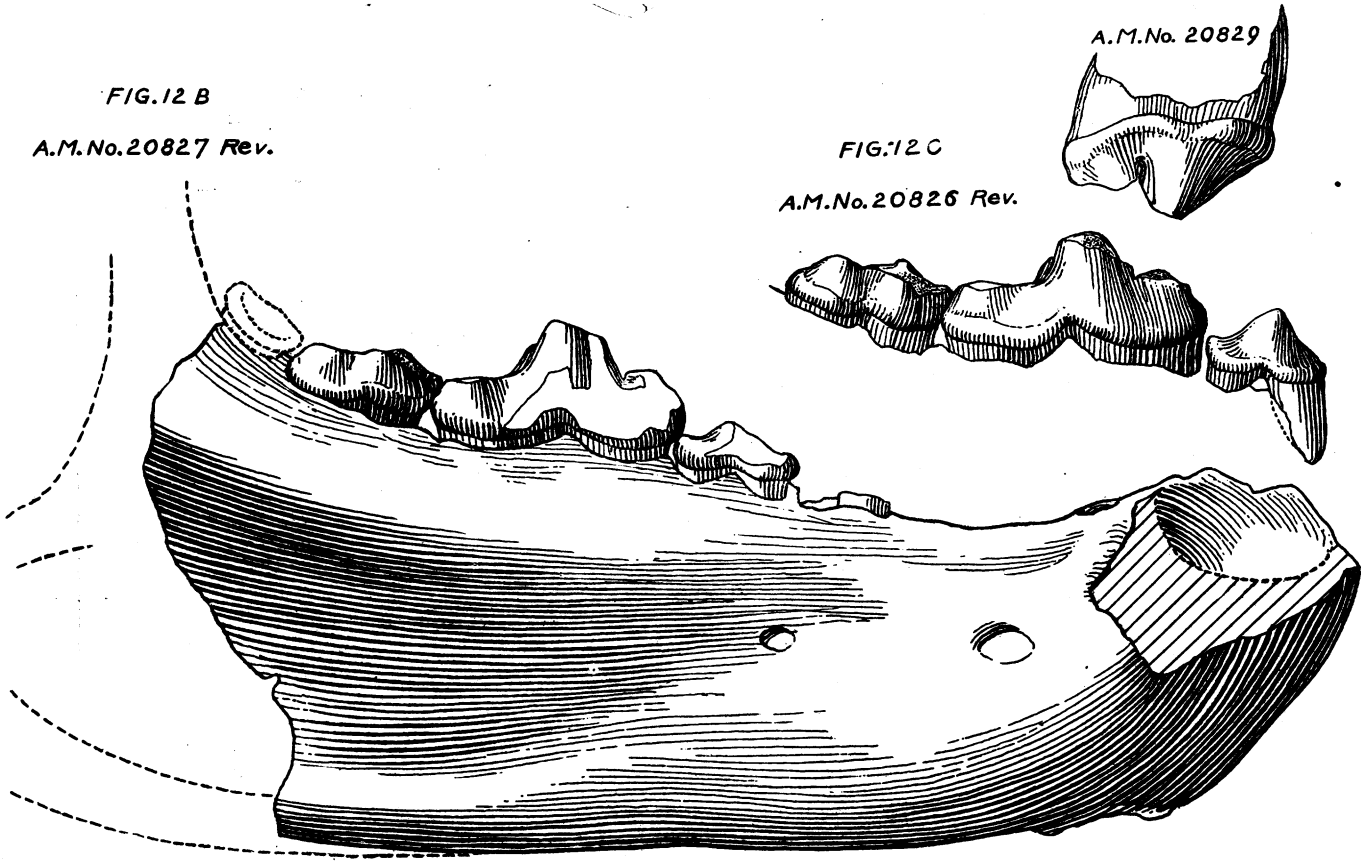


Fig. 12A. *Hemicyon barstowensis*, new species, skull fragment containing canine to m^2; and mandible containing p_1-m_3 of newly secured paratypes. Outer viwes. Natural size. Amer. Mus. Nos. 20821 and 20820. Type locality, Barstow Miocene, California.



Figs. 12B-C. *Hemicyon californicus*, new species, Barstow Miocene, Mohave Desert, California. (B) Portion of left ramus containing p_4-m_2 and alveoli of canine, p_1, and p_2. Outer view, reversed. Natural size. Amer. Mus. No. 20827. (C) P_4-m_2 of fragment of left ramus; and a p^4. Outer view, reversed. Natural size. Am.Mus. Nos. 20826 and 20829.

(f) m_2, lighter-proportioned and heel more narrowed, metaconid much less prominent than protoconid, and cusplet anterior to metaconid less prominent than figured by Toula.

Compared to *Ursavus primævus* Gaillard, from La Grive St. Alban, France (Figs. 42–46, 50B, and 11B).

(a) Much larger.

(b) carnassiform p_4 very similar in blade development, placing of deuterocone, and anteroposterior diameter relative to that of m^1.

(c) Upper molars similar in the general arrangement of the cusps and presence of post-cingulum cusplet; but differing in actual cusp development, and in greater relative transverse breadth.

(d) m_1[1] the more central protocone resulting in the trigonid being longer and the talonid being shorter and narrower than in *U. primævus*, which more resembles the m_1 of *Hyænarctos*.

Hemicyon californicus, new species

Figures 12B and C

TYPE.—Anterior portion of left ramus containing p_4 (broken), m_1 (broken), m_2, and alveoli of canine, p_1, p_2 and p_3. Fig. 12B. Amer. Mus. No. 20827. Collected by Mr. Joseph Rak, *Hemicyon* Stratum, Barstow Miocene, Mohave Desert, California.

PARATYPE.—Section of left ramus containing p_4-m_2. Fig. 12C. Amer. Mus. No. 20826. Type locality.

Right maxillary fragment with m^1 (broken)-m^2. Amer. Mus. No. 20828. Type locality.

P^4 right. Fig. 12C. Amer. Mus. No. 20829.

CHARACTERS.—Large size; m_2 relatively short compared to m_1, as in *H. barstowensis* versus *H. ursinus*; anterior-posterior diameter of teeth averaging 17% greater than in *H. barstowensis* type specimen.

DISCUSSION.—Preliminary work of the 1925–1926 season at the Barstow type locality has resulted in the discovery of the presence of a second and much larger *Hemicyon* species. The discovery is of extreme interest in showing the occurrence in one well-defined stratum of two forms of *Hemicyon* differing from each other as do species of recent *Canis*, or as does *Amphicyon major* from *A.* (*minor*) *sansaniensis* of the same horizon. The discovery thus affords additional evidence of the former broad specific range of this hitherto little-known but once widely distributed genus. The difference, as noted in tooth diameters, between the larger and the smaller Barstow species is equivalent to that occurring between the type of *A. major* and *A.* (*minor*) *sansaniensis*, or 17% of the measurement of the smaller. In the case of recent *Canis*,

[1] m_1, type of *Lutra dubia* Depéret, differs from the m_1 referred to *U. primævus* in the protoconid being even slightly more anterior and the heel longer-proportioned (further, the external border of the trigonid appears more swollen, and the posterior inner accessory cusp more reduced than as usually figured).

large skulls of *C. latrans* may approximate in total length small specimens of *C. occidentalis*,[1] though a difference of more than 70% is seen to exist between larger American specimens of *C. occidentalis* and the smaller of those representative of *C. latrans*. It must be remarked, however, that among a large collection of recent wolves from a single locality, a difference between the largest and smallest specimens of as much as 19% of the latter has been noted.

MEASUREMENTS

	p^4	m^1	m^2	p_4	m_1	m_2	m_3	p_1 alveolus to m_1 inclusive
H. barstowensis paratype A. M. 20820	22	19	13.5	15	29	17	(11)	76½
H. californicus type A. M. 20827				15½	33	20		91
A. M. 20826, paratype				16	34.5	20.5		
A. M. 20829, paratype	26.5							
A. M. 20828, paratype		(23)	15.5					
H. ursinus neotype A. M. 21101	26	23	16	16	35	23		78–84

Hemicyon (Canis) ursinus (Cope)

Frontispiece, Figures 4, 5A and B, 9, 10 and 10A, 13A and B, 14, 15

Canis ursinus COPE, E. D., 1875, Proc. Acad. Nat. Sci. Phila., XXVII, p. 256; Ann. Rept. Chief of Engineers, Appendix LL, p. 988, Extract Ann. Rept. Chief of Engineers, Appendix LL, p. 68; 1877, Geog. Surv. West of 100th Merid. (Wheeler), IV, p. 304, Pl. LXIX, Figs. 1–1c.

(?)*Amphicyon ursinus* COPE, E. D., 1880, Bull. U. S. Geol. and Geog. Surv. Terr., V, p. 46; 1882, Bull. U. S. Geol. and Geog. Surv. Terr., VI, p. 178; 1883, Amer. Nat., XVII, p. 242; 1884–85, Bull. U. S. Geol. and Geog. Surv. Terr., III, p. 39. MATTHEW, W. D., 1902, Bull. Amer. Mus. Nat. Hist., IX, p. 290. TROUESSART, 1905, Catalogus Mammalium, III, p. 220.

Ælurodon ursinus (Cope) SCOTT, 1890, Bull. Mus. Comp. Zool., II, p. 68. MATTHEW, W. D., 1899, Bull. Amer. Mus. Nat. Hist., p. 67. HAY, O. P., 1902, Bull. U. S. Geol. Surv., p. 774.

(?)*Dinocyon ursinus* (Cope) MATTHEW, 1909, Bull. U. S. Geol. Surv., p. 115.

Canis ?ursinus (Cope) MERRIAM, J. C., 1919, Univ. Cal. Pub. Dept. Geol., p. 536.

Pliocyon ursinus (Cope) MATTHEW, W. D., 1924, Bull. Amer. Mus. Nat. Hist., L, p. 113.

TYPE.—Portion of right ramus of mandible containing broken base of c, single-rooted p_1, roots of p_2–p_4, broken m_1 showing roots and worn heel, m_2 greatly worn,

[1]Allen, J. A., 1876, Bull. U. S. Geol. and Geog. Surv. Terr., II, p. 309, see tables.

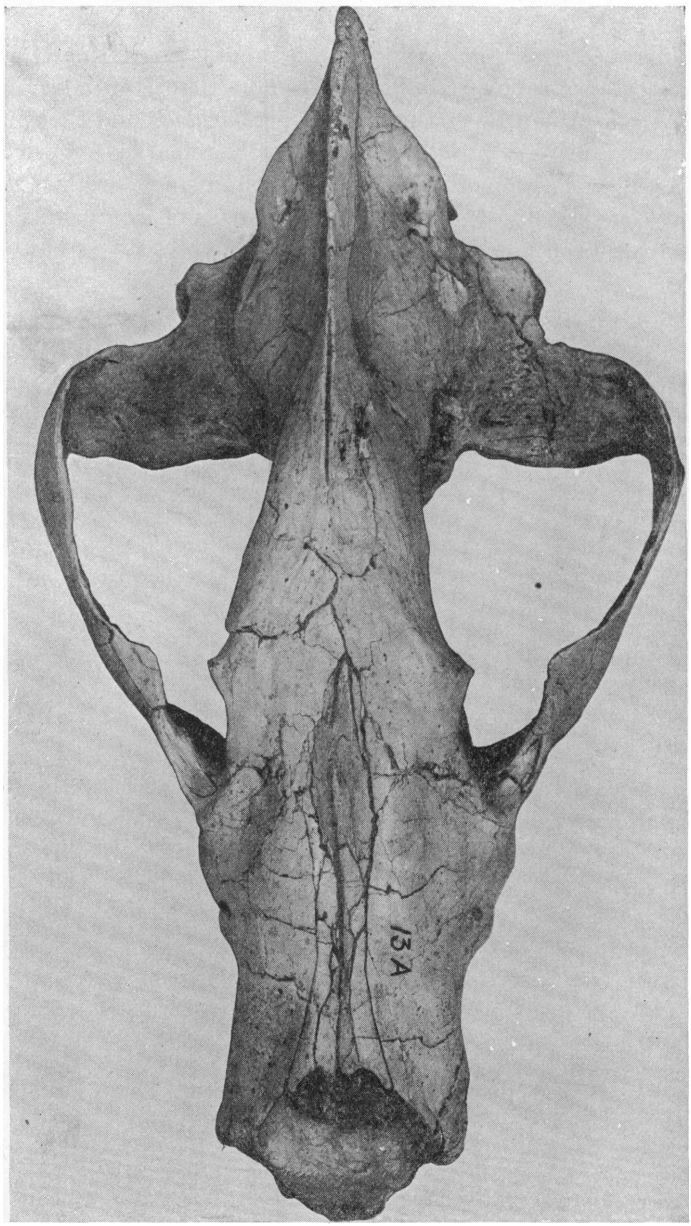


Fig. 13A. *Hemicyon* (*Canis*) *ursinus* (Cope), dorsal view of skull of neotype from Santa Fé Miocene, New Mexico, Amer. Mus. No. 21101. ×¾.

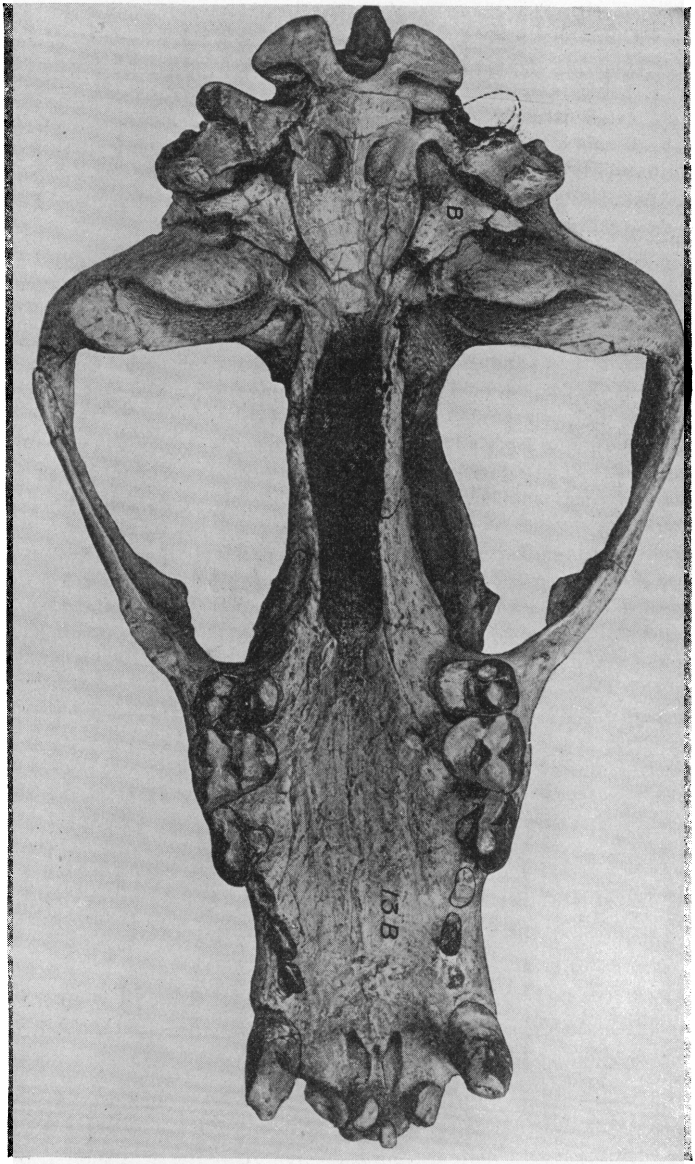


Fig. 13B. *Hemicyon* (*Canis*) *ursinus* (Cope), palatal view of skull of neotype from Santa Fé Miocene, New Mexico, Amer. Mus. No. 21101. ×¾.

and alveolus m_3, from the Santa Fé Miocene, New Mexico, U. S. Nat. Mus. No. 2040. Figured 1877, Pl. LXIX, Figs. 1–1c. Figured this paper, Fig. 4.

NEOTYPE.—Associated skull and mandible, with vertebral column (excepting atlas), ribs, pelvis, scapula, humerus, radius, tibia, fibula, cuboid, astragalus, and calcaneum. Amer. Mus. No. 21101. Frontispiece; Figs. 5, 9, 10 and 10A, 13A and B, 14 and 15. Found by Messrs. Falkenbach and Simpson of American Museum party, in the Santa Fé Miocene, New Mexico, October, 1924.

REFERRED.—Maxillary fragment with m^{1-2} much worn, from Santa Fé Miocene, New Mexico, Amer. Mus. No. 21102.

CHARACTERS OF TYPE AS GIVEN BY COPE.—Prominent premasseteric fossa; tuberculars unusually large relative to premolars; anterior premolars separated by diastema; posterior mental foramen below anterior edge of p_4.

Cope notes in 1877 (p. 304: "... a curious species, ... the outline of the mandible is peculiar in its great depth posteriorly as compared with the wolf ... exterior (face of ramus) is deeply concave from below the anterior margin of sectorial tooth to the line of the posterior border of the second tubercular. ... The excavation is below the extension of the roots of the molars, and is bounded below by the everted lower border of the jaw. This border is narrow, but thickens forward so as to be massive at the symphysis. ... The external face, immediately below the tubercular molars, is convex instead of concave, as in *C. wheelerianus* and *C. lupus*. ... The disproportion in the size of the premolar and tubercular teeth strikingly distinguishes this species from those of the type of *C. lupus*. ... From *C. haydeni* it differs widely in the absence of the upward direction of the alveolar border, the excavation of the external face of the ramus, the one-rooted second tubercular molar, etc. ..." And again in 1882 (p. 178): "On account of the large development of the inferior tubercular teeth I have suspected that *Canis ursinus* Cope, from the Loup Fork of New Mexico, would prove to be an *Amphicyon*."

DESCRIPTION OF NEOTYPIC SKULL AND ASSOCIATED MANDIBLE AND SKELETAL ELEMENTS, AMER. MUS. NO. 21101

Frontispiece; Figures 5A and B, 9, 10, 10A, 13A and B, 14 and 15

The teeth and mandible of our neotypic specimen, except for the slightly larger size and the presence of a double-rooted m_3, are, so far as visible, very similar to the Cope type.

DENTITION.—The teeth are in an advanced stage of wear.

The lower incisors are missing; the upper incisors are represented. i^3 is much enlarged; in the specimen it is worn to a stub. The canines are heavy, particularly at the base; they are greatly worn, especially the upper pair, through attrition with c_1 and i_3.

The non-carnassiform premolars are unusually small relative to the molars, though tending to be slightly larger in the lower than in the upper jaw. The upper premolars are very similar to those of the type specimen of *H. göriachensis* Toula (Hofmann, 1893, Pl. v), and thus differ from those of the Filhol neotype. In this the premolars are ex-

ternally flat-sided and inwardly rounded, and p^3 is moderately enlarged, filling the space between p^2 and p^4. The first premolars are single-rooted and separated from the canines (versus adjacent in the bear).

The second premolars are double-rooted and very slightly separated from premolars $_1$ and $_3$; premolars $_1$ and $_2$ are missing, but represented by alveoli. p^2 is short and triangular, differing from the tooth as seen in *H. sansaniensis*. p^3 is believed to be represented by a premolar found adhering to the matrix of the right maxilla; this agrees with the p^3 of *H. barstowensis*. It is small relative to p^2 (see restoration in figures); the protocone is slightly anterior and the tooth is curved outwardly as in *H. göriachensis*. p_3 has a relatively tall crown, and is large-proportioned compared to p^3, as in *Amphicyon* versus *Canis*.

p^4–m^2 and m_{1-3} are of typically hemicyonid type. So far as comparable in their worn state, these teeth are very similar to the Barstow; except for their much greater size, the perhaps greater elongation of the lingual half of the upper molars, and the presence of two roots to m_3 (it must be noted that the m_3 of the Cope mandible was apparently single-rooted). p^4, in the thickness of the paracone and considerable length of paracone relative to the metacone, apparently more resembles the p^4 of *H. göriachensis* than that of the Filhol neotype of *H. sansaniensis* (in which the parastyle that is practically absent in one example is slightly suggested). m_3 is situated in the base of the vertical ramus, the crown being set at an angle to the m_2.

In occlusion, the premolars of *H. ursinus* do not meet; the paraconid shear of m_1 strikes between the paracone and deuterocone of p^4, and thus falls directly superior to the deuterocone root, instead of well posterior of the deuterocone as in *Canis* and *Amphicyon* (compare Fig. 1); and the wedge-shaped inner ridge areas of the upper molars strike into the basin areas of the lowers.

MANDIBLE.—The uppermost portions of both the vertical rami are missing and the condition of the coronoid processes, therefore, unknown. (Frontispiece, and Fig. 5.) The horizontal ramus is moderately deep, deepest directly beneath the molars. The inferior border is strongly flared outwardly, suddenly constricted at the anterior edge of the main masseteric fossa, and slightly constricted inferior to m_1. The outer surface is deeply hollowed through the presence of the premasseteric fossa. The symphysis is long. The condyles are angulated relative to one another and their inner surfaces are narrowed inwardly and raised outwardly. This latter conformation of the condyles is apparently correlated with the more than usual angulation of the planes of the

horizontal rami with respect to one another, and with the angulation of the glenoid fossæ. The angle is prominent. A glance at the frontispiece shows that the deepest portion of the premasseteric fossa lies directly inferior to the broad and unusual depression at the root of the malar. While this mandibular adaptation is paralleled in *Tremarctos* and in the arctotheres, reference to the comparative figures (Figs. 55A and E) indicates how widely the same differs in the two forms. In *Tremarctos* the anterior fossa is thus restricted to the posterior area and is generally continuous with the alveolar border; in *Hemicyon* it is markedly elongate anteroposteriorly and separated from the alveolar border by the prominent convexity of that area. The parallelism between the development of the fossa and teeth in the respective forms is immediately apparent, in each case being adjusted to the work in hand. The trace of a perhaps somewhat similar adaptation may occur (as noted above) at times in the mandible of *Procyon* (Fig. 55C) and to a less degree in *Ælurus* (Fig. 55H). In the cats and in the Creodonta (see *Dissacus* and *Hyænodon*), the masseteric fossa is continuous forward to the region of the mental foramina, and neither divided, as in *Hemicyon* and the arctotheres, nor restricted to the posterior area alone, as in the dogs and bears (Fig. 55D–G).

Skull.—The specimen is the only skull in existence. It is perfectly preserved, except for a slight dorsoventral compression of the frontal and of the palatal regions, and a slight lateral compression of the brain case. (Frontispiece, and Figs. 13A and B.) The great skull of *Hyænarctos* evidently had much in common with the present specimen, as: the almost rectilinear line of the profile of the face, the slight degree of convexity of the posterior profile, the abruptness and prominence of the sagittal crest, the broad frontal region, the obtuseness of the muzzle, the considerable obliquity of the orbits, the great depth and extent of the temporal fossa, the strong longitudinal and transverse arching of the palate and its non-extension backward of the molars. The skull in size equals that of a large grizzly bear. The cranium is low, the sagittal and lambdoidal crests and occipital spine are very remarkably developed. The muzzle is broad and expanded over the canines. The brain case is small, the parietal region low and much constricted, the frontals low and narrow relative to the muzzle. The palate is broad and but very slightly narrowed anterior to the p^4s. The zygomatic arches are only

[1]Two partial skulls recently obtained in the Barstow indicate that certain characters, as the great development of the crest and constriction of the brain, may be largely a resultant of the specimen's size and age.

moderately wide. Slight postorbital processes are present on both the frontals and zygomata. The orbits are small and diagonally elongated. The mastoids are prominent and fan-like. The paroccipital processes are directed inferoposteriorly and lie well backward of the bullæ, which are remarkably small and anteriorly placed. The auditory meati are noticeably projecting. The post-glenoid processes and the anterior lip of the glenoid both arch over the glenoid cavities, which are directed posteroinwardly. The prominence of the mastoid and paroccipital processes, the general condition of the occipital region, and of the sagittal crest and occipital spine may be correlated to a certain degree with the relatively small size of the roof of the cranium itself and the need of a sufficient area for muscular attachment. The condylar foramina are slit-like and well separated from the posterior lacerated foramina. Deep muscular pits are present in the basioccipital, and marked pits also occur in the postero-inferior borders of the parietals, as in *Amphicyon* and certain early Carnivora. Other prominent depressions for muscular attachment lie just inferior to the malars (see above under mandible), and on the inferior border of the orbit; these occur to a less degree in *Pliocyon* and *Amphicyon*. The somewhat similar depressions in *Arctonyx* (and the peccary) have to do with the muscles of the snout.

The broad muzzle, non-projecting premaxilla, the wide and somewhat arched palate, the angulation of the glenoid surfaces and locked type of fossæ, and the general appearance of the basicranial region are non-dog-like, and approach in a variable degree the condition in *Pliocyon*, in certain procyonids, and in *Ursus*. The high sagittal, knife-like lambdoidal area and the strongly projecting inion, the low, diagonally elongate orbits, the anteriorly placed infra-orbital foramina, the lack of posterior production of the palate, and the length of the nasals, all so different from the bear (recalling the not too well-known *Hyænarctos*), are most closely approached in *Amphicyon*. A slightly similar development is seen in the hyena and even suggested to a very minor degree in the dog. It is not surprising that the skull characters of this small-brained Miocene form should be more nearly approached by a small-brained contemporary than by recent genera specialized from early times along contrary lines. (It must be noted, however, that, coexistent with the small-brained Miocene *Hemicyon*, were *Tephrocyon-Tomarctus* forms whose crania were practically as well domed as those of the wolves of today. In other words, the ancestors of the recent bears and *Procyon* as early as the Miocene also may have attained to moderate-sized brains with an attendant degree of doming of the crania.) A comparison

of the specimen with the two extremes represented by *Amphicyon* and *Pliocyon*, as seen in the two well-preserved Snake Creek skulls of *Amphicyon idoneus* Matthew and *Pliocyon medius* Matthew,[1] is of considerable interest. The *Hemicyon* skull, though exceeding both of the latter in the narrowness of the brain case, the relative breadth of the muzzle, etc., and approximating the first in the actual distances between foramen magnum, glenoid, posterior edge of m^2 and incisive border, entirely differs in transverse development from this dolichocephalic type, and more resembles the broad and much shorter-proportioned skull of the latter, as: in the breadth and strength of the basioccipital area, angulation of the glenoid region, unnarrowed palate, and greater heaviness of the molar series.

In position, the bullæ of *Hemicyon* parallel *Amphicyon* and *Pliocyon*, though in the latter they apparently lie slightly more inward of the postglenoid processes and may be even slightly more anterior. The bullæ in *Amphicyon* and *Pliocyon*, however, while placed much the same as in *Hemicyon*, are more globular and slightly more swollen, standing well above the plane of the basioccipital-sphenoidal suture. The bullæ quite lack the backward extension and posterior swelling seen in aged *Ursus* and highly developed in *Canis*. (In *Hemicyon* and in *Ursus* the lateral edges of the broadly extended basioccipital lie well up and slightly over the sides of the bullæ, the same being less noticeable in *Amphicyon* and the dogs through the crowding and protrusion of the bullæ.) The auditory bullæ, however, vary throughout the "*Arctoidea*" in position, degree of inflation, shape, and in the development of the external auditory meati. Thus the bullæ of immature *Ursus* and *Tremarctos*, of *Helarctos*, and of *Pararctotherium pamparum* (as seen in cast), unlike in aged *Ursus*, are well inflated, tend to lie in contact with the paroccipital and postglenoid processes, and to lack a well-developed meatus. In the specimen, the bullæ are noticeably anterior in position and so little inflated that they barely extend beyond the plane of the basioccipital. They are limited posteriorly by the line of the meati (when imaginarily extended), the posterior edges lying approximately opposite the anterior one-third of the mastoids. In the bear the bullæ are posterior, and as in the dogs reach well posterior of the meati and opposite the posterior extremity of the mastoid and adjacent to the paroccipitals. The large vacuities prominent in the basicranium of *Hemicyon* and *Pliocyon* are filled in the bear and dog by these large posteriorly developed bullæ. The basi-

[1]Matthew, W. D., 1924, Bull. Amer. Mus. Nat. Hist., L, p. 108, Fig. 27.

occipital is moderately wide as in *Pliocyon*, versus narrow in the dog and extremely wide in the bear. The basioccipital-basisphenoidal suture lies at the anterior edge of the bulla in the dog and approximately the same in the bear and hyena; in the specimen, on the contrary, it apparently lay median to the bullæ.

COMPARATIVE MEASUREMENTS OF SKULLS

	H. (Canis) ursinus, Neotype	*Amphicyon idoneus*, Amer. Mus. No. 20495	*Amphicyon sinapius*	*Pliocyon medius*, Amer. Mus. No. 17207	*Canis lupus*, Amer. Mus. No. 2383	*Hyæna striata*, Amer. Mus. No. 6247	*Tremarctos*, Amer. Mus. No. 35539
Greatest length over all	357				234	243	242
Basal length	311	312	(370)	280	202	212	222
Distance m^2 to incisive border	146	147	193	132	112	111	98
Greatest breadth over arches	201		(194)	198	130	146	149
Width over mastoids	120	91	125	115	74	82	120
Distance between centers of foramina ovale	35	(35)	(44)	50	29	31	45
Width palate ant. ext. to m^1s	90	77	(90)	90	71	57	59
Width muzzle ext. to canines	73	(62)	(66)	(72)	45	56	57
incisive border to m^2	147	150	183	(135)	115	(111 to m^1)	100
p^4-m^2	62	58	75	61	43	"	55
m^1-m^2	39	36	47	(49)	225	"	42
Width between post-glenoid foramina	76	68	(86)	88	60	55 (in bullæ?)	77
Width palate antero-externally to m^1s	90	77	((90))	90	71	57 (ant. edge p^4)	59
Width muzzle external to canine bases	73	(62)	(66)	(72)	45	56	57
m^1-m^2	39	36	49	38	22	nil	42
Posterior edge of canine-m^2	101	108	136	92	80	75	68

SKELETON.—In the characters of the skeleton (Figs. 14 and 15), *Hemicyon* differs from the highly specialized bear and from the mustelines and, while somewhat more resembling the cat and primitive felines than the dog, in some characters rather suggests recent *Procyon*. The resemblance to the latter is particularly marked in the tarsus, in the relative proportions of the known limb elements, in the axis, and to a less degree in the character of the vertebral column. Compared with a

large-sized specimen of the Alaskan grizzly (Amer. Mus. No. 70330), the individual skeletal elements are of quite different proportions, the skull is very slightly longer, the scapula and pelvis are approximately of similar length, the humerus slightly shorter, the radius and tibia somewhat longer, and the vertebral column (axis to posterior lumbar inclusive) one-third longer (approximate length 1200 mm.). The form of the brain case and of the teeth, the proportions of the lighter limb bones, the flat narrow pelvis, the unusually elongate and tall-spined vertebra, and the tall-proportioned tarsus, are quite unbear-like.

THE VERTEBRAL COLUMN.—This consists of seven cervicals, fourteen thoracics, and six lumbars; the number of the sacrals is in question.

The atlas is missing (the atlas of *I. oregonensis* is more like that of *Procyon*, the cat, and the bear than the dog, but differs from *Procyon* and the cat in the vertebral canal being roofed over anteriorly as in the bear).

The axis is relatively long. The odontoid process is broken, the neural spine large and plate-like and continued in a prominent spike far to the rear of the posterior zygapophyses, more as in *Procyon* than in the cat or in *Smilodon*, where the posterior border is notched, or in the dog and bear, where the same is blunt and unprojecting. The ventral keel is without the post-hypapophysial tubercle occurring in the dog; the vertebraterial canal is long and the anterior opening extremely far forward. The spine of the third cervical is rudimentary, that of the fourth is high, and those of the succeeding vertebræ increase in height to about the fifth thoracic (dorsoventral height of this vertebra and spine inclusive being 117 mm.), versus the abrupt increase in height at the first thoracic vertebra in the dogs and bears. The eleventh thoracic is the "anticlinal." The last three thoracics are lumbar-form, except for rib facets replacing the transverse processes. The vertebræ of the lumbar region are extremely elongate, high, narrowed transversely, deeply keeled ventrally, and furnished with prominent transverse processes and broad spines. They thus resemble *Procyon* or the cat, as contrasted with the dog and bear, in which the vertebræ are broader transversely than anteroposteriorly and lack the ventral keels. The first sacral alone is in contact with the ilium, as in the cat, versus the two sacrals in *Procyon* and two or more in the bear. The first sacral vertebra equals the last lumbar vertebra in length, being narrower and much more elongate than in the cat or *Procyon;* in the bear it is remarkably short. Two sacral vertebræ remain, the second being noticeably narrower than the first. The rudimentary spines of the latter might suggest that the tail possibly may have been reduced, as in the bear.

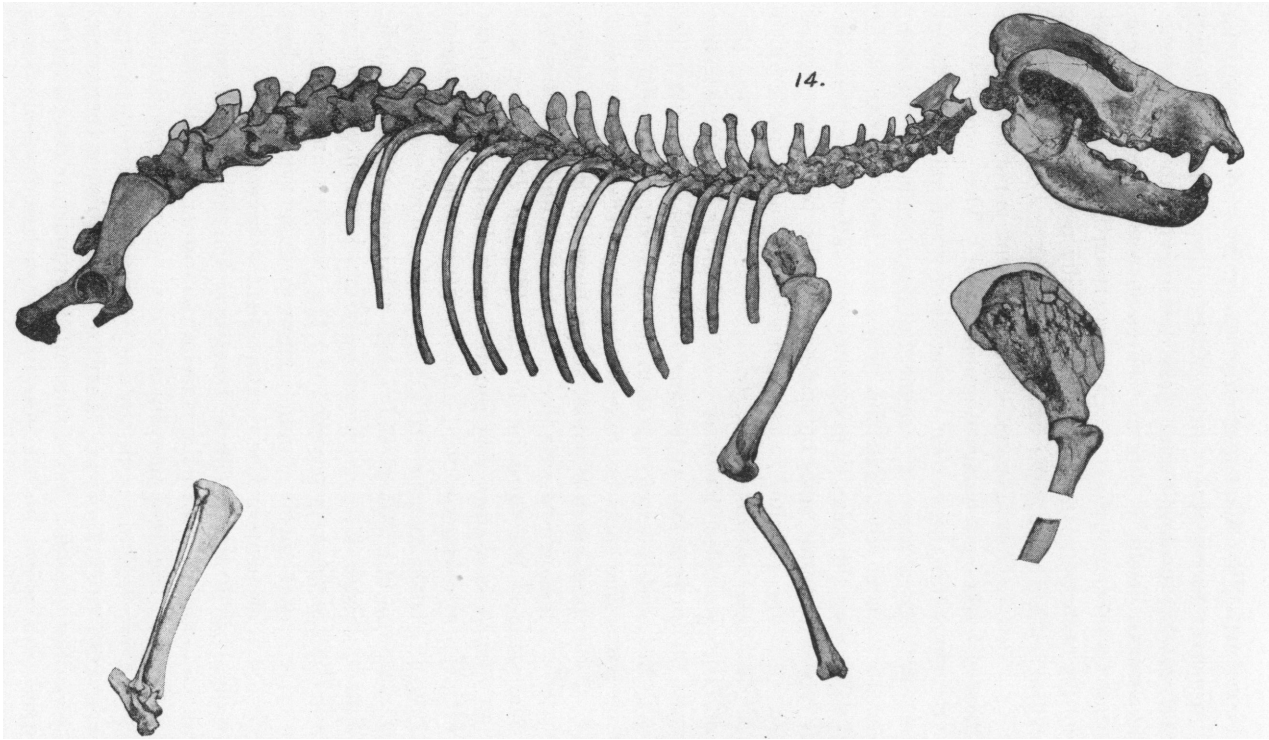


Fig. 14. *Hemicyon* (*Canis*) *ursinus* (Cope), skull, mandible, and portions of skeleton (left scapula reversed) of neotype from Santa Fé Miocene, New Mexico, Amer. Mus. No. 21101.

THE SCAPULA.—The distal portion of the spine and the proximal posterior border of the scapula are broken. The scapula is taller-proportioned and the posterior plate less developed than in the bear. The distal posterior border is thin and flares outwardly as in *Procyon*, differing from the bear, in which it is further strengthened by a prominent ridge. The anterior plate is swollen outwardly parallel to the spine as in *Phlaocyon*, in this again differing from the bear.

FIG. 15

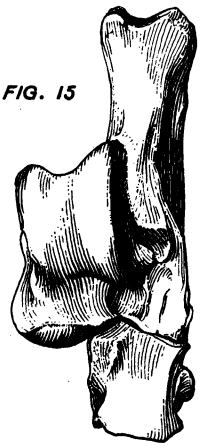


Fig. 15. *Hemicyon* (*Canis*) *ursinus* (Cope), right astragalus, calcaneum, and cuboid, neotype specimen (in part), Amer. Mus. No. 21101. × ½

THE PELVIS.—This element is noticeably narrow and elongate-proportioned. The symphysis is long, the plates of the ilia vertical and as unflared as in the cat, versus the broadly flared condition in *Procyon* and the bear. The anterior edge of the acetabulum is approximately half-way between the anterior edge of the ilia and the posterior edge of the ischium, versus considerably more posterior in the cat, *Procyon*, etc.

THE HUMERUS.—The shaft is less arched than in *Procyon* or the bear. The distal end is much less widely expanded than in the bear, and radial and ulnar surfaces are separated by a well-marked groove, much as in *Procyon*, where, however, the ulnar trochlea edge is knife-like. The entepicondylar foramina are present as in the cat, *Pliocyon*, *Phlaocyon*, and *Tremarctos*. The radius is only slightly shorter than the humerus (95%), the condition being approximated in the raccoon (97%), versus the much shorter radius in the bear (87%), and wolverene (83%); table, page 47. (In *I. oregonensis*, a large entepicondylar foramen is present, and the humerus and ulna are said to be of much more massive type than these elements in the Californian *A. simum*).

THE TIBIA AND FIBULA.—These bones are relatively long-proportioned, and the distal articulatory surface of the former is small relative to that of the bear. The tibia laterally is straight as in *Procyon* and the bear, not bowed outwardly as in the cat. (A femur, tentatively referred by Lydekker, 1883, to *H. sivalensis*, is said to be notable for the general stoutness, broadness, and flatness of its shaft, the moderate development of its terminal expansions, and the shortness of the poorly defined constriction below its head, etc.)

THE FEET.—The bones of the feet are represented alone by the astragalus, calcaneum, and cuboid. The proportions of the tarsus are somewhat the same as in the dog or the cat, but the known elements differ in the presence of an astragalar facet on the cuboid and the deeper grooving of the astragalus. The tarsal arrangement differs markedly from that in *Ursus* and *Gulo*. In the two latter there is a somewhat similar astragalar facet on the cuboid, but the cuboid and astragalus are much compressed dorsoventrally and expanded dorsally, the head and shaft of the astragalus are angulated, the astragalar grooves short, and the calcaneum correspondingly short. The cuboid is tall, the astragalar facet broad, and the facets for the fourth and fifth metatarsals prominent. The proportions of the astragalus, the large size of the tibial compared to the fibular trochlea, the grooving of the proximal surfaces, and the continuance of the grooving on to the posterior surface, all much suggest the condition in recent *Procyon*. (The cuboid of *I. oregonensis* is said to more nearly approach a cuboid form than does the corresponding element in the recent *Ursus*, and is compressed dorsoventrally to a much greater degree than in the present specimen. An astragalar facet is also well developed in the Oregon specimen. Metacarpal No. 5 of the latter form is said to resemble in general that in *Arctotherium*, though to differ greatly in proportions. Metatarsal No. 2 is said to be even relatively more like that of *Arctotherium* [Merriam, 1916, p. 97].)

	H. (Canis) ursinus, Neotype		*Amphicyon major*, casts	*Procyon*	*Canis lupus*, Amer. Mus. No. 16138	*Ursus dalli*, Alaska Amer. Mus. No. 70330	*Gulo*	*Felis*	*Phlaocyon*
Greatest length humerus	320			104	220	330	140	143	91.5
" " radius	305		298	101	221	288	118	120	62.5
" " tibia	327		317	121	242	298	141	164	84.5
PERCENTAGES									
radius / humerus	95%		97%	100%	87%	84%	84%	68%	
tibia / humerus	102%		107%	110%	90%	100%	115%	92%	
radius / tibia	93%	94%	83%	91%	97%	83%	73%	74%	

Hemicyon sansaniensis Lartet, 1851
(Genotypic Species)
Figure 2

"Un vrai chien," LARTET, 1837, Annales Sci. Nat., Ser. 2, VII, p. 119; Compte rendu heb. Acad. Sci. (Paris), IV, p. 90; 1838, idem, VI, p. 655; idem, VII, p. 1157; 1839, idem, VIII, p. 498.

Hemicyon sansaniensis LARTET, 1851, 'Notice sur la Colline de Sansan,' p. 16.

Amphicyon major ("de plus taille," in part) BLAINVILLE, 1839–1864, Ostéographie, Pl. XIV (left top).

Amphicyon (?) *minor* BLAINVILLE (in part), 1839–1864, Ostéographie, p^4, figured Pl. XVI (left center), text p. 92.

Amphicyon laurillardi (in part) POMEL, 1853, 'Catalogue méthodique . . . des vertébrés fossiles decouverts dans le bassin . . . de la Loire . . . et . . . l'Allier,' p. 72 (small mandible figured by BLAINVILLE under *A. major*).

Hyænarctos hemicyon GERVAIS, 1848–1852, Zoologie et Paléontologie français, 1st Ed., unfigured, p. 193, Note 1; Expl. Pls. XXVI–XXVIII, p. 13; Expl. Pl. XXIII; 1852–1853, Bull. Soc. Géol. Fr., Ser. 2, X, p. 154, Pl. IV, Fig. 2; 1853, Annales Sci. Nat., Ser. 3, XX, p. 232; 1855–1859, Zoologie et Paléontologie français, 2d Ed., p. 210, Pl. LXXXI, Fig. 8 (not Fig. 9). GAUDRY, 1878, 'Les Enchainements du Monde Animal . . . Mammifères tertiaries,' p. 212, Fig. 278.

Hemicyon sansaniensis LARTET, GAUDRY, 1876, 'Matériaux pour l'Histoire des Temps quaternais,' Pl. XXI, Fig. 1, and Pl. XXII, Fig. 1. FILHOL, 1891, 'Étude sur les Mammifères fossiles de Sansan,' Annales Sci. Géol., XXI. ZITTEL, 1894, 'Traité de Paléontologie,' Part 1, p. 642, Fig. 534. WOODWARD, 1898, Vert. Pal., p. 394.

Dinocyon hemicyon GERVAIS (in part), LYDEKKER, 1883, Pal. Indica, Ser. 10, II, p. 202, footnote; 1885, Catalogue of the Fossil Mammalia in the British Museum, Part 1, p. 156. SCHLOSSER, 1898, Beiträge Pal. Osterreich-Ungarn., VII, p. 83.

Dinocyon laurillardi POMEL, DEPÉRET, 1892, Arch. Mus. Lyon, p. 39.

Hemicyon göriachensis id *H. sansaniensis* SCHLOSSER, 1899, Palæontographica, XLVI, p. 108.

Hemicyon LARTET, GAUDRY, 1896, 'Essai de Paléontologie philosophique,' p. 190, Fig. 195. WEBER, 1904, 'Die Säugetiere,' p. 535. BOULE, 1919, 'Les Grottes de Grimaldi,' I, p. 254. ZITTEL, 1923, Grundzüge der Paläontologie, II, p. 469.

I take as the lectotype of *Hemicyon sansaniensis* Lartet (see above under history of the genus *Hemicyon*) the mandible of the Lartet collection at present in the Muséum d'Histoire Naturelle, Paris, which Pomel referred to *Amphicyon laurillardi* Pomel, and which Blainville figured under *A. major* (1839–64, left top, Pl. XIV). I refer to this as cotypes the maxillary specimen with m^1-m^2 and broken roots of p^4, figured by Gervais (1859, Pl. LXXXI, Fig. 8, etc.) and by Filhol (1891, Pl. VIII, Fig. 4), and the p^4 figured by Blainville, Gervais, and Filhol. I refer, as a neotype, the fine specimen of associated palate and mandible found and figured by Filhol (1891, Pls. VII and IX). These specimens, while showing considerable variation in size, are closely similar in character. A difference of 20%, however, observed between the anteroposterior diameters

of the m_1 of the type and a large detached specimen implies the presence of a second and unnamed species, this difference being equivalent to that existing between the type specimens of the two Barstow species.

TYPE.—Portion of a mandible containing p_1-p_4 alveoli, m_1-m_2 slightly worn, and alveolus m_3 from Sansan, France, Lartet Coll., Mus. d'Hist. Nat., Paris. Figured by Blainville, left top, Pl. XIV. This paper, Fig. 2. The premasseteric fossa runs forward in a shallow extension to the vicinity of the mental foramen inferior to p_4. The inner cusps of m_1 and metaconid of m_2 are very little worn; the enamel of the main external cusps is worn through (the protoconid of m_1 is very slightly lower-crowned than in Blainville's figure). m_3, alveolus elongate, and noticeably narrowed posteriorly.

NEOTYPE.—Portion of a skull and mandible with the dentition completely represented, mandible showing premasseteric fossa, from type locality. Filhol Coll., Mus. d'Hist Nat., Paris. Figured by Filhol, 1891, Pls. VII and IX, and text figure, p. 304 (m_3). The two lower molars are very slightly shorter than those of the type specimen.

Description of Filhol neotype, palate-mandible specimen:

PALATE.—The teeth are practically unworn; incisors ^{1} and ^{2} (shown in Filhol's figure) are missing; incisors ^{3} are both present, and slightly separated from the upper canines; upper canines are long and slight, left is unbroken.

p^1, of right side, is indicated by an alveolus, which is slightly separated from c and from p^2.

p^2-p^3 are present on right side; p^3 (17 mm.) is much larger relative to p^2 (9.1 mm.) than drawn by Filhol.

p^3 is surrounded by a cingulum; this is especially noticeable on the inner, and on the posterior border where it is extended backward contrary to Filhol's figure.

p^4 has a slight external cingulum, a prominent cingulum cusplet at the anterior extremity of the tooth (an incipient parastyle), and a strong inner cingulum continuous with the medianly placed deuterocone, as in the case of the "parastyle"; the summit of the deuterocone cusplet is posterior (Filhol figures the deuterocone too long anteroposteriorly and not cut-in enough posteriorly); the anterior corner of the tooth is produced forward, not rounded inwardly as in *Hyænarctos insignis*; and the rudimentary parastyle lies outward of anterior edge of the paracone (versus rather inward in *H. insignis*). Were the anterior-exterior cingulum and the bulge of inner margin of deuterocone of the p^4 of Filhol's neotype removed through abrasion, the p^4 would resemble the large Sansan p^4 (Filhol, Pl. VIII, Fig. 3) as well as that of the Barstow and Göriach specimens.

m^1 and m^2 are furnished with external cingula; and an inner ridge (perhaps figured too near the inner margin by Filhol) with small but distinct tubercles, the inner ridge being relatively high posteriorly and low forwardly; a prominent cingulum cusp lies at the posterior inner corner,—this is not shown in Filhol's figure. (In biting, the two inner accessory cusps of heel of m_1 fit over anterior area of the inner ridge of m^1.)

The nasal foramina, shown by Filhol, are not visible in the specimen. These in the Santa Fé skull are relatively short, the premaxilla not projecting far forward as in the dog.

MANDIBLE.—Left ramus with c (broken); an indication of alveolus of p_1; p_2 small; alveoli of p_2 and p_3; m_1-m_3 entire (excepting that m_1 is repaired between paraconid and protoconid); and right ramus (anterior alveolar border broken) with m_2-m_3.

The sulcus is deep; the posterior inferior border of the mandible is inflected outwardly below the deep and anteriorly extended premasseteric fossa. The region of the masseteric ridge is noted, in comparison with the type specimen, to be slightly distorted.

p_2 is narrow, elongate (a. p. diam. 8.5), and separated by slight diastemata from the alveoli of p_1 and p_3.

p_3 and p_4 are each represented by double and slightly separated alveoli.

m_1 has a diminutive cusplet postero-adjacent to metaconid.

m_2, the metaconid is slightly more prominent than paraconid, and external cingulum is present.

COTYPES.—Right maxillary fragment with p^4 represented by broken roots, m^1 (external half missing), and m^2. The posterior inner borders of m^1 and m^2 are greatly worn. From the type locality. Lartet Collection, Mus. d'Hist. Nat., Paris. Figured by Filhol (*loc. cit.*), 1891, Pl. VIII, Fig. 4 (reversed). Figured by Gervais (*loc. cit.*), 1852, 1–3, Pl. IV, and 1859, Pl. LXXXI, Fig. 8. Figured by Gaudry, *loc. cit.*, 1878, Fig. 278. Figured by Zittel, *loc. cit.*, 1894, Fig. 534.

p^4, right, Mus. d'Hist. Nat., Paris. Figured under "*A. minor*" by Blainville (*loc. cit.*), Pl. XVI. Figured under *H. sansaniensis* by Filhol, 1891, *loc. cit.*, Pl. VIII, Fig. 3. Blainville (p. 92) lists under "petite *Amphicyon*" with other material (which he considers may represent one or many forms) a p^4 (as of the left side), which he notes differs from its analogue in the great *Amphicyon*, in that the inner lobe, in place of being quite anterior, as in *Amphicyon* and the dog, or nearly posterior as in the bears, is in the middle. He believes it to represent a form intermediate between the bear, great *Amphicyon*, and *Canis*; that it does not represent *Agnotherium* Kaup.

The stage of wear and the broken condition of the maxilla make comparison with Filhol's neotype (palate-mandible specimen) difficult. Filhol's and Gervais' figures do not show the worn condition of the posterior edge of the upper molars. An examination of the specimen itself shows the three roots of p^4, the inner and rather posteriorly placed root indicating the former presence of the typical anteromedian-lying deuterocone.

REFERRED SPECIMENS.—m^1, left, slightly broken. Mus. d'Hist. Nat., Paris, Box 359, "*A. minor*" of Blainville's text figured under "*A. major*," Ostéographie, Pl. XIV (upper left corner).

m^1, right, Mus. d'Hist. Nat., Paris, Box 369 (in part).

Four teeth that are somewhat larger than the foregoing may represent a second species. These approximate those of the Santa Fé neotype in size. They are:

m_1, right, unworn. The outline is slightly more sinuous and heel more swollen than in above molars. (This tooth measures 35.1 × 14.5.) It is of the same yellowish-white color as the p^4 of a fragment figured by Blainville, Pl. XVI (see above). The metaconid is low, heavy, and rather unusually distinct from protoconid; and the anterior tooth base is more swollen than in the other specimens. It probably represents a second Sansan species.

m_1, left, broken, in fragment of mandible, is identical with right m_1.

p^4, right, broken.

Two metatarsals and several phalanges (not seen by the writer), which Filhol states are remarkably long and slender but more suggestive of the hyena than of the cat.

The Sansan collection includes two mandibular specimens of the general size of the type mandible of *H. sansaniensis*, but which differ from the latter and also from one another. The first (No. 90, Mus. d'Hist. Nat., Paris) is distinctly amphicyonid. I here refer it to *A. minor*, which is represented in the Sansan Collection by other material that similarly differs in notably smaller size from the material representative of the larger Sansan *Amphicyon, A. major*. This particular mandible was taken by Filhol as the type for his "*Pseudocyon sansaniensis*" (1891, *loc. cit.*, p. 153, Pl. x, Figs. 1–3). Pomel (1853, *loc. cit.*, p. 72) and Lydekker (1883, *loc. cit.*, p. 248, footnote) have referred it to *A. laurillardi* Pomel. The second mandibular specimen (No. 89, Mus. d'Hist. Nat., Paris) is distinctly non-amphicyonid. A premasseteric fossa was apparently present. This is the mandible which Filhol, in later discovered error (*loc. cit.*, pp. 148 and 150), described and figured (*loc. cit.*, mid-page 127–137, Pl. VIII, Figs. 1–3) as "*H. sansaniensis*" Lartet. I here place it, with great reservation, together with the lost uppers of Gervais' type of "*Hyænarctos hemicyon*," under (*?*)*Dinocyon sansaniensis* (see below).

Hemicyon göriachensis (*D. göriachensis* Toula, in part)

Figure 16

Amphicyon species, TOULA, 1884, Jahrb. K. K. Geol. Reich., XXXIV, p. 391, Pl. VIII, Figs. 12–14.

Amphicyon göriachensis TOULA, 1884, 1885, pub., Sitzungsb. K. K. Akad. Wissen., XC, p. 407, Pls. I–III; Verhandl. K. K. Geol. Reich., p. 451.

Dinocyon göriachensis TOULA, HOFMANN, 1886 (part), Beiträge Pal. Österreich-Ungarn., VII, p. 84. SCHLOSSER, 1888 (part). FILHOL, 1891, 'Étude sur les Mammifères fossiles de Sansan,' p. 136. DEPÉRET, 1892, Arch. Mus. Lyon, p. 38. HOFMANN, 1893, Abhandl. K. K. Geol. Reich., XV, p. 24, Pls. IV–VI.

Hemicyon göriachensis TOULA, SCHLOSSER, 1899, Palæontographica, XLVI, p. 107.

TYPE.—A crushed palate with the dentition completely represented. The teeth are slightly worn, c is broken and out of position, a diastema is suggested between p^1 and p^2. From Göriach, Steiermark. Cast Mus. d'Hist. Nat., Paris. Figured by Toula, 1884, Sitzungsb. K. K. Akad. Wissen., XC, pt. 1, Pls. I–II. Hofmann, 1893, Abhandl. K. K. Geol. Reich., Pls. V and VI.

REFERRED SPECIMENS.—Mandible portions with right p_4-m_1 and m_3, and left m_1-m_3. From Göriach, Steiermark, Brit. Mus. cast marked "*Dinocyon göriachensis*," No. 12120 (Hillier Coll. purch. 1922). Fig. 16 this paper. Specimen represents a larger individual than the type specimen, approaching the neotype of *H. ursinus*.

Lower incisor to p_4 from Göriach. Figured by Toula, 1884, Pl. III, Figs. 1–3. Hofmann, 1893, Pls. V and VI.

p_4, m_1 talonid, and m_2, of left side. Figured by Toula, 1884, Pl. VIII, Figs. 12–14.

Left mandible portion with c-m_1 (cast Paris), and figured by Hofmann, 1893, Pl. IV.

CHARACTERS.—Peculiar form p^2-p^3 as noted by Filhol.
Upper molars, tendency to be wide transversely.
m^2, long anteroposteriorly, and unusually large proportionate to m^1.
m_2 of referred mandible likewise unusually large relative to m_1.

Compared to *H. sansaniensis*.—Note that certain seeming differences may be accounted for by the stage of wear (possibly others may be due to reconstruction of the specimen).

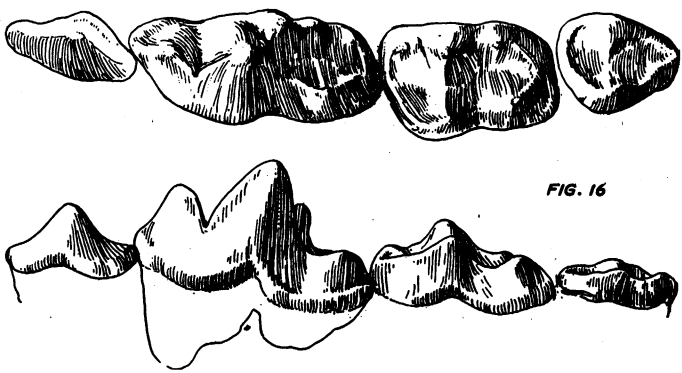


FIG. 16

Fig. 16. *Hemicyon göriachensis* Toula, referred p_4–m_3, left, from Göriach, after cast, Brit. Mus. No. 12120. (p_4 supplied from unfigured right series.) Drawn by Miss Woodward. Natural size.

The generally slightly smaller size, as seen in the teeth and in the considerably narrower palate (this narrowness somewhat accentuated by crushing).

p^2-p^3, of somewhat peculiar form, the p^2 being broader transversely, and thus apparently very like the p^2 of Santa Fé neotype.

p^3 is much shorter anteroposteriorly, the outer border is rounded and the inner face flat, versus the reverse in the Sansan specimen.

p^4 is broad transversely, but shorter anteroposteriorly; an external cingulum is present, and the parastyle is absent (as in large p^4, referred, from Sansan).

m^1 is slightly smaller, but very similar to the Filhol Sansan neotype.

m^2 relative to m^1 is definitely larger, m^2 being actually slightly larger than m^2 of the otherwise larger *H. sansaniensis;* the inner ridge is slightly less prominent.

Hemicyon grivensis, new species

Figure 17

"*Dinocyon laurillardi* POMEL" and "*Dinocyon göriachensis* TOULA," according to Lyon. Museum label.

TYPE.—m^2, right, unworn, from La Grive St. Alban. Mus. Sci. Nat., Lyon. (Fig. 17 this paper, previously unfigured.) Cast Amer. Mus. Nat. Hist.

The metacone is small, and greatly angulated relative to the paracone; inner ridge very weak. The cingulum cusp of the posterior inner corner of the lingual exten-

Hemicyon

Measurements of Dentitions

		H. sansaniensis Lartet			*H. grivensis*, n. sp.	*H. göriachensis* (Toula)	*H. ursinus* (Cope)		*H. barstowensis*, n. sp.			*H. californicus*, n. sp.	
	Type mandible (fig'd Blv., Pl. XIV)	Neotype (fig'd Filhol)	"Laurillard" maxilla (fig'd Gerv., Pl. LXXXI, Fig. 8)	Disassociated specimens	Type tooth, M.S.N. Lyon, Fig. 9	Type maxilla, cast M. H. N., Paris	Type mandible (fig'd Cope)	Neotype A. M. 21101	Type A. M. 20810 Figs. 6 and 11	Paratypes A. M. 20811 Fig. 7	Paratypes A. M. 20816 Fig. 8	Type A. M. 20827	Paratypes
(post-canine m^2)		99				(93–6)		103					A. M. 20829
p^4-m^2		62				(59)		62	54.5		(56)		
p^1				(fig'd Blv., Pl. XIV)				9					
p^2		9.2				9.5		11.7					
p^3		16.7				12.5					12		
p^4		25×16.8	((26))(a)	26.8×16.5 (also fig'd Gerv. & Filh.)		22.6×16.5		26.2×17.2	22.5×13.3	21.8×—	24.4×15.9		26.8×(16)
													A. M. 20828
m^1		22×22.5	(22)	22.1×22.8		19.5×24.1		23.5×25.4	19.5×20	20.5×20	(22)×22		(23)×22.5
m^2		16×21[1]	16.5×21.1		19.8×23.6	17.8×23		16.5×24.5	14×17.5	14.5×18.5	14.9×17.5		15.5×20
						Brit. Mus. cast No. 12120				A. M. 20813 Figs. 3, 12	A. M. 20819		A. M. 20826
Post c-m_1		94					91	93		93.5			
Post c-alv. m_2				(unfigured)	*H. göriachensis* Toula, Hofmann, 1893, Pl. IV		121	(130)		(121)			
p_1		left present								7.7			
p_2													
p_3								10		11.1			
p_4					14	18		16.5		16.5		15.5	16.
m_1	30.6	32.5		35.1×14.5	29[2]	32.5×13–14	32	35.4×15	29.2×12.7	(30.5)	31×14	33×15	34.5×15
m_2	18.8	19.4				23.6×14.5 ant.	21	23×15	17.7×12			20×13.5	20.5×14
m_3	14.5 (alv.)	12				16×12		(17 alv.)	10.5×8.5				
Diameter c							23	(25)		20			
Depth sulcus p_2		44.5					38	44		37		42	
Depth anterior end m_1	50	45					45	49		44		54	44
Depth between p_3 and p_4	43.5	41.5						45		40		48	
Depth at posterior border m_2							55	61		50			

(a) = estimated.
( ) = approximate.

[1] H. stätslingii (figured Roger, Pl. III, Fig. 8), m^2 type measures 15×19.5. H. (?) race minor (fig'd Depéret, 1887, Pl. XIII, Fig. 8), m^2 type measures 15×17 mm.
[2] Toula 1884, Pl. VIII, figures Göriach p_4-m_2, m_2 measuring (20×14), of unusually small size.

sion is very prominent. The tooth is similar to that of *H. sansaniensis*, except for its much larger size and weakness of the inner ridge. Compared to *H. barstowensis*, it is much larger, the hypocone is relatively more elevated and prominent, and the inner ridge weaker.

The specimen is sufficient to definitely establish the presence of *Hemicyon* at La Grive St. Alban and thereby the contemporaneity of *Hemicyon, Dinocyon thenardi*, and *Ursavus primævus*. The species was apparently of unusually large size.

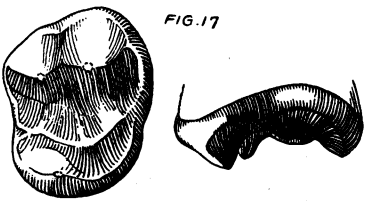


Fig. 17. *Hemicyon grivensis*, new species, m^2, right, from La Grive St. Alban, crown and anterior views, after Amer. Mus. cast of type specimen in Mus. Sci. Nat., Lyon. Natural size.

Hemicyon stätzlingii, new species

Hemicyon sansaniensis LARTET, ROGER, 1898 (in part), Bericht. Naturwiss. Verein für Schwab. und Neuburg in Augsburg, XXXIII, p. 5, Pl. III, Fig. 8.

Hemicyon göriachensis SCHLOSSER, 1899, Palæontographica, XLVI, p. 109.

TYPE.—m^2, right, from Dinothere Sands of bayerisch-schwabischen Hochebene (Stätzling near Augsburg). Figured by Roger, Pl. III, Fig. 8.

CHARACTERS.—The tooth as figured by Roger, except for its much smaller size, is indistinguishable from the m^2s of the Sansan and Göriach types. The tooth, though of somewhat similar size to the La Grive St. Alban m^2 described by Depéret under *Hemicyon, race minor* (see below), differs in its very typical and striking hemicyonid proportion and character.

(?) **Hemicyon minor** Depéret

Hyænarctos hemicyon (Lartet), *race minor* DEPÉRET, 1887, Arch. Mus. Lyon, p. 98, Pl. XIII, Fig. 8.

Dinocyon laurillardi POMEL, by present Museum label.

TYPE.—A small m^2. From La Grive St. Alban. Coll. Mus. Lyon. Figured by Depéret, 1887, Pl. XIII, Fig. 8.

Depéret (1887) considers that the specimen represents an m^1, and that it strongly recalls the form of the m^1 in the considerably larger *H. sansaniensis*. He thus provisionally refers it to *H. sansaniensis* under "race minor.". Schlosser (1899, p. 109) is doubtful whether, on account of its very small size, this Depéret specimen may be correctly referred to *H. göriachensis*, which he considers to be inclusive of *H. sansaniensis*. The tooth is not of typical hemicyonid form (as I have noted above under *H. stätzlingii*). It may perhaps more resemble *Cephalogale geoffroyi*. For the present this species must remain indeterminate.

DINOCYON Jourdan, 1861

Dinocyon thenardi Jourdan, which authorities have tended to place with the canids,[1] is ostensibly a member of the group Hemicyoninæ. It agrees with *Hemicyon* and *Hyænarctos* in the proportion of the antero-posterior diameters of m_2 and m_1, and in the loss of m^3, and with them and *Ursavus* differs from all other known *megalocreodontic* Carnivora in the presence in the mandible of a premasseteric fossa. The character of the deuterocone of the upper carnassial is unfortunately indeterminate, as this tooth is so far unknown. [The shape and the direction of the worn surfaces of the paraconid-protoconid of m_1, however, suggest that the p^4 deuterocone was anteromedian and that this tooth was of *Hemicyon-Hyænarctos* type.] Strictly, the genus *Dinocyon* is alone represented by the huge *Dinocyon thenardi*,[2] but to the genus broadly considered I tentatively refer as belonging to a second species certain fore-mentioned specimens from Sansan, which though somewhat resembling *Hemicyon* are clearly not referable to the Sansan species. [Two large American forms originally referred to *Dinocyon*[3] are now recognized as species of *Amphicyon*.] As seen in the m^1, the genus is nearer to *Hemicyon* than to *Hyænarctos*.

Dinocyon thenardi Jourdan, 1861

Dinocyon thenardi JOURDAN, 1861, Compte rendu heb. Acad. Sci. (Paris), LIII, p. 959; 1862, Bull. Soc. savantes. FILHOL, 1883, Arch. Mus. Lyon, III, p. 43, Pl. III, Figs. 1–14. DEPÉRET, 1887, idem, IV, p. 94, reviews Filhol (*loc. cit.*). LYDEKKER, 1883, Pal. Indica, Ser 10, II, p. 202; 1885, Catalogue of the Fossil Mammalia in the British Museum, Part I, p. 150. SCHLOSSER, 1888, Beiträge Pal. Osterreich-Ungarn., VII, p. 81. DEPÉRET, 1892, Arch. Mus. Lyon, Pl. I, Figs. 20 and 20A. ZITTEL, 1923, Grundzüge der Paläontologie, p. 469.

TYPE.—A portion of the right ramus of the mandible with m_1-m_3 from La Grive St. Alban, Coll. Mus. Lyon (cast Amer. Mus.). Figured by Filhol, 1888, *loc. cit.*, Pl. III, Figs. 4 and 5 reversed.

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[1]Osborn, H. F., 1910, 'Age of Mammals,' p. 529 (note by Matthew); Boule, M., 1919, 'Les Grottes de Grimaldi,' I, p. 254. Filhol, as Lydekker (1883, Pal. Indica, Ser. 10, II, p. 202) points out, was led astray in considering that *D. thenardi* had no affinity with *Hyænarctos* through Owen's erroneous characterization of the lower carnassial of *Hyænarctos*. Lydekker himself notes, and contrary to present evidence, that the lower carnassials of *Hyænarctos*, *Dinocyon*, and *Hemicyon* are constructed on the type of the dogs, that in the upper molars there is an almost complete transition from the true bears through *Hyænarctos* to *Dinocyon*, and that it is impossible to determine with which of the two, ursids or canids, *Dinocyon* should be classed. Lydekker (1885) refers both *Dinocyon* and *Hyænarctos* to the Ursinæ.

[2]Zittel, in evident error, notes the occurrence of the genotypic species at Sansan, Steiermark, and in the Lower Pliocene of Frohnstetten, Eppelsheim. The p^4 from La Grive St. Alban figured by Depéret (Fig. 17), in its greatly reduced and anteriorly lying deuterocone, and the huge p^4 from Baden figured by Schlosser (1899, Palæontographica, XLVI, p. 122, Pl. XIV, Fig. 32, measuring 34×28 mm.), in its broadly and anteriorly placed deuterocone, etc., differ entirely from the *Hyænarctos-Hemicyon* type and are not believed to be correctly referable to *D. thenardi*.

[3]*Amphicyon* (*D.*) *gidleyi* Matthew, and *Amphicyon* (*D.*) *ossifragus* Douglass, of the North American Tertiary, which approach *Dinocyon thenardi* in size, and agree with it and *Hemicyon* in the loss of m^3, are typically amphicyonid in their transversely elongated molars with prominent crescentic protocones, anteriorly situated deuterocones, and (as may be seen in the case of *A. gidleyi* in which the mandible is known) in the non-hemicyonid character of the mandible. (See in part, Matthew, 1923.)

REFERRED MATERIAL FROM TYPE LOCALITY.—Coll. Mus. Lyon (casts Amer. Mus.):

m^1 right. Figured by Filhol, *loc. cit.*, Pl. III, Figs. 11, and 6 reversed.

Portion of m^2 left in maxillary fragment (external half of tooth missing). Figured by Filhol, *loc. cit.*, Pl. III, Fig. 12.

Two incisors, c, and 5 metacarpals of right side, collected 1847–61. (*Loc. cit.*, Figs. 7–10 and 13–14).

m_3, from La Grive St. Alban, referred by Depéret (1892). Reference in question (see below).

CHARACTERS OF *Dinocyon thenardi* JOURDAN

Presence of premasseteric fossa; enormous proportions, teeth exceeding in size those of the mandible referred by Lydekker to *Indarctos* (*Hyænarctos*) *punjabiensis*.

m_1, paraconid broad, lateral tooth borders unindented; protoconid median.

m_2, and m_3, markedly elongate.

m_2, paraconid remarkably developed and separated on inner tooth surface by a small valley from metaconid (not shown in cast).

m^1 (referred), transverse diameter exceeding anteroposterior diameter, inner ridge weak, post-cingulum cusplet present (as in *Hemicyon*).

m^3, absent.

The presence of the premasseteric fossa, shortness of the talonid, and weakness of the hypoconid of m_1, the unusual development of the trigonid of m_2, and the weakness of the inner ridge of the referred m^1 prove the wide separation of this form from *Amphicyon*.

DESCRIPTION OF TYPE MANDIBLE.—The teeth are of unusually large size, being longer anteroposteriorly and higher-crowned than those of the large mandible referred by Lydekker to *I.* (*H.*) *punjabiensis*.

The teeth are moderately worn (length of m_1-m_3 equals 95 mm., measurement reduced through the m_3 lying in the base of the ascending ramus; m_1-m_2 equals 78 mm.; and m_3 equals 23 mm.).

m_1, even sweep of the outer and inner tooth borders, absence of median external indentation usually separating trigonid from talonid; trigonid broad, width of paraconid slightly exceeding that of talonid; heel straight and slightly narrowed, inner posterior border (endoconid) rudimentary and low, hypoconid moderate and slightly worn, basin absent.

The tooth differs from *Hemicyon* and even more from *Hyænarctos* in relative broadness of the paraconid and narrowness of the talonid, and in the absence of any real constriction between the trigonid and talonid. The paraconid and protoconid blades are slightly worn, the worn surface sloping externally as in *Hemicyon* versus inwardly as in *Canis*. This condition (?) suggests the presence of an anteromedianly placed deuterocone in p^4 as in *Hemicyon*.

m_2, elongated, paraconid bold and separated by a small intervening valley from the metaconid (as noted in the actual type specimen, not shown in casts); protoconid much more prominent than metaconid; hypoconid developed, worn inner border of heel low and without developed cusp. In its relative greater elongation and the prominence of the outer cusps, the specimen differs from *Hyænarctos*.

m_3 is situate in the base of the ascending ramus (greatly foreshortened in occlusal view as figured by Filhol); elongated, tapering posteriorly; root anteroposteriorly elongated ((?) two-rooted). The tooth somewhat suggests the m_3 of *Hemicyon*; it differs markedly from the tooth of *Hyænarctos* (at least as seen in *I.* (*H.*) *punjabiensis* referred).

DESCRIPTION OF REFERRED MOLARS:—

m^1, right, broadly triangular; anteroposterior diameter slightly exceeded by transverse diameter, as may occur in *Hemicyon*, but not seen in *Hyænarctos*; lingual portion of tooth narrower, protocone and inner ridge weaker than in *Hemicyon*; posterior root slightly larger than anterior root. Post-cingulum cusplet small, but present as in *Hemicyon* versus absent in *Hyænarctos*.

m^2 left (broken, the main external cusps missing); lingual portion broader transversely than in m^1, as typical in *Hemicyon*, *Hyænarctos*, and also in *Amphicyon*.

m_3 (referred by Depéret, 1892), considerably smaller than that of the type specimen, measuring according to Depéret's text 18×13 mm. (by Depéret's figure 18×11), versus 23×16.4 of the *D. thenardi* type mandible. The specimen as figured is of the general proportions of the *D. thenardi* m_3. It is slightly larger than the m_3 of any thus far known species of *Hemicyon*.

COMPARISON OF *D. thenardi and Hemicyon:*—

m_1, talonid slightly narrower and shorter; trigonid relatively fuller and undivided from talonid; talonid rounded off postero-inwardly much as in *Hemicyon*; hypoconid more external and relatively slightly larger; metaconid more posterior; basin undeveloped.

m_2, anteriorly well developed and postero-inner corner reduced as in *Hemicyon*.

m_3, more elongate than in *Hemicyon*.

In *D. thenardi* $\frac{m_1}{m_2}$ = 77%, versus 61% in *Hemicyon*, and 71–74% in *Hyænarctos*.

m^1 and m^2, referred, differing from, but suggestive of, *Hemicyon*, as noted above.

(?) **Dinocyon sansaniensis,** new species

I take as the type of this somewhat indeterminate species the m^1 and m^2 (which Gervais credits to the Lartet Sansan Collection), figured by Gervais, 1852; and 1859, Zoologie et Paléontologie français (Pl. LXXXI, Fig. 9). Gervais considered this specimen as representing the same species as the Laurillard maxilla, which he figures on the same plate, and which I have taken as the paratype of *Hemicyon sansaniensis*. Gervais (1853) states that Laurillard's discovery at Sansan represents a third species of *Hyænarctos*, and (in 1859) places these Laurillard and Lartet maxilla specimens together under *Hyænarctos hemicyon*. Lydekker (1883, *loc. cit.*, p. 202) notes a slight difference between the two specimens (as figured by Gervais), but states that this may not be more than individual variation. As he considers that there is some doubt whether the specimens are the same as Lartet's *Hemicyon*, he thinks it best to adopt the name *Dinocyon* for the genus to which they belong. Filhol (1891, *loc. cit.*) notes a similarity between the m^1 and that of *D. thenardi*,

that the m^2 differs from the m^2 of *D. thenardi*, but that the two are closer to each other than to *Hyænarctos sivalensis* or *H. insignis*. He considers that *Hemicyon* itself, particularly in the presumably digitigrade feet, shows a resemblance more to *Cephalogale* than to *Dinocyon*.

I very tentatively refer to the above Sansan species the mandible with evident intermasseteric ridge, figured by Filhol (*loc. cit.*, Pl. x) under "*Hemicyon sansaniensis*." Filhol, on discovery of his neotypic specimen of *H. sansaniensis*, called attention to the error of such reference. The dentition of this mandible somewhat resembles that of *H. sansaniensis* and definitely differs from that which Filhol figures under *Pseudocyon sansaniensis*, which, as noted above, represents *Amphicyon*. The characters of the former mandible seem homologous with the characters of the upper molars. The specimen represents a much smaller species than the genotypic species, but, as noted by Filhol, suggests the Jourdan genus.

(?) *D. sansaniensis*, new species

Hyænarctos hemicyon GERVAIS, 1853, Bull. Soc. Géol. Fr., Ser. 2, X, 1852–3, p. 154, Pl. IV, Fig. 2; 1859, Zoologie et Paléontologie français, p. 210, Pl. LXXXI, Fig. 9.

Dinocyon hemicyon GERVAIS, LYDEKKER, 1883, Pal. Indica, Ser. 10, II, p. 202, footnote; 1885, Catalogue of the Fossil Mammalia in the British Museum, Part I, p. 156. SCHLOSSER, 1887, Beiträge Pal. Osterreich-Ungarn., VII, p. 81. FILHOL, 1891, 'Etude sur les Mammifères fossiles de Sansan' (Pl. VIII, Figs. 1–3, p. 149, bottom, p. 127, middle).

TYPE.—m^1 and m^2, right, according to Gervais were found by Lartet (specimens now lost ?). Figured by Gervais, 1852, 1859, Pl. LXXXI, Fig. 9.

REFERRED (very tentatively).—Mandible No. 89, Lartet Coll., Mus. d'Hist. Nat., Paris, from Sansan. Figured in self-admitted error as "*Hemicyon sansaniensis*. Lartet" by Filhol, 1891, Pl. VIII, Figs. 1 and 5 reversed, Fig. 2 not reversed. (Specimens labeled "*Pseudocyon*.")

DISCUSSION OF THE TYPE M^1 AND M^2.—The present whereabouts of the two Gervais-"Lartet" molars, which I take as the type of the species, is unknown; they are not in the collection of the Muséum d'Histoire Naturelle, Paris. As figured by Gervais, the teeth are considerably larger than the teeth of any known species of *Hemicyon*. Further, the m^1 distinctly differs from that of *Hemicyon*.

Compared to the Filhol neotype of *H. sansaniensis*, the two "Lartet" molars (Gervais, *loc. cit.*, Pl. LXXXI, Fig. 9) are considerably larger; the paracone of m^1 is (as drawn) smaller rather than larger than the metacone; m^1 is relatively more produced inwardly, the tooth being broader transversely, the lingual portion more narrowed, and the inner ridge unusually near the inner tooth border; m^1, however, in the position of the protocone, of the metacone, and the nub-like development of the postero-inner cingulum, strongly resembles *Hemicyon*. The teeth are much smaller than those referred to *D. thenardi;* the inner ridge is low, as in the latter form, but is placed more inwardly versus more centrally in *D. thenardi*.

I personally am very doubtful, as above noted, of the correctness of the reference of the specimen to *Dinocyon*, though Schlosser (1887, p. 83) "considers it only a weaker individual of *Dinocyon thenardi*."

DESCRIPTION OF REFERRED MANDIBLE No. 89.—The dorsoventral narrowness of the mandible and the crowded and unworn condition of the premolars may be partly due to the (probable) immaturity of the specimen. Both the m_2 and the m_3 have been broken, and I have doubt as to the correctness of the reconstruction, particularly of the m_3.

The former presence of a premasseteric fossa is indicated by a depression below m_3; the region of the sulcus, unlike in *H. sansaniensis*, is narrowed dorsoventrally.

p_{3-4} are relatively large and quite unworn; the inner cingula are prominent.

p_2 alveolus and p_1 are separated by a distinct diastema (5 mm.+); p_2 is more crowded on p_3 than in either the type or the Filhol neotype mandible of *H. sansaniensis*.

m_1 is high-crowned; the hypoconid is considerably less prominent, the two posterior accessory inner cusps less prominent, and the heel actually narrower than in Filhol's neotype *H. sansaniensis*.

m_2 (broken posteriorly) is, relative to m_1, actually larger and heavier than in *H. sansaniensis*.

m_3 (crown separated from roots and present replacing questionable) is obovate, and short anteroposteriorly, versus *Hemicyon*.

The specimen differs from *Hemicyon* in the extreme heaviness of the m_2 relative to m_1, the character of the m_1, and the peculiar shape of m_3.

Compared to *Amphicyon*, the upper molars are elongate transversely, but not as extremely elongate as is the tendency in *Amphicyon*. The protocone and hypocone are fused into a low ridge, versus the high and prominent crescentic protocone of *Amphicyon*. The metacone is larger than the paracone, the post-inner cingulum cusplet is prominent, and the metacone root is slightly heavier than the paracone root, all versus *Amphicyon*.

FIG. 18

Fig. 18. (?) *Dinocyon aurelianensis*, new species, m_1–m_2, right, from Sables d'Orleans, Mus. Hist. Nat., Paris, No. 228, after rough cast Amer. Mus.

(?) **Dinocyon aurelianensis,** new species

Figure 18

A hitherto undescribed specimen from the Orleans Lower Miocene (or Oligocene) includes an m_2 of most interesting and primitive character in that the same has a distinctly tricuspid trigonid. The m_1 is strongly suggestive of *Hemicyon*, and, so far as the scant but nevertheless im-

portant evidence goes, the specimen might well represent a form lying near the ancestral line of the Hemicyoninæ. Pending further study, I tentatively refer the specimen, which is undoubtedly worthy of generic rank, to the above genus as a new species.

TYPE.—m_1 and m_2, right, with mandibular and canine fragments, from Sables d'Orleans, Mus. d'Hist. Nat., Paris, No. 228. Figured this paper, Fig. 18. The two molars are both moderately worn, have the same peculiar pitted texture, were evidently found together, and are believed to represent the same individual.

CHARACTERS.—m_2 trigonid tricuspid; paraconid unusually developed, and situate directly anterior to metaconid, from which it is separated by a deep valley. Anteroposterior diameter of m_2 relative to m_1 shorter than in *D. thenardi* and more as in *Hemicyon*.

DESCRIPTION.—m_1, elongate, narrowed anteriorly, more resembling *Hemicyon* than *Dinocyon thenardi*, slightly longer, but very similar to m_1 of specimen (No. 89) figured by Filhol (Pl. VIII, Figs. 1, 2, and 5); accessory cusplets posterior to metaconid were very weak, if ever present.

m_2, length relative to m_1 as in *Hemicyon*, less than in *D. thenardi*.

The tooth is of approximately the same length as the m_2 of the Sansan specimen (No. 89), but is narrower and differs further and markedly in the prominent paraconid cusp that lies directly anterior to the metaconid, and which, separated on the inner side by a deep valley from the metaconid, is joined to the protoconid by a worn ridge.

ANTEROPOSTERIOR DIAMETER OF M_2 RELATIVE TO M_1, IN THE ORLEANS SPECIMEN, *Hemicyon*, *Amphicyon*, AND IN *Hyænarctos* AND *D. thenardi*

$\frac{m_2}{m_1}$	*H. barstowensis*, n. sp.	(?) *H. aurelianensis*, n. sp.	*Amphicyon* Barstow	*Hyænarctos*	*D. thenardi* Jourdan
	$\frac{17.8}{29}$ 61%	$\frac{22}{35}$ 63%	$\frac{21}{31}$ 68%	71–74%	$\frac{33}{44}$ 77%

HYÆNARCTOS Falconer and Cautley

Figures 1, 19–41

GENERAL DISCUSSION.—The great extinct species from the sub-Himalaya, on which the genus *Hyænarctos* is now based, was first described by Falconer and Cautley in 1836 as *Ursus sivalensis*, but later[1] placed by them under the present well-known title. Falconer remarks that the teeth are constructed more after the type of the higher Carnivora than any described species of *Ursus*. He mentions in particular the three-lobed carnassial, the anterior lobe being well developed as in the

[1]Owen, Richard, 1840–45, Odontography, p. 150, notes that the term *Hyænarctos sivalensis* has been provisionally assigned by Falconer and Cautley to *U. sivalensis*. Gervais, Zoologie et Paléontologie français, 1859, p. 208, notes that Wagner as early as 1837 (Munch,. Geol. Anz.), established the genus *Agriotherium* for this form. Pictet, F. J.,1844, Traité de Paléontologie, I, p. 153, credits the same to the genus *Amphiarctus*. Lydekker, 1883, Pal. Indica, Ser. 10, II, p. 220, considers that the name *Hyænarctos* has "acquired such a general acceptation that it seems best that it should be retained, although it is a somewhat misleading one."

higher Carnivora, and the tubercle of the inside, instead of lying at the rear as in other species, being advanced forward opposite the middle lobe, and he is particularly struck with the great size of the type skull, the absence of any notable curvature in the profile, and the salient sagittal crest.

Specimens broadly referable to the genus are known from the supposed Pliocene of India, China, Greece, France, Spain, Italy, Great Britain, Mexico, Florida, California, Oregon, and Nebraska; these include some thirty-five different occurrences, sixteen of portions of upper and nineteen of portions of lower dentitions. Of the seventeen named or recognized species, which include six from Asia, six from Europe, and five from America, ten are based on upper and seven on lower teeth. Unfortunately, only in one case, that of the m_2 of *I. oregonensis* Merriam, has a tooth of the lower jaw been found directly associated with teeth of the upper jaw. Variation in size, and in appearance, due to different stage of wear, makes the definite reference of the lower teeth to the species based on upper teeth, and vice versa, impossible. It has, therefore, been deemed best here to consider the upper and lower material in two separate sections (A and B). Under the description of the upper material, however, the previous references of lower material are noted. In one case at least (that of the mandible placed by Falconer and Cautley with the type skull of *H. sivalensis*), this is seen to be in evident error, and the correctness of all references must for the present remain in serious doubt. The previous references are noted again and discussed in order under the section dealing with the lower teeth.

A. Upper Teeth.—The various dental types distinguished by previously referred material of the upper jaw may best be considered under three subgeneric heads, represented respectively by

Hyænarctos sivalensis Falconer and Cautley,
Indarctos (*H.*) *punjabiensis* Lydekker,
Lydekkerion (*H.*) *palæindicus*, new subgenus.

Hemicyon, which is much like the typical section of *Hyænarctos*, differs from *Hyænarctos*, broadly considered, in that:

The premolars are less reduced.

The p^4 parastyle is characteristically absent instead of being prominent (a slight parastyle occurs in p^4 of the Sansan neotype specimen).

The upper molars have more prominent outer cusps, their transevrse are greater than their anteroposterior diameters, and their inner ridges are directed antero-inwardly, instead of antero-outwardly as in

Hyænarctos. In the m^1 of *Hemicyon*, the post-inner cusplet is here interpreted as a cingulum cusplet, and the next inner cusplet as the hypocone (or fused hypocone-metaconule); the protocone is noted to lie well separated from the base of the paracone. In *Hyænarctos*, the post-inner cusplet is interpreted as representing the fused cingulum cusplet and hypocone, the metaconule being considered as absent; the protocone is seen to be (more) adjacent to the base of the paracone.

The dentition of *Hyænarctos*, as that of *Hemicyon*, predicates a combined sectorial crushing action, that of the bear a more grinding action—in *Hyænarctos* and in *Hemicyon* powerful sectorials are present, and the wedge of the inner ridge of the upper molars strikes into the talonid basin of the lower molars, versus in the bears, true carnassials are absent, and the flattened m_2-m_3 grind over the elongated and flattened m^2.

The subgenera of *Hyænarctos*, specifically considered, resemble or differ from *Hemicyon* as follows:

(a) *Hyænarctos sivalensis* Falconer and Cautley (Fig. 21), except as noted above, strongly suggests *Hemicyon*, and may be said to be "*Hemicyon*-like."

(b) *Indarctos* (*H.*) *punjabiensis* Lydekker, (Fig. 23), which may be said to be more "*Ursavus*-like," is further distinguished from *Hemicyon* in that the upper molars are notably elongate and transversely narrowed, the main cusps reduced, and a distinct talon is present in m^2.

(c) *Lydekkerion* (*H.*) *palæindicus*, new subgenus (Fig. 25), which may be as yet but tentatively referred to the genus, differs from *Hemicyon* in that: the p^4 parastyle is unusually developed, the deuterocone is slightly less posterior, the main cusps are low, the lingual angles of the upper molars are more rounded, the post-inner corner of m^2 is cut away, the transverse diameters are more narrowed, and the inner ridges are more prominent, especially anteriorly.

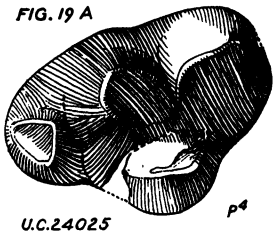
It must be noted, however, that both Messrs. Pilgrim and Lydekker considered *L.* (*H.*) *palæindicus* to be more "*Hemicyon*-like" than the other species of *Hyænarctos*, in the rounded inner corners and shortness of m^1, and the obliqueness of the external cusps of m^2.

(d) The form tentatively referred to *Hyænarctos*[1] from the Snake Creek is even less *Hemicyon*-like, in that the inner angles of m^2 (as presumably the case in m^1) are unusually reduced, and the transverse diameter exceeded by the anteroposterior.

The three hyænarctid subgenera, the subgenotypic species, and the species which I tentatively group with each (including the authority,

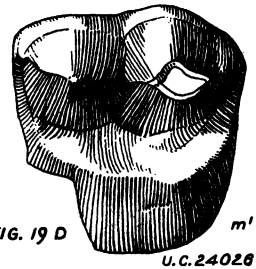
[1]Matthew, W. D., 1924, Bull. Amer. Mus. Nat. Hist., L, p. 65, *Hyænarctos* species, m^2 from Upper Snake Creek.

FIG. 19 A



U.C.24025 P^4

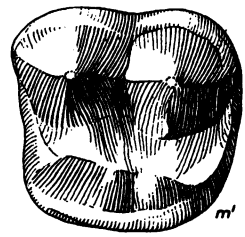
FIG. 19 D



M^1

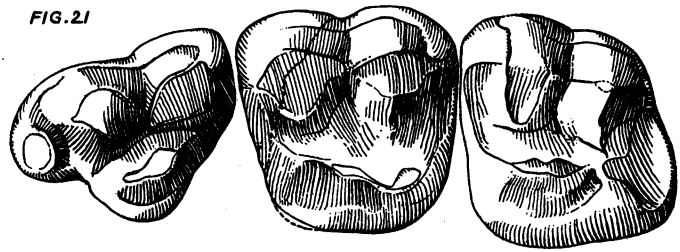
U.C.24026

FIG. 20



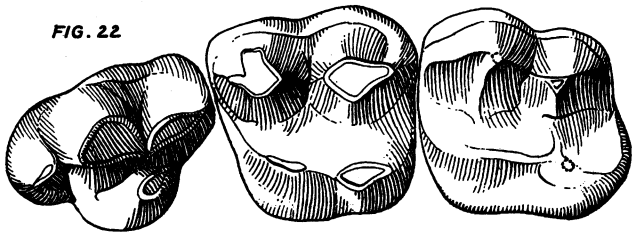
M^1

FIG. 21



19B 19C

FIG. 22



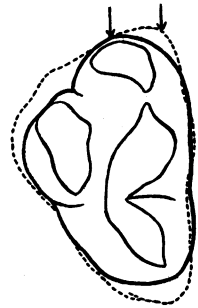
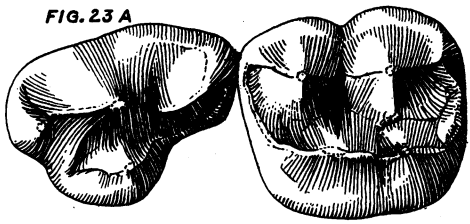
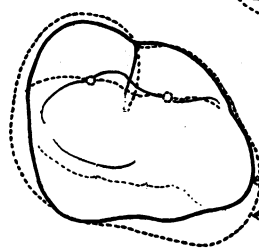


FIG. 23 A





23B

24

FIG. 25

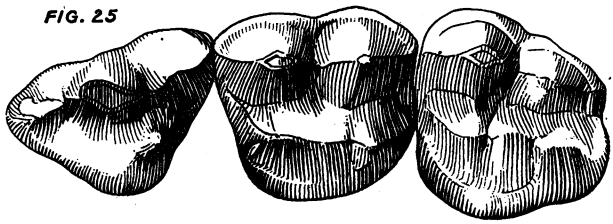
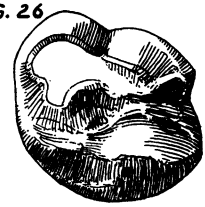


FIG. 26



Hyænarctos, upper dentition, occlusal views. Natural size.

Fig. 19. *Hyænarctos gregori* Frick, from type locality, Eden, Cal.; 19A, p^4, referred, Amer. Mus. No. 18121A; 19B, p^4, (?) referred, Univ. Cal. No. 24027 in outline; 19C, p^4, type, Univ. Cal. No. 24025 in dotted outline; 19D, m^1, referred, Univ. Cal. No. 20026 (reversed).

Fig. 20. *Hyænarctos* species, Flower, m^1, from the Red Crag.

Fig. 21. *Hyænarctos sivalensis* Falconer and Cautley, p^4–m^2 of type specimen from the Siwaliks, after sketch of original and Amer. Mus. cast.

Fig. 22. *Hyænarctos insignis* Gervais, p^4–m^2 of type specimen, from Montpellier, after Gervais and rough cast Amer. Mus.

Fig. 23. *Indarctos* (*Hyænarctos*) *punjabiensis* Lydekker; 23A, p^4–m^1 of type specimen, from the Siwaliks, after Amer. Mus. cast; 23B, m^2, referred by Lydekker, in outline [after Lydekker, 1883, Fig. 6].

Fig. 24. *Indarctos salmontanus* Pilgrim, m^2 of type specimen, from Salt Range, in dotted outline, after Pilgrim.

Fig. 25. *Lydekkerion* (*H.*) *palæindicus* Lydekker, p^4–m^2 of type specimen, after cast Amer. Mus., reversed.

Fig. 26. (*?*) *Hyænarctos* species, Matthew, m^2, from Snake Creek, Amer. Mus. cast.

Fig. 26A. *Hyænarctos "schneideri,"* m^1 referred, from Bone Valley, Florida. Fla. Geol. Surv. Coll. No. 6858.

locality, and date described) are as follows (see subsequent pages for synonymy and description, also for those species based on specimens of the lower dentition):

1. Typical *Hyænarctos* Falconer and Cautley.

CHARACTERS.—

m^2 without definite heel (Red Crag, Alcoi, and Eden m^2s unknown).
p^4, external border indented at mid-post base paracone (Red Crag p^4 unknown).
m^1 broad transversely, inner ridge near inner tooth border (Alcoi m^1 unknown).

H. sivalensis FALCONER AND CAUTLEY, 1836, Genotypic species. Type, broken skull, from the mid-Siwaliks.

H. species, GERVAIS, 1853, Type, p^4, from Alcoi.

H. insignis GERVAIS, 1853, Type, c, p^1, p^4-m^2, from Montpellier.

H. species, FLOWER, 1877, Type, m^1, from the Red Crag.

H. gregori FRICK, 1921, Type, p^4, and referred specimens from Eden (Fig. 27).

H. "*schneideri* SELLARDS," m^1, referred from Florida. Fig. 26A.

2. Subgenus *Indarctos* Pilgrim.

CHARACTERS.—

m^2 with prominent talon variably developed.
p^4 parastyle less developed, post-paracone outer base swollen, deuterocone more inward (p^4 *I. salmontanus* unknown).
m^1 narrowed transversely and elongate anteroposteriorly, outer cusps reduced.

I. salmontanus PILGRIM, 1913, Genotypic species. Type, maxillary fragment with m^2, from the Salt Range.

I. (*H.*) *punjabiensis* LYDEKKER, 1878, Type, p^4-m^2, from the Siwaliks (m^2 referred).

I. oregonensis MERRIAM, 1916, Type, p^4, m^2, m_2, etc., from the Rattlesnake.

3. Subgenus *Lydekkerion*, new subgenus, distinguished by:

CHARACTERS.—

Smaller size, reduced lingual angles of molars.
m^2 unusually constricted postero-inwardly, external cusps much angulated.
m^1 metacone and inner wedge more prominent.
p^4 relatively short anteroposteriorly, parastyle relatively long.

L. (*H.*) *palæindicus* LYDEKKER, 1878, Genotypic species. Type, p^4-m^2, from the Siwaliks.

B. LOWER TEETH.—There exist in addition, as noted above, some 19 interesting specimens of portions of the lower dentition which have been referred to *Hyænarctos*, all of which, excepting that of the broken Oregon m_2, were found unassociated with teeth of the upper jaw. Of

these specimens, seven have been taken as the types of the following additional species:

Hyænarctos (*A.*) *schneideri* SELLARDS, 1916, Figs. 26, 36, right ramus with c-m_2, and alveolus of m_3 from Florida.

H. arctoides DEPÉRET, 1895, portion of mandible with p_4-m_2 from Montredont.

H. atticus DAMES, 1883, m_1-m_3 from Pikermi.

H. maraghanus MECQUENEN, 1925, mandible with c-m_2, from Maragha, Persia.

H. laurillardi MENEGHINI, 1863, Figs. 34, 41, portion of mandible with c-m_3 from Monte Bamboli.

H. species, FREUDENBERG, 1910, Type, m_1 from Mexico.

H. species, LYDEKKER, 1884, Type, m_2 from China.

The remaining twelve specimens, including the three here described for the first time, have been referred to species based on upper teeth. A definite comparison of the different specimens with one another is difficult to impossible, on account of differences in the stage of wear and the lack of any knowledge as to limit of size and other variation within the species. Unlike in *Hemicyon*, in these short-jawed *Hyænarctos* species the p_1

Figs. 27–41. *Hyænarctos*, lower dentition, occlusal views, natural size; lateral views, × ½.

Figs. 27 and 35. *Hyænarctos gregori* Frick, p_4–m_2, referred, from type locality. Amer. Mus. No. 18120; 27A and 35A, (?) *Hyænarctos gregori* Frick, tentatively referred, m_3 fragment from type locality. Amer. Mus. No. 18121.

Figs. 28 and 36. *Hyænarctos schneideri* Sellards, p_4–m_2 and alveolus m_3 of type mandible, from Bone Valley, Florida, after Amer. Mus. cast No. 14448.

Figs. 29 and 38. *Hyænarctos* species, Freudenberg, m_1, from Mexico, after Amer. Mus. casts, reversed.

Fig. 30. *Indarctos oregonensis* Merriam, m_2 (broken) of type specimen, from Rattlesnake, Oregon, after Merriam.

Figs. 31 and 37. p_4–m_2, alveoli of p_2, p_3, and m_3 of specimen referred by Falconer to "*H. sivalensis*," from the Siwaliks, drawn by Miss Woodward from original in Brit. Mus.

Figs. 32A and 39A. p_4–m_1 and double alveolus p_3 of specimen referred by Lydekker to "*L. palæindicus*," from the Siwaliks, after Amer. Mus. cast, reversed.

Figs. 32B and 39B. m_2 of specimen referred by Lydekker to "*H. palæindicus*," from the Siwaliks, after Amer. Mus. cast.

Figs. 33 and 40. m_1-m_3 and alveoli of p_1, p_3, and p_4 of specimen referred by Lydekker to "*I.* (*H.*) *punjabiensis*," from the Siwaliks, after Amer. Mus. cast No. 9900.

Figs. 34 and 41. *Hyænarctos laurillardi* Meneghini, p_3–m_3 of type specimen, from Monte Bamboli, drawn by Miss Woodward, after Brit. Mus. cast.

Figs. 27–34. *Hyænarctos* species, lower teeth, occlusal views. × 1.

FIG. 27 A

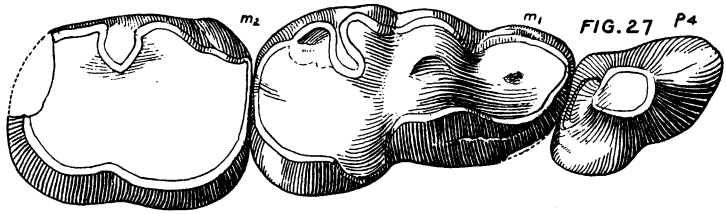


FIG. 27

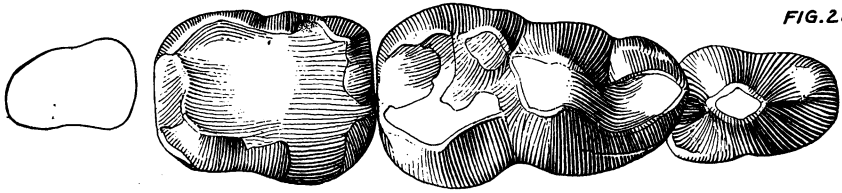


FIG. 28

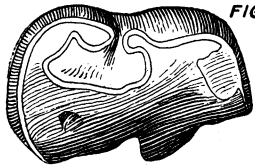


FIG. 30

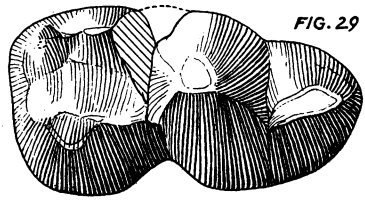


FIG. 29

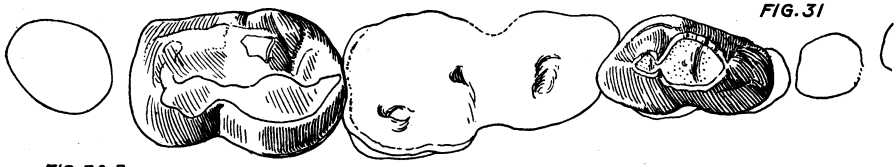


FIG. 31

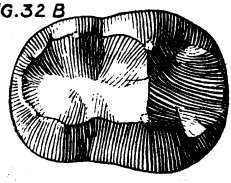


FIG. 32 B

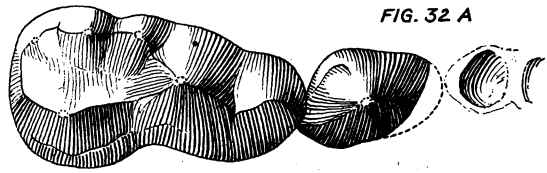


FIG. 32 A

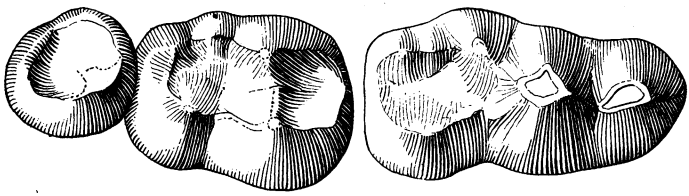


FIG. 33

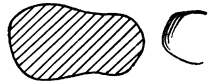
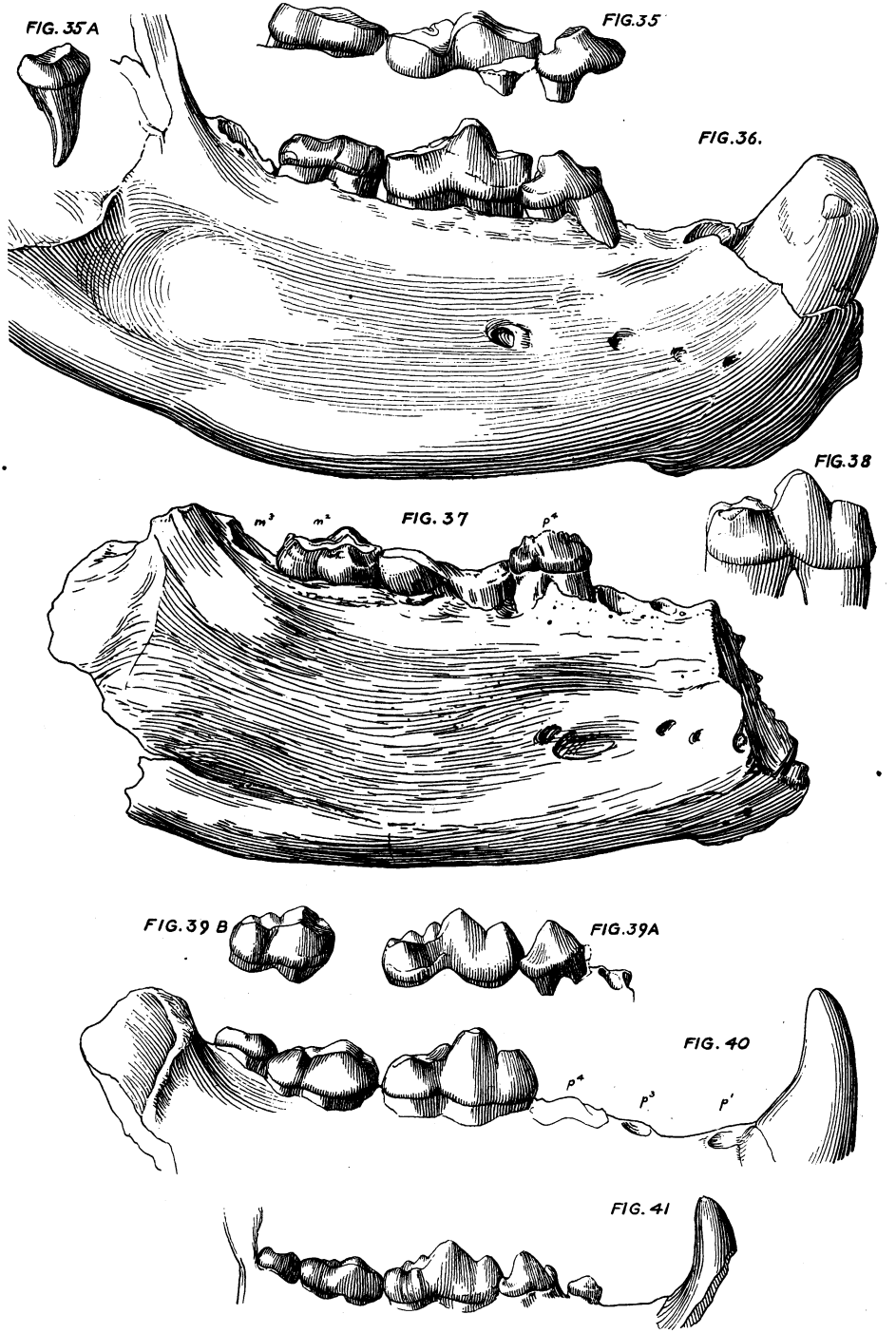


FIG. 34



Figs. 35–41. *Hyænarctos* species, mandibular fragments and teeth, lateral views, showing premasseteric fossa. × ½.

closely adjoins the canine. The p_2 is apparently single-rooted, and with the p_3 tends to be early lost, as is seen in *H. laurillardi*, and in *H. schneideri*. The alveolus of the latter suggests that both teeth may have been present, as in the Maragha specimen, in *H. "sivalensis,"* referred, and as in *H. "punjabiensis,"* referred (a remnant of p_2 alveolus being seen in cast). The Oregon form witnesses the one definite association of a lower tooth (m_2) with teeth of the upper dentition. The m^1 referred to *H. schneideri*, however, may have belonged to the same individual as the type mandible; and the Eden mandibular specimen very probably belongs to the same species as the upper teeth. For hypothetical correlation purposes, as the respective m^1s and the teeth of the lower jaw seem generally similar in the two last species, it may be well to tentatively consider the *H. schneideri* mandible as typical of the lower dentition of the *H. sivalensis* group. (In m_3, an elongated form is typically hemicyonid, a more enlarged form ursid, and a reduced circular form ursavid and to a certain degree helarctid. The indication of a somewhat elongate m_3 in *H. schneideri* and *H. gregori* need not be interpreted as suggesting the development of a talon in m^2, for this is not the case in *Hemicyon*. As opposed to the elongate condition, it will be noted that the crown of the m_3 was apparently round in *H. "sivalensis,"* referred, as in *H. "punjabiensis,"* referred, and in *H. laurillardi*). Should the mandibular specimen associated by Falconer with *H. "sivalensis"* be included in the above section, it must be noted that the m_2 is unusually long-proportioned, and the distance anterior to p_4 relatively longer than in the Florida specimen. But while these lowers may be of one broad general type, marked differences exist between certain specimens, for example: cingula are present on the inner and external borders of the trigonid of the m_1 of the Eden and Florida teeth only; and the Florida m_2 is much shorter-proportioned than the Eden, etc. The p_4-m_1 referred by Lydekker to *L. (H.) palæindicus*, except for slightly smaller size and lower tooth crowns, are also of very similar general form. The mandible referred by Lydekker to *I. (H.) punjabiensis*, and the smaller mandible on which Meneghini based *H. laurillardi*, are notably different from all the above specimens and from each other:

The *"I. (H.) punjabiensis"* specimen is particularly characterized by the greater breadth of the paraconid, lack of the typical swelling of the inner border of talonid, and the tallness of the protoconid of m_1.

The *H. laurillardi* type mandible is characterized by the unusually small size and narrow proportions of the teeth, loss of p_1–p_2, and in the low crown and accessory cusplets of m_1.

The mandibular material (as above noted) is listed and considered in detail under Section B.

The interpretation of the time relations of the fossil data must vary to a certain extent as the views of the observer, and whether *Hemicyon* may yet be considered as an indication of the Miocene and *Hyænarctos* of the Pliocene, as before noted, must still remain in question. The evidence, at any rate, is that the typical section of the genus *Hyænarctos* was very widely distributed; and we may reason that what is known of its distribution is but a bare outline of the actual. New material will be reported from time to time and other forms may even yet be recognized amid that already collected. The species of the typical section of *Hyænarctos* are seen to be much larger and shorter-jawed than *Hemicyon*, but to resemble *Hemicyon* more than do the species of the subgenera. The *Hyænarctos* faunas are correlated with the Lower to Upper Pliocene by American writers, and mid-Miocene to Upper Pliocene by European writers. These place the respective faunas of Monte Bamboli, Pikermi, Upper Siwaliks, and Red Crag,[1] as mid-Miocene, Upper Miocene, Lower Pliocene, and Upper Pliocene.[2] The mandibles here very tentatively referred to the typical section include forms with variable degree of development of m_3, some of which may possibly on knowledge of m^2 be found to approach or actually lie near to the *Indarctos* section. The remains grouped under the typical section are generally referable to the late lower half of the Pliocene. The *Indarctos* section is represented by two forms from the mid-Siwaliks (as distinguished by Pilgrim (1913), from the Upper Siwalik horizon containing *H. sivalensis*), and that from the Oregon Rattlesnake, which have been broadly considered as all of Pikermi age. Two of the three remaining *Hyænarctos* forms, *Lydekkerion palæindicus* and the Upper Snake Creek species, have been similarly correlated with the Upper Miocene of the European scale and Lower Pliocene of the American. On the other hand, the associated fauna of the unique species, *Hyænarctos laurillardi* of Monte Bamboli (Gervais has also referred the Alcoi horizon to this age) interestingly enough is reported to represent the Middle Miocene.

Section A. Specimens of the Superior Series

Of the sixteen occurrences of material representative of the upper series, some ten have been taken as the types of as many species (starred

[1] *Loc. cit.*, footnote, Introduction.

[2] Dr. Matthew's recent study of the Bone Valley faunas leads him to place the same as approximately equivalent to the Blanco (communicated). The writer tentatively interprets (as noted elsewhere) *Borophagus* as a possible hyænarctid species.

below); the remaining material has been variously referred. The occurrences (see the sequel for details), with the name of the first describer, and date described, may be listed as follows:

*Portion of skull with etc. teeth from the typical Siwaliks, type of *Hyænarctos sivalensis* Falconer and Cautley, 1836.

*Fragment of a maxilla and etc. teeth from Montpellier, France, type of *Hyænarctos insignis* Gervais, 1853.

*Maxillary fragment with p^4, etc., from Alcoi, Spain, described as *Hyænarctos* species Gervais, 1853.

*m^1, right, broken, from the Red Crag of Felixstow, described as *Hyænarctos* species, Flower, 1857.

m^1 left, unworn, referred by Flower to the above.

*p^4 left, worn, from Eden Pliocene, type of *Hyænarctos gregori* Frick, 1921.

p^4 left, small, worn, referred to the above in type description.

m^1 left, referred to above in type description.

p^4 left, unworn, here first described and referred to the above.

m^1 right, from Bone Valley, Florida, referred to *H. schneideri* this paper.

*left maxillary fragment with m^2, etc., from near Asnot, Siwaliks, type *Indarctos salmontanus* Pilgrim, 1913.

*p^4–m^1 of both jaws from Hasnot, Siwaliks, type *Indarctos* (*H*). *punjabiensis* Lydekker, 1878.

p^4-m^2, etc., from type locality, and referred to the above by Lydekker.

*Portion of dentition, including etc. skeletal elements from the Rattlesnake of Oregon, type *Indarctos oregonensis* Merriam, 1916.

*Right maxilla with p^4–m^2 from Punjab Siwaliks, India, type *Lydekkerion* (*H.*) *palæindicus* Lydekker, 1878.

*m^2 right, from Lower Snake Creek, described as *Hyænarctos* species, Matthew, 1918.

Subgenus **HYÆNARCTOS**

Hyænarctos sivalensis Falconer and Cautley, 1836

(Genotypic Species)

Figure 21

Ursus sivalensis FALCONER AND CAUTLEY, 1836, Asiatic Researches, XIX, pt. 1, p. 193.

"Sivalours" BLAINVILLE, 1839, Ostéographie, p. 96.

Amphiarctus sivalensis BLAINVILLE, 1839, Ostéographie, pp. 96–102.

Ursus sivalensis BLAINVILLE, 1841, Compte rendu heb. Acad. Sci. (Paris), XIII, pp. 68 and 165.

Hyænarctos sivalensis FALCONER AND CAUTLEY, OWEN, 1840–45, Odontography, p. 505, Pl. CXXXI.

U. (*Hyænarctos*) *sivalensis* FALCONER, 1848, 'Fauna Antiqua Sivalensis,' p. 9, (unpub.) Pl. o.

Hyænarctos sivalensis FALCONER AND CAUTLEY, GERVAIS, 1853, Bull. Soc. Géol. Fr., Ser. 10, p. 147, Pl. IV; 1859, Zoologie et Paléontologie français, Pl. LXXXV, Fig. 1 (figured as of right side and unworn). FALCONER-MURCHISON, 1868, Palæontological

Memoirs, p. 321, Pl. XXVI, Figs. 1 and 2, reprint of unpublished plate. LYDEKKER, 1877, Rec. Geol. Surv. India, X, p. 33; 1878, XI, p. 103; 1883, Pal. Indica, Ser. 10, II, Pl. XXX, Fig. 5 (reversed). WOODWARD, 1898, Vert. Pal., p. 394, Fig. 221. TROUESSART, 1899, Cat. Mam., p. 247, and 1905, p. 178.

TYPE.—Portion of skull with canines, p^2 and p^3 alveoli, and p^4–m^2, Brit. Mus. No. 39721, from the typical Siwaliks. Figured unpub. Pl. o, 'Fauna Antiqua Sivalensis,' with referred limb elements, executed about 1848; in part by Owen, 1840; Gervais, 1859 (figured as of right side and unworn): Falconer and Murchison, 1868; Lydekker, 1883; and this paper, Fig. 21.

Falconer and Cautley (1836) remark that the teeth are constructed more after the type of the higher Carnivora than any described species of bear, and consider that the large size of the outer lobes and presence of an inner ridge indicate a transition from the bears to the dogs. They state that the most striking feature of the skull is the almost rectilinear line of the cranium, as seen in profile, from the anterior nasals to between the interorbitary process and the but slight degree of convexity from there backwards. They further note the abruptness and prominence of the sagittal crest, the broad frontal region (the breadth somewhat reduced by fracture), the considerable obliquity of the orbits, the great depth and extent of the temporal fossæ, the breadth and obtuseness of the muzzle (in length approximating one-fourth the length of the skull, and being a little wider than the interorbitary portions of the frontals), the strong arching both longitudinally and transversely of the palate, non-extension of the palate beyond the rear molars, and apparent subdivision of the infraorbital foramen. The describers find that the specimen in many respects deviates from the type of the genus *Ursus* and approximates that of the more perfect Carnivora.

DENTITION.—Three alveoli between the canine and p^4 are interpreted as representing the single alveolus of p^2 and double alveolus of p^3. Left p^4–m^2 perfect, teeth of right side damaged (posterior and lower portions of occipit, both zygomatic arches, and anterior portion of nasals missing).

p^4, moderately worn, cusps relatively low, paracone-metacone shear massive, external border indented anterior to paracone-metacone division, and swollen over the antero-external base of the paracone. (The anterior base of the deuterocone and the antero-inner base of the parastyle are more convex than in Lydekker's figure.) The external cingulum is slight, and a slight cingulum is present about the base of the deuterocone, which lies at the base of the paracone.

m^1 is cracked through the antero-external corner. The metacone is lower than the paracone, but was evidently slightly heavier than the paracone, as in the case of the Red Crag tooth. (The inner ridge is more angulated in respect to the inner border and line of the external cusps, and the antero-inner corner is more prominent and longer-sloping than evident in Lydekker's figure.) The antero-innermost corner is broken in both molars, but is believed to have been prominent and similar to the condition in the Red Crag tooth. The tooth is longer anteroposteriorly than the m^2.

m^2, the crown of the paracone is broken, the postero-inner area is considerably worn, the paracone and metacone are strongly angulated, the inner ridge approximately parallels the line of the outer cones (the inner ridge is more angulated relative to the inner tooth border in m^1-m^2 than previously figured). The inner margin is broader anteroposteriorly than the outer margin, versus the reverse in m^1, as usual in *Hyænarctos*, *Hemicyon*, and likewise in *Amphicyon*. The condition of the postero-inner tooth corner suggests a tendency to the development of a very rudimentary heel.

LOWER TEETH.—The portion of a mandible with worn and broken teeth, which Falconer and Cautley state was acquired a season previous to the above skull (figured beside the specimen by Falconer and Cautley and reproduced by Owen and Murchison), is very evidently, because of its moderate size and narrow teeth proportions, not directly referable to the individual described above, if even to the same species.

Hyænarctos insignis Gervais, 1853

Figure 22

Hyænarctos insignis GERVAIS, 1853, Bull. Soc. Geol. Fr., Ser. 2, X, p. 152, Pl. IV, Fig. 1; 1853, Compte rendu heb. Acad. Sci. (Paris), XXXVII, p. 354 (not 253); 1853, Annales Sci. Nat., Ser. 3, XX, pp. 233 and 234, Pl. XII; 1859, Zoologie et Paléontologie français, p. 209, Pl. LXXXI, Figs. 2–3 (3 and 4 reversed); 1865–7, Mem. Acad. Sci. Montpellier, III, p. 142 (idem, Bull. Geol. Fr.). LYDEKKER, 1883, Pal. Indica, Ser. 10, II, pp. 220 and 232. SCHLOSSER, 1887, Palæontographica, VII, p. 86. STEHLIN, 1907, Bull. Soc. Géol. Fr., Ser. 4, VII, p. 220, Fig. 1.

TYPE.—Certain upper teeth and fragments of the maxilla, incisive border, glenoid, etc., of one individual from the Montpellier Pliocene, France.

Portion left maxilla with p^4-m^2 figured by Gervais, 1853, Annales Sci. Nat., Pl. XII (rev.); 1859, Zoologie et Paléontologie français, Pl. LXXXI, Figs. 3 and 4 (rev.); this paper, Fig. 22.

Right upper canine and p^1-m^2 figured by Gervais, 1853, Pl. XII; 1859, Pl. LXXXI, Fig. 7 (p^1 only).

Right p^4 figured by Gervais, 1853, Pl. XII; 1859, Pl. LXXXI, Fig. 5 (rev.).

Incisors figured by Gervais, 1853, Pl. XII, Fig. 1; 1859, Pl. LXXXI, Fig. 6.

The teeth are somewhat worn. They greatly resemble the slightly more worn teeth of the type of *H. sivalensis*. The Montpellier teeth differ from the latter mainly in their slightly smaller size (see table), the general greater lightness of the cusps and cingula, the disproportionate shortness of p^4 due to the small size of the parastyle, and the peculiar prominence of the external base of p^4 anterior to the protocone-metacone division (indented in *H. sivalensis*). [The anterior lip of the glenoid fossa, as seen in the supposedly associated fragment, is flat, suggesting an unlocked rather than locked articulation.]

LOWER DENTITION.—Stehlin (1907, *loc. cit.*) calls attention to certain lower teeth of typical hyænarctid form from Boutonnet, Montpellier, in the Deluc Collection, Geneva Museum, described by Cuvier in 1822 as representing a species of (?) *Lophiodon*, and suggests that they may represent *Hyænarctos insignis*. See under Lower Teeth, Section B.

Hyænarctos species, Gervais, 1853, from Alcoi

Hyænarctos species GERVAIS, 1853, Bull. Soc. Géol. Fr., Ser. 2, X, p. 152, Pl. IV, Fig. 3. Annales Sci. Nat., Ser. 3, XX, p. 233 (no figure; mention of *H. insignis*); 1859, Zoologie et Paléontologie français, p. 210, Pl. LXXXI, Fig. 2. LYDEKKER, 1883, Pal. Indica, Ser. 10, II, pp. 220 and 232. SCHLOSSER, 1887, Palæontographica, VIII, p. 87.

TYPE.—Maxillary fragment with p^4, portion of anterior base of m^1, and suggestion of the alveoli of p^3 and p^2, from Alcoi, Spain. Figured by Gervais, 1853, Pl. IV, Fig. 3; 1859, Pl. LXXXI, Fig. 2.

The tooth is unworn, and, according to Gervais' figure, seems to more resemble *H. sivalensis* than *H. insignis*. Gervais considered it doubtfully distinct from either.

Hyænarctos species, Flower, 1877, from Red Crag

Figure 20

Hyænarctos sivalensis FLOWER, W. H., 1877, Quart. Journ. Geol. Soc. London, XXXIII, p. 534, Figs. A and B. LYDEKKER, 1878, Rec. Geol. Surv. India, XI, p. 104.

Hyænarctos species, LYDEKKER, 1883, Pal. Indica, Ser. 10, II, p. 227, Figs. 5A and B (reversed); 1885, Catalogue of the Fossil Mammalia in the British Museum, Part I, p. 155, Fig. 22 (reversed). SCHLOSSER, 1887, Palæontographica, VII, p. 87. NEWTON, E. T., 1891, 'The Vertebrata of the Pliocene Deposits of Britian,' (Pal.) Mem. Geol. Surv. United Kingdom, p. 14, Pl. I, Fig. 20.

TYPE.—m^1, right (broken), from the Red Crag of Felixstow (near Waldringfield), Ipswich Mus. Figured by Flower and Lydekker.

REFERRED.—m^1, left, unworn, and canine tooth, from type locality, Reed Coll., York Mus. Figured by Newton, 1890, Pl. I, Figs. 20A and B; this paper, Fig. 20, after casts in Brit. Mus. and Amer. Mus.

The anterior edge of the left m^1 is indented deeper (for the reception of the protoconid of m_1), the lingual border is broader-proportioned, and the inner ridge lies slightly more inwardly and is possibly slightly more prominent than in the *H. sivalensis* tooth. The outer cusps are stronger, the tooth is broader-proportioned transversely, and the antero-inner corner more prominent than in the m^1 of *I. punjabiensis*. The referred tooth apparently agrees with the type (broken).

Flower noted that the cusps of the inner ridge were not as prominent as in *H. insignis*, and provisionally referred his specimen to *H. sivalensis*. Lydekker considered the specimen to be near *H. sivalensis* but to represent a distinct species.

LOWER DENTITION.—The specimen superimposes moderately well on the m_1-m_2 of the mandible referred by Lydekker to *I.* (*H.*) *punjabiensis*, but not on that referred to *L. palæindicus*. An m_2, right, from the type locality, Reed Coll., York Mus., has been referred to this form by Newton, 1891. Recent authority, as noted above, contends

that the terrestrial remains of the Red Crag were derived from the earlier Coralline Crag deposits and that the Red Crag itself represents the Pleistocene. See under Lower Teeth, Section B.

Hyænarctos gregori Frick, 1921

Figures 19A-D, 27, 27A, 35, 35A

Hyænarctos gregori FRICK, 1921, Univ. Cal. Pub. Dept. Geol., XII, p. 342.

TYPE.—p^4, left, worn, from Eden Pliocene, Univ. Cal. No. 24025. Figured 1921, p. 343, Fig. 49; this paper in outline, Fig. 19B.

Type and referred specimens collected at Eden, Cal., by Mr. Joseph Rak.

REFERRED.—p^4, left, unworn, Amer. Mus. No. 18121A. Figured this paper, Fig. 19A.

p^4, left, (?) small, worn, Univ. Cal., No. 24027. Figured, 1921, p. 343, Fig. 50; this paper, Fig. 19C.

m^1, left, Univ. Cal., No. 24026. Figured, 1921, p. 343, Fig. 51; this paper, Fig. 19D (reversed).

Portion of mandible, etc., teeth. Figured this paper, Figs. 27, 27A, 35, and 35A (see Section B).

CHARACTERS.—

p^4 type, large size; the direct anterior position of the parastyle in relation to the protocone, large size of the parastyle, anterior extension of the deuterocone, and massive metacone.

m^1 referred, large size, the considerable transverse breadth relative to the antero-posterior length, the mid-position of the inner ridge in relation to the line of the main cusps and the inner tooth margin, the broad lingual expanse of the strong inner ridge, the lack of a marked cingulum.

REFERRED LOWER DENTITION.—The relative transverse shortness and heaviness of m_2 as compared to m_1, and the more hemicyonid character of the very tentatively referred m_3 fragment, are discussed in detail under lower dentition section.

DISCUSSION.—The type p^4 is greatly worn. The sectorial character of the unworn p^4 of similar size, the powerful wedge-like blade of the metacone, the relative moderate size of the parastyle surface in relation to that of the paracone, the anteromedian position of the deuterocone, the tendency for the inner cingulum to connect the deuterocone with the anterior and posterior extremity, and the lightness of the external cingulum, are all shown by Amer. Mus. No. 18121A (Fig. 19A).

The small p^4 (Fig. 19B), figured in solid outline with the dotted outline of the type tooth (Fig. 19C), exhibits approximately the same stage of wear as the type tooth, to which it appears to conform in all but size. The specimen possibly represents a separate species, exceeding in antero-posterior diameter the referred unworn p^4 (Fig. 19A) by 13 per cent., but is here interpreted to represent no more than individual or sexual variation within the species. The remaining specimens of both the upper and lower jaw dentition are larger than any known Asiatic or European

specimens, excepting the equally large Persian mandibular specimen, and are apparently only slightly exceeded in size by the form represented by the Mexican m_1.

The m^1 referred (Fig. 19D) is very slightly worn; the tip of the metacone and the antero-inner corner are somewhat broken. The metacone is slightly heavier, but was evidently lower than the paracone; the inner ridge and its lingual expanse are unusually prominent.

For the discussions of the tentatively referred lower teeth of large proportionate size, see Section B.

Hyænarctos "schneideri" Sellards, ref. (see Section B for type)

Figure 26A

REFERRED SPECIMEN.—m^1 left, worn, from Brewster, Polk County, Florida. Coll. Florida Geol. Surv. No. 6858 (cast Amer. Mus.). Figured this paper, Fig. 26A.

DESCRIPTION.—The specimen is much worn, it is provided with three powerful roots, and has a crown of typical hyænarctid character. It much resembles the m^1 referred to *H. gregori*, which superimposes moderately well upon the teeth of the type mandible of *H. schneideri*, and, being slightly less extended on the lingual border, is believed might itself exactly superimpose on the latter. (Anteroposterior diameter 29.8 mm., greatest transverse diameter 30.2 mm.)

DISCUSSION.—The writer was apprised of the existence of this specimen by Doctor Matthew, who had identified the same as representing *Hyænarctos* during the course of a recent examination of the collections of the Florida Geological Survey.[1] The specimen was secured in 1916 by the (Amalgamate Phosphate Company) American Cyanide Company during the progress of the excavation that yielded the type mandible of *H. schneideri* Sellards. I am able to reproduce the tooth in the present paper through the kindly co-operation of Doctor Gunter of the Florida Survey. It is of the same proportionate size and state of wear and of the same coloration and texture as the m_{1-2} of the type specimen, and it may very possibly represent the same individual. The tooth is of the form of m^1 of the typical section of the genus, being very slightly narrower but much resembling the Eden tooth referred to *H. gregori*.

Subgenus INDARCTOS

Indarctos salmontanus Pilgrim, 1913

Figure 24

Indarctos salmontanus PILGRIM, 1913, Rec. Geol. Surv. India, XLIII, pp. 281 and 290; 1914, XLIV, p. 225, Pl. XX, Figs. 1–3. MERRIAM, 1916, Univ. Cal. Pub. Dept. Geol., X, p. 94, Fig. 12.

[1]See Matthew, W. D., forthcoming article in the Amer. Mus. Bull., 'Observations upon Fossil Mammalian Faunas of Florida.'

TYPE.—Left maxillary fragment with m^2, broken base of m^1, and indication of alveolus of posterior root of p^4, from near Hasnot, north of Salt Range and west of Tilla Ridge, according to Pilgrim, "probably Dhok Pathan zone, possibly, but less likely, Tatrot beds," India Mus. Coll., cast in Brit. Mus. Figured by Pilgrim, 1914, Pl. xx, Figs. 1–3. Outline drawing this paper, of m^2 (Fig. 24).

CHARACTERS.—Evidence of p^4 and m^1 being of hyænarctid type. m^2 talon unusually developed. Tooth, except for size, suggesting the much smaller m^2 of *Ursavus primævus*.

Pilgrim infers that the protocone of p^4 rested on a separate root and lay farther forward than in *Helarctos*. He notes that the occlusal surface of m^2 is quite smooth (this probably is an age character), and that the talon is much depressed. The antero-inferior corner of the zygomatic arch lies opposite the indentation between the paracone and metacone of m^2, versus opposite the posterior edge of m^2 in *H. sivalensis*. Lydekker notes (1883, p. 228) that m^2 extends back of the root of the zygomatic arch in the same way as in *I. (H.) punjabiensis*. Pilgrim (1914) withdraws his suggestion of 1913 that *Helarctos* might represent a degenerate descendent of *Indarctos* and suggests that it is not beyond the bounds of possibility that *Indarctos* may have come from *Ursavus*.

VARIABLY REFERRED LOWER DENTITION.—The above m^2 (of the British Museum cast) is noted to superimpose remarkably well over the talonid of m_2 and anterior edge of m_3 of the mandible referred to *I. (H.) punjabiensis* (though the m^1 might seem to lie too far outward for this reference, the position might well be accounted for by individual variation or crushing). Pilgrim notes that the mandible referred by Lydekker to *I. (H.) punjabiensis* is not of the same individual as the type specimen, and may have belonged to the species *I. salmontanus*. He withdraws his tentative (1913) suggestion that the mandible referred by Lydekker to *H. palæindicus* might possibly belong to *Indarctos*, in view of the relative lightness of the specimen and other doglike characters pointed out by Lydekker. He considers both *H. sivalensis* and *H. insignis* to have belonged to a higher geological level than *I. salmontanus* and *I. punjabiensis*, which he believes to have come from one level and to be descended from a smaller and yet unknown hyænarctid ancestor. He wonders whether the m^2 of either *H. laurillardi* or *H. atticus* had an embryonic talon. He suggests the possible connection of *Indarctos*, *H. arctoides*, and *Ursavus depereti*. (See under Section B).

Indarctos (H.) punjabiensis Lydekker, 1878

Figures 23A and 23B

Hyænarctos punjabiensis LYDEKKER, 1878, Rec. Geol. Surv. India, X, p. 103; 1883, Pal. Indica, Ser. 10, II, p. 226, Pl. xxx, Fig. 2; 1885, Catalogue of the Fossil Mammalia in the British Museum, Part I, p. 153, Fig. 21. PILGRIM, 1914, Rec. Geol. Surv. India, XLIV, pp. 227, 231. MERRIAM, 1916, Univ. Cal. Pub. Dept. Geol., X, p. 107.

TYPE.—p^4-m^1 of both sides, and a probably associated upper premolar, from the Punjab, Hasnot, Siwaliks, Theobald Coll., 1877, India Mus. (assembled on plaster). Figured by Lydekker, 1883, Pl. xxx, Fig. 2. This paper, Fig. 23A.

REFERRED.—p^4-m^2 (p^4-m^1 much broken) from the Siwaliks, Punjab, Theobald Coll. India Mus. m^2 figured by Lydekker, 1883, p. 228, Fig. 6; 1885, Fig. 21. This paper, Fig. 23B (outline).

DESCRIPTION OF TYPE.—The teeth are unworn, low-crowned, and relatively narrow transversely.

p^2 (?), small with two fangs (versus probable single root in *H. sivalensis*).

p^4 parastyle slight, paracone-metacone moderately developed, external tooth border rounded and but slightly indented, outer and inner cingula weak, deuterocone bold and placed at base of paracone.

m^1 tending to be relatively elongate anteroposteriorly and narrow transversely, main cusps unusually weak, external cingulum light, antero-outwardly directed inner ridge strong and lying midway between outer cones and inner tooth border (nearer the main cones than in *H. sivalensis*), the hypocone area being nearer the metacone than in *H. sivalensis* and more elongated than that of the protocone. The anterior tooth edge is slightly indented for necessary accommodation for the protoconid of m_1; the posterior edge is convex and the inner mid-border rounded and prominent.

REFERRED MATERIAL.—m^2 referred specimen, a well-developed talon is present, but the same is considerably less prominently developed than in *I. salmontanus*, as is shown by the superimposed outline drawing of the two teeth, Figs. 23B and 24.

Lydekker notes that the anterior border of the orbit of the referred specimen is nearly as far forward as the middle of m^1 (this is the condition in *Hemicyon*); that m^2 extends behind the anterior root of the zygoma, versus lying entirely in advance of same as in *H. sivalensis*, and that the zygomatic root is lighter than in *H. sivalensis*, thus suggesting a less ponderous skull. Lydekker (1878), in first describing the specimen, considered it represented a second maxilla of *H. sivalensis*, and at the same time noted the close agreement of the m^1 of the specimen with the Red Crag tooth. Pilgrim held it highly reasonable that *I. salmontanus* and *I. punjabiensis* should represent slightly different lines of development from a small and highly specialized ("arctoid") ancestor, such as is suggested by *H. laurillardi* or *H. atticus*, either of which might have possessed an m^2 with similar embryonic talon. He believed that both *I. salmontanus* and *I. punjabiensis* were from a lower level than *H. sivalensis*, that *H. sivalensis* was descended from a species which in the talon of m^2 was more primitive, but more "degraded" in the p^2 (if this was single-rooted as in the allied *H. insignis*).

LOWER DENTITION.—Lydekker has referred two specimens of the lower dentition to the type. See under Lower Teeth, Section B.

Indarctos oregonensis Merriam, 1916

Indarctos (?) *oregonensis* MERRIAM, 1916, Univ. Cal. Pub. Dept. Geol., X, p. 87; 1921, Proc. Nat. Acad. Sci., VII, p. 184.

TYPE.—Portion of dentition and etc. skeletal elements, collected by Messrs. Stock and Moody in the Rattlesnake, Oregon, Univ. Cal. No. 22362, including:

2 upper incisors and 2 lower canines. Figured by Merriam, Pl. XVI, Fig. 2.

p^1. Figured by Merriam, Pl. XVI, Fig. 3.

2 p^4s. Figured by Merriam, Pl. XVI, Fig. 4.

2 m^2s. Figured by Merriam, Pl. XVI, Figs. 8 and 9.

m_2 (broken). Figured by Merriam, Pl. XVI, Fig. 13. Refigured this paper, Fig. 30.

The teeth are greatly worn.

CHARACTERS.—

p^4 typically hyænarctid.

m^2 with well developed talon as in *Indarctos* Pilgrim.

The describer notes that the upper canines are large, the roots of the lower canines relatively larger than the corresponding element in the California arctothere;

p^1 a single-rooted cusp;

p^4 parastyle large, protocone larger than the metacone, deuterocone very large and supported on a widely divergent root, an indentation of the outer cingulum occurring opposite the posterior side of the protocone;

m^2, allowing for individual variation, the resemblance to *I. salmontanus* is close; small differences, such as the smaller hypocone, slightly longer heel, and wider trigon region, "suggest specific distinction such as would be expected in individuals so widely separated geographically. . . distinguished from that of *Arctotherium* by its greater width and much shorter talon" and in that the cusps are less strongly compressed laterally;

m_2 very greatly worn and external border broken; tooth exhibits the usual division between the trigonid and talonid, and seemingly the usual hyænarctid proportions (again noted under Lower Teeth, Section B).

LIMBS.—"The characters of the massive limb elements of the Oregon specimen, so far as they are known, suggest the limb type of *Hyænarctos*, and indicate a rather wide separation from *Arctotherium*.

"The sum of the known characters of the Oregon bear represent a type near *Hyænarctos*, but tending toward *Arctotherium* in the development of its last upper molar. The Oregon form cannot be sharply separated from the Siwalik type of *Indarctos* on the basis of available material. Differences in proportions of the tubercles of m^2 suggest the specific divergence which is to be expected in forms found in regions so widely separated geographically as India and Oregon. . .

"The occurrence in the Oregon Pliocene of a form closely allied to an Indian Siwalik type suggests close faunal relationship of Asia and North America in early Pliocene times. The presence of a form of the *Hyænarctos* type with characters tending toward those of *Arctotherium* in the North American Pliocene also gives support to the assumption that the American *Arctotherium* is derived from a line passing near that of *Hyænarctos*. It is now possible to consider the origin of *Arctotherium* in America rather than in Eurasia. As no bears of the *Ursus* type are known from the Pliocene of America, we may conceive of *Arctotherium* as originating in North America in the Pliocene and entering South America before *Ursus* was present in the New World. This would account for the large Pleistocene development of *Arctotherium* in South America in absence of *Ursus*, though the two groups appear together in the North American Pleistocene."[1]

[1]Merriam, J. C., 1916, Univ. Cal. Pub. Dept. Geol., X, pp. 106 and 107.

HORIZON.—Pliocene of Rattlesnake, approximately the age of Thousand Creek, Eden, Upper Snake Creek, and the Hipparion faunas of the Siwaliks and Pikermi.[1]

LYDEKKERION, new subgenus

Lydekkerion (H.) palæindicus Lydekker, 1878

Figure 25

Hyænarctos palæindicus LYDEKKER, 1878, Rec. Geol. Surv. India, XI, pt. 1, p. 103; 1883, Pal. Indica, Ser 10, II, p. 232, Pl. XXX, Fig. 1. PILGRIM, 1914, Rec. Geol. Surv. India, XIV, pp. 225–233.

TYPE.—Right maxilla with p^4–m^2, from the Siwaliks, Punjab, Theobald Coll., India Mus. Figured by Lydekker, 1883, Pl. XXX, Fig. 1. This paper (Amer. Mus. cast), Fig. 25.

CHARACTERS.—Relatively small size of upper molars, unusual rounding of inner posterior corners, and prominence of antero-inner faces. The teeth according to Lydekker are but very slightly abraded by wear.

DESCRIPTION.—p^4, parastyle and deuterocone largely developed, deuterocone tending to be posteromedian and having a relatively prominent cusp. (Absence of palatal depression between p^4 and m^1 indicates protocone of m^1 was low.)

m^1, relatively short anteroposteriorly, paracone higher than metacone, external cingulum especially strong on base of metacone; inner ridge formed of protocone and hypocone and directed antero-externally; antero-inner corner with long antero-inward sloping surface, which would abut against the metaconid and posterior accessory cusplet of m_1 (suggesting that the metaconid was probably relatively large and posteriorly placed). The protocone ridge is wedge-shaped and strong.

m^2, large relative to m^1, main cusps strongly diagonal, tooth much narrowed posteriorly and without talon. Anterior inner corner depressed (suggesting an unusual development of the metaconid of m_2). Postero-inner corner narrowed (a slight projection suggesting an incipient heel), outer cusps strongly diagonal.

Lydekker notes that the m^2 is farther from the bear than in either *I.* (*H.*) *punjabiensis* or *H. sivalensis*, both in entire lack of a talon and the dog- or "*Dinocyon*-like" obliqueness of the external lobes. He states that the maxilla indicates that the profile was angulated at the orbit as in *Ursus spelæus*, versus the straightness of the profile occurring in *H. sivalensis* and *H. punjabiensis*. He notes (p. 232) that in *Hemicyon* (Gervais, Pl. LXXXI) the inner root of the carnassial was placed as in *Hyænarctos*. He believes that it is but a step further to *Cephalogale*, where the deuterocone is confluent with the blade, large, and opposite to the first lobe, and but another step further to the dog, where the deuterocone is small and at the antero-inner angle of the crown. Lydekker (1878) considers that m^1 is somewhat like that tooth in *Hemicyon* of Sansan, both approaching the dogs and *Amphicyon*. He notes, however,

[1]Merriam, J. C., 1919, Univ. Cal. Pub. Dept. Geol., XI, p. 454. Frick, C., 1921, Univ. Cal. Pub. Dept. Geol., XII, No. 5, p. 287.

that the tooth lacks the inner cingulum present in *Hemicyon*, and that the p^4 and m^2 are like *H. sivalensis*, but that the crown of m^1 is triangular and the inner ridge higher and shorter than in *H. sivalensis*. In the writer's opinion a better understanding of the characters of *Hemicyon* shows no very close resemblance between *Hemicyon* and *L. palæindicus*. On account of the above noted peculiarities, I have felt it advisable to refer the latter to a new subgenus, *Lydekkerion*.

LOWER DENTITION.—Lydekker refers to the type a left mandibular fragment with p_3–m_1, a right mandibular fragment with m_2, and tentatively refers a canine tooth. See under lower tooth section, B (p. 82).

(?) **Hyænarctos** species, Matthew, from Upper Snake Creek

Figure 26

Indarctos species, MATTHEW, W. D., 1918, Bull. Amer. Mus. Nat. Hist., XXXVIII, p. 185.

Hyænarctos species, MATTHEW, W. D., 1924, Bull. Amer. Mus. Nat. Hist., L, p. 165.

TYPE.—m^2, right, from Upper Snake Creek, Amer. Mus. cast No. 14450. Harold Cook Coll. This paper, figure 26.

CHARACTERS.—Transverse narrowness, especially posteriorly, and unusual reduction of the antero-inner corner.

DESCRIPTION.—Low-crowned, strongly diagonal condition of the outer cusps, unusual transverse narrowness, paracone and hypocone considerably developed, protocone and metacone reduced, antero-inner border much reduced, inner root posterior and larger than two outer roots, its greatest diameter being directed antero-externally. It is much worn.

HORIZON.—Upper Snake Creek correlated with the Republican River Pliocene. The specimen apparently represents the earliest known American occurrence of a possible *Hyænarctos* form.

The tooth is low-crowned, and relatively small-sized compared to the described forms of *Hyænarctos*, but large relative to *Hemicyon*. It is evidently not directly referable to any present known form. The strongly diagonal position of the paracone and metacone indicates that the specimen represents m^2.

The tooth perhaps resembles *H. palæindicus* more than any other described form, but evidently cannot well be referred to the same genus. Compared to *Hemicyon barstowensis*, it is much larger, more narrow-proportioned transversely, and lacks the typical lingual production characteristic of *Hemicyon* and developed to much greater degree in *Amphicyon*.

Hyænarctos

MEASUREMENTS OF UPPER TEETH

	H. gregori (from material)	*H.* sp., Red Crag (after cast)	*H. sivalensis* (from type)	*H. schneideri* ref. (from specimen)	*H.* sp., Alcoi (after Gerv. illusts.)	*H. insignis* (from type)	*I. punjabiensis* (after cast)	*I. salmontanus* (from cast)	*I. oregonensis* (after Merriam)	*L. (H.) palæindicus* (from cast)	*H.* sp., Snake Creek (from cast)
p^4	U. C. 24027 32.3×21.7		32×22		30×23	29.1×21	32×22.5		31.7×22.6	(29)	
	type A.M.24025 35.4×25.8										
	ref.A.M.18121A 36.5 2.5										
m^1	U. C. 24026 30.5×(32.3)*	30×30	29×29.9	29.8×30.2		27.8×27.5	30×28	(29×25.5)		27×25.5	
m^2			29×30.5			27.4×26.5	31×27 (ref.)	35×27	35.3×27.2	27×27.5	26×24

*Measurements parallel or perpendicular to imaginary line through centers of main cusps.

Section B. Specimens of the Inferior Series

Authorities have taken seven of the nineteen disassociated specimens believed to be representative of the lower dentition of *Hyænarctos*, as the types of as many species (starred below), and have variously referred the other specimens. The material (considered in the same order and in detail in the sequel), with the name of the first describer, date described, and occurrence, may be listed as follows:

Portion of mandible with p_4–m_2, etc.; and a second similar fragment from Eden, tentatively referred in this paper to *Hyænarctos gregori* Frick.

Portion of m_3, from Eden, tentatively referred in this paper to *Hyænarctos gregori* Frick.

*Right ramus with c–m_2 and alveolus of m_3, from Florida, type of *Hyænarctos (A.) schneideri* Sellards, 1916.

*m_1 from Mexico, *Hyænarctos* species, Freudenberg, 1916.

Ramus and poorly preserved c–m_3, from Siwaliks, described by Falconer and Cautley in 1836 with *H. sivalensis* skull specimen.

m_2 from Norwich Crag, referred by Newton, 1891?, to *Hyænarctos* species, Falconer.

*m_2, from South China, referred by Lydekker, 1884, to *Hyænarctos* species.

m_3, from China, referred to the above species by Schlosser, 1903.

p_4-m_2, from Montpellier ("Lophyodont," Cuvier, 1822), referred by Stehlin, 1902, to *H. insignis* Gervais.

m_2, from Aubignas, tentatively referred, this paper, to *H. insignis* Gervais.

*m_{1-3}, from Pikermi, the type specimen of *H. atticus* Dames, 1883.

*Left ramus with incisors, c, and p_1–m_2 from Maragha, Persia, described by Mecquenen, 1925, as *Hyænarctos maraghanus*.

m_2 (broken), from Rattlesnake, part of type of *I. oregonensis* Merriam, 1916.

*Portion of mandible with p_4-m_2, from Montredont, type of *I. (H.) arctoides* Depéret, 1895.

Nearly complete mandible and teeth, from the Siwaliks, referred by Lydekker, 1878, to *I. (H.) punjabiensis*.

Fragment of symphysis with p_2, from the Siwaliks, referred by Lydekker, 1883, to *I. (H.) punjabiensis*.

Fragment with p_4-m_1, from the Siwaliks, referred by Lydekker, 1883, to *H. palæindicus* Lydekker.

Fragment with m_2, from the Siwaliks, referred by Lydekker, 1883, to *H. palæindicus* Lydekker.

*Portion of mandible with c-m_3, from Monte Bamboli, type of *H. laurillardi* Meneghini, 1863.

Other specimens have doubtlessly been found which a correct determination might prove to represent this genus, such as the now lost type specimen *Borophagus diversidens* Cope (see below).

Hyænarctos "gregori" Frick, referred

Figures 27, 27A, 35, 35A

Hyænarctos gregori FRICK, C., 1921, Univ. Cal. Pub. Dept. Geol., XII, p. 342.

REFERRED SPECIMENS.—Portion left mandible with p_4-m_2, Amer. Mus. No. 18120. Heretofore undescribed. Figured this paper, Figs. 27 and 35.

m_1 right, in mandibular fragment, Amer. Mus. No. 18120B.

Portion m_1 trigonid, Amer. Mus. No. 18120C.

c (?), Amer. Mus. No. 18120D.

Posterior portion m_3, left, Amer. Mus. No. 18121. Figured this paper, Figs. 27A and 35A.

CHARACTERS.—The relative shortness of m_2 as compared to m_1, the transverse heaviness of the m_2 as compared to the trigonid of m_1; the considerable development of m_1 and evident presence of an enlarged post-metaconid cusplet.

m_3 (broken), suggested hemicyonid (*H. schneideri*) characters.

DISCUSSION.—The referred mandibular specimen seemingly indicates the former presence of a premasseteric fossa. The teeth are much worn.

The p_4 is double-rooted, enlarged posteriorly, and with prominent anterior and posterior cingula. It is inserted externally and diagonally to m_1, as usual in *Hyænarctos*. The carnassial is long, narrowed anteriorly, and noticeably broad posteriorly. The trigonid is relatively long, the paraconid, protoconid, and metaconid are greatly worn, but were once well developed. The talon id is very broad; the cusps of the inner margin were evidently unusually well developed. The inner and outer walls of the trigonid are provided with weak cingula. The outer border is typically grooved at the posterior base of the protoconid, through abrasion of the paracone of m^1. The pattern of m_2 is obliterated and the tooth is broken at the posterior inner corner. The specimen is of wide and somewhat rectangular form, though characteristically broader anteriorly than posteriorly. A facet evidences the former presence of m_3

Specimen No. 18121 (Figs. 27A and 35A) is believed to represent the posterior portion of m_3 of the left side, through its general resemblance to the m_3 of *Hemicyon ursinus*. The crown is somewhat worn, is supported on a heavy and strongly inwardly curved fang, and is broken across near its greatest transverse diameter. The specimen can be only most tentatively referred to the mandible and the upper teeth, but is so referred on account of its undoubted hemicyonid character, its apparent agreement in size with the teeth of the large Eden form, and the recognition so far of but a single species in this locality. The more hemicyonid than typical hyænarctid character (m_3 was evidently elongate in *H. schneideri* but was rounded in "*H. sivalensis*" referred, "*H. punjabiensis*" referred, and *H. laurillardi*) of the fragment, how-

ever, suggests that it may well represent a different species from the other teeth.

A large referred lower left canine tooth held in a fragment of the jaw, Amer. Mus. No. 18120D. The specimen was found near the above mandible and is believed to be referable to the same individual. It would indicate the rather small size of the lower canine of this large form. The crown is much worn, somewhat transversely compressed, and shows two continuous deep grooves, one anteroventral, due to the attrition of the upper third incisor, and one postero-external, through attrition of the upper canine. The tooth is larger than one tentatively referred to *Hyænarctos* by Lydekker (Fig. 3), but is much smaller than the upper canine of the type specimen of *Hyænarctos sivalensis*, the lower canine of the mandible referred to *I. punjabiensis*, and the canine of the Florida mandible. It is much larger than the canine of *I. oregonensis*.)

Hyænarctos schneideri Sellards, 1916

Figures 28 and 36

Hyænarctos schneideri Sellards, 1916, Eighth Ann. Rept. Florida State Geol. Surv., p. 98, Pl. xii.

Type.—Right ramus of mandible with c, alveolus of p_1, p_4–m_2, and alveolus m_3, from Bone Valley formation, Brewster, Fla., No. 6856, Fla. Survey Coll. (U. S. Nat. Mus.). Figured by Sellards, Pl. xii. This paper, Figs. 28 and 36 (cast Amer. Mus.).

Characters.—The mandible and teeth are large, approaching in size those of the specimen referred to *H. gregori*, and to the but slightly larger m_1 from Mexico. The mandible is splendidly preserved and illustrates the great depth of the jaw and prominence of the premasseteric fossa in these forms. The teeth are considerably worn, especially m_2. The incisors are suggested by closely crowded alveoli. The canine was large, with a swollen and laterally compressed base.

The (?) p_1 is represented by the alveolus, which is separated from p_4 by a diastema; this is relatively shorter than that occurring in *I. punjabiensis*. The alveolar border is somewhat rugose, but shows no definite indication of the former presence of p_2 or p_3.

The breadth and fullness of the heel and the evident development of the post-accessory metaconid cusplet and the position of the metaconid of m_1 suggest the teeth referred to *L. palæindicus* by Lydekker, and those here referred to *H. gregori*.

The m_2 is more worn and unusually short relative to m_1. The apparent shortness of the tooth is doubtlessly due to some extent to the advanced stage of wear. The antero-outer corner has been deeply abraded by the metacone of m^1.

The m_3 was single-rooted, but evidently relatively large as in *Hemicyon*, and as suggested by the fragment referred to *H. gregori* (versus smaller and round in *I.* (*H.*) *punjabiensis* ref.).

The teeth are typical of the genus, except perhaps for the reduction of the premolars (which, however, at the best is as yet uncertain), and perhaps for the unusual relatively small size of m_2. Overlooking the

small size of this tooth, as in the case of the referred m^1 (see above), the specimen might represent a form closely allied to *H. gregori*. Similarly it might be argued that m^2 would have had a relatively long and somewhat narrowed and deflected heel (on account of the evident large proportions of m_3, which was set partly in the vertical ramus), but the protocone area of the inner ridge must have been relatively shorter than in the hypothetical m^2 of *H. gregori* (on account of the shortness of the talonid of m_2).

Compared to *Arctotherium haplodon*, the present mandible is deeper, the anteroposterior length of the series is greater, and the teeth are much larger and heavier, except the m_2 (which is relatively very short). It should be remarked, however, that the mandible, so far as visible in the specimen, follows *Tremarctos* very much more closely than *Hemicyon*, in the tendency to restriction of the premasseteric fossa to the posterior area, and the strong constriction of the inferior border below m_3.

	Hyænarctos schneideri		*Hemicyon ursinus*
Length posterior edge of $\frac{c\text{-}m_3}{}$	$\frac{146}{}$	196% versus $\frac{128}{}$	241%
Gr. depth ramus post. to m_1	74.5		53

The Bone Valley formation has yielded, besides this interesting mandible and the m^1, specimens of rhinoceros, of mastodon, camel, and of hipparion.

Hyænarctos species, Freudenberg, 1910, from Mexico

Figures 29 and 38

(?) *Hyænarctos* species, Freudenberg, 1910, Geol. Pal. Abhandl., N. F., IX, pt. 3, p. 205, Pl. III, Fig. 2; 1921, Geol. von Mexiko, p. 131. Merriam, 1916, Univ. Cal. Pub. Dept. Geol., X, p. 108.

Type.—m_1, left, from (?) Tehuichila Pliocene, Mexico. Figured by Freudenberg, 1910; Merriam, 1916; and this paper, Figs. 29 and 38.

Tooth formerly broken in two (mended), metaconid lost; and only slightly worn.

The specimen evidently represents an hyænarctid species of unusual size.

Freudenberg notes the indentation of the antero-external midborder, the four separate cusplets and the wrinkling of the enamel of the heel. At the time of Freudenberg's description, *Hyænarctos* had been unreported from America. He interpreted the specimen as representing a more primitive form than the Indian, believing it to have had unreduced premolars and to have been ancestral to the South American arctotheres.

Hyænarctos "sivalensis," referred Falconer and Cautley

Figures 31 and 37

Hyænarctos "sivalensis" FALCONER AND CAUTLEY, 1836, Asiatic Researches, XIX, p. 193. OWEN, R., 1840–1845, Odontography, Pl. CXXXI. FALCONER AND CAUTLEY, 1848, 'Fauna Antiqua Sivalensis.' FALCONER, 1868, Palæontological Memoirs, I, p. 321, Pl. XXVI, Figs. 3 and 4.

Portion of right ramus of mandible with c (broken)–m_2 from typical Siwaliks, Brit. Mus. Coll. No. 39722. Figured by Owen, 1840, Pl. CXXXI; Falconer and Cautley, 1848, Pl. o, Fig. 2 (unpub.); Falconer, 1868, Pl. XXVI, Figs. 3 and 4. This paper, Figs. 31 and 37.

The specimen is much too slender-proportioned and the teeth are too worn for direct reference to the skull of *H. sivalensis*, which was found a season later. The mandible shows a remnant of a deep pre-masseteric fossa continued forward under m_1 and less prominently under the alveoli of the premolars.

The lower canine, which is represented by its broken base, was apparently considerably compressed transversely (1.6 inches by .95 inches according to Lydekker).

Two alveoli, posterior to the canine, are interpreted by Lydekker as representing single-rooted p_2-p_3, rather than as a double-rooted p_3.

p_4, double-rooted, main cusp broken, posteriorly enlarged, and with inner cingulum (versus p_4 of *L. palæindicus* referred).

m_1, worn to root, short anteroposteriorly compared to *L. palæindicus* referred.

m_2 but moderately worn, of approximately same anteroposterior diameter as *L. palæindicus*, but much narrower. The metaconid is much more prominent than the paraconid.

m_3, represented by a single circular alveolus placed in the base of the ascending ramus; this would indicate that the crown of the tooth lay somewhat obliquely to the m_2.

The mandible and m_1 are much smaller than the corresponding elements of the specimen referred to *I. punjabiensis*.

Falconer and Cautley note that the lower edge of the mandible exhibits a considerable backward curvature and that the outer surface is deeply indented by a muscular hollow towards the angle. Lydekker and subsequent writers have accepted Falconer and Cautley's reference of the specimen to *H. sivalensis* (Lydekker, 1883, p. 223, notes Owen's error [p. 504] in interpreting the p_4 as representing m_1 and thus stating the m_1 to lack a metaconid). The specimen may represent an undescribed species.

Hyænarctos "species," Flower, referred Newton, 1891, from Red Crag

Hyænarctos species, NEWTON, E. T., 1891, 'The Vertebrata of the Pliocene Deposits of Britain,' (Pal.) Mem. Geol. Surv. United Kingdom, p. 14.

SPECIMEN.—m_2, right, from the Red Crag of Felixstow, Reed Coll., York Mus. Figured by Newton, 1891, Pl. I, Figs. 21*a* and *b*.

Newton notes the presence of a strong cingulum on the external side, and the manner in which the crown narrows upward. The specimen may represent the same form as the two upper teeth. The tooth is here tentatively referred to the upper teeth, pending evidence of the occurrence of more than one form of *Hyænarctos* in the Red Crag.

Hyænarctos species, Lydekker, 1884, from China

Hyænarctos species, LYDEKKER, 1884, Geol. Mag., Ser. 3, I, p. 444; 1885, Catalogue of the Fossil Mammalia in the British Museum, Part 1, p. 157, Fig. 23. SCHLOSSER, 1903, Abhandl. der k. Bayer. Akad. der Wiss., XII, p. 23, Pl. I, Fig. 3. *H. "sinensis* Owen," TROUESSART, Cat. Mam., 1898, p. 247, and 1905, p. 178.

TYPE.—m_2 right, from the (?)Pliocene of South China, Hamburg, 1853, Coll. Brit. Mus. No. 28588. Figured by Lydekker, 1885, p. 157, Fig. 23.

(?) REFERRED.—m_3, left, from China. Figured by Schlosser, 1903, p. 23, Pl. I, fig. 3 (part), from Pliocene or (?) Pleistocene.

The specimen is somewhat worn. Its most marked character appears to be the presence of a small swelling on the antero-outer face. The tooth is only slightly larger, and, except for the external swelling, rather similar to the m_2 of the mandible referred by Lydekker to *L. palæindicus*. It is much broader than the narrow, elongate m_2 of the mandible that has been referred to the skull of *H. sivalensis*.

Schlosser refers the somewhat indeterminate m_3 but tentatively to the former tooth (which he figures as of the "left side").

Hyænarctos "insignis," referred Stehlin

(?) *Lophiodon* species, CUVIER, 1822, 'Recherches sur les Ossemens fossiles . . ,' Second Edition, I, partie 2, p. 217, Pl. XI, Figs. 7–9.

"Ours" BRAVARD, 1828, Introduction, Monog. de Perrier, Mem. Soc. Hist. Nat., Ser. 2, IV, p. 368.

Lophiodon CRISTOL, 1835, Annales Sci. Nat., Ser. 2, IV, p. 225 (lists remains as rare).

"Not *Lophiodon*" BLAINVILLE, 1839–64, Ostéographie, IV, p. 103, Pl. II, center (reduced after Cuvier).

Lophiodon monspeliense M. DE SERRES, Cav. de Lunel-Viel, p. 249

(?) *Hyænarctos* or *Ursus* GERVAIS, 1853, Annales Sci. Nat., Ser. 3, XX, p. 236.

(?) *Lophiodon* GERVAIS, 1859, Zoologie et Paléontologie français, pp. 118 and 206.

Questions GERVAIS, 1865–7, Mem. Acad. Sci. Montpellier, III, p. 142.

(?) *Hyænarctos* FILHOL, 1888, Mem. Soc. Géol. Fr., Ser. 3, V, p. 159.

Hyænarctos insignis STEHLIN, 1907, Bull. Soc. Géol. Fr., Ser. 4, VII, p. 220, Fig. 1.

MATERIAL.—

p_4-m_2 from Boutonnet, Montpellier, in the Deluc Coll., Geneva Museum, referred by Stehlin, 1907, to *H. insignis* Gervais, 1853:

p_4, right. Figured by Cuvier, 1822, Pl. XI, Fig. 9. Stehlin, 1907, p. 223, Fig. 1.

m_1, right.

m_1 left. Figured by Cuvier, Pl. XI, Fig. 7. Stehlin, Fig. 1.
m_2 left. Figured by Cuvier, Pl. XI, Fig. 8. Stehlin, Fig. 1.
canines, etc. Figured by Cuvier, Pls. IX and XI.

REFERRED SPECIMEN.—m_2 from Aubignas, France. Mus. Hist. Nat., Paris, Coll.

The lower molars of the Deluc Collection, though much worn, are characteristically hyænarctid. A facet on the posterior border of m_2 attests to the former presence of m_3. As noted by Stehlin, the teeth are very like those of the mandible referred by Lydekker to *I.* (*H.*) *punjabiensis*. They differ from the latter in the (perhaps) larger proportions of p_2, the presence of cingula on the outer and inner base of m_1 (may occur in American forms), and the prominence of the metaconid of m_1 and m_2.

I very tentatively refer to the same species an unfigured m_2 from Aubignas. The tooth is in advanced stage of wear. A facet on the posterior face indicates the former presence of m_3. The tooth is similar, so far as may be seen by Stehlin's figure (Bull. Soc. Géol. Fr., 1907, Ser. 4, VII, p. 219, Fig. 1, p. 223), to the m_2 of the lower series from Montpellier. The tooth also resembles the slightly less worn m_2 from China, figured by Lydekker (Cat. Fos. Mam. Brit. Mus., p. 157, Fig. 23), differing mainly in the apparent presence of a slightly greater constriction between the trigonid and talonid, and absence of the pronounced swelling on the antero-external border. It differs from the narrow-proportioned m_2 of the mandible referred by Falconer to *H. sivalensis*, being only slightly longer but much broader, and (formerly) evidently having a prominent mid-accessory cusp.[1]

Indarctos (H.) atticus Dames

Hyænarctos atticus DAMES, 1883, Sitzung. Gesell. Naturf. Freunde [on discovery of *Hyænarctos* in Pliocene of Pikermi.] SCHLOSSER, 1887, Beiträge zur Pal. Osterreich Ungarn., VII, p. 311. WEITHOFER, 1888, Beiträge zur Pal. Osterreich-Ungarn., p. 231, Pl. XII, Figs. 1–2.

TYPE.—Portion of mandible with m_1 (crown poorly preserved), m_2, and trace alveolus m_3, from the upper Pontian of Pikermi. Figured by Weithofer, 1888.

The specimen measures larger according to the principal Weithofer figure than according to his measurements (m_1 40 mm., versus 35 mm.; m_2 29 mm., versus 28 mm.). By this figure, the specimen is approximately the size of the mandible referred by Lydekker to *H. punja-*

[1]In the same box with the above I note a p_4 and the anterior portion of an m_1, which are both of a more hyænarctid than amphicyonid aspect. The m_1 fragment is worn, very low-crowned, and too small and narrow-proportioned to be referred to the above m_2. (Distance between anterior end and division between paraconid and metaconid, 20 mm., transverse width over protoconid, 14.5 mm.) There is a trace of an inner cingulum on the anterior base. The tooth is too large for known *Hemicyon*.

biensis; m_2 is short relative to m_1, the protoconid was evidently high relative to the metaconid, and the talonid is reduced. The alveolus of m_3 is round as in *Hyænarctos*. The rough figure does not indicate the presence of a premasseteric fossa, and the external mid-indentation of m_1, as drawn, is more anterior than is usual in *Hyænarctos*.

Hyænarctos maraghanus Mecquenen, 1925

Hyænarctos maraghanus Mecquenen, 1925, Annales de Paléontologie, XIII, p 135, and XIV, p. 47, Pl. ix, Fig. 8.

Type.—Left ramus with incisor, canine, p_1-m_2, from Maragha, Persia. Mus. Hist. Nat., Paris. Collected in 1904. Figured by Mecquenen, Pl. ix, Fig. 8.

It is stated that the specimen appears to represent a species near to the mandible referred by Lydekker to "*L.* (*H.*) *palæindicus* (? ," but is a little stronger.

Description (after author and figure).—All premolars present, p_{1-2} reduced, and scarcely used.

p_1, near to canine; slight diastema anterior and posterior to small p_2; p_1 and p_2 probably single-rooted.

p_3, slightly stronger and two-rooted.

p_4, closely pressed against m_1, triangular-shaped, light external cingulum present with anterior and posterior cusplets.

m_1, large relative to the other teeth; considerably worn; paraconid united by wear to protoconid, metaconid, and large postero-adjacen cusplet; trigonid somewhat narrowed, talonid broad.

m_2, talonid and trigonid approximately equal, external cusp much worn. Tooth large relative to m_1. (m_3 unknown).

Messrs. Boule and Depéret consider the Maragha deposits as of Pikermi-Samos age (Upper Miocene). It is presumed that a well developed premasseteric fossa, unmentioned by the author, was present. The specimen is of unusual interest in showing the retention of all four premolars (though p_2 is considerably reduced). It differs from *Hemicyon* in its much greater size, shortness of the jaw, nearness of p_1 to c, single root of p_2, relatively large size of p_4, and relative width of trigonid of m_1. The most interesting specimen may eventually prove no more than a large individual of the present very indefinitely known *H. atticus* Dames.

Indarctos oregonensis Merriam, 1916 (in part)

Figure 30

(See above under Upper Teeth, Section A)

Type (in part).—m_2 (broken) associated with type specimen, Univ. Cal. No. 22362, from the Rattlesnake, Oregon. Figured by Merriam, 1916, Fig. 13. Refigured this paper, Fig. 30.

As noted above, the tooth is greatly worn and the external border is broken. A facet on the posterior extremity evidences the occurrence

of m_3. It exhibits no unusual character, but is of particular interest as representing the only known recorded case of the finding of a lower tooth of *Hyænarctos* in association with teeth of the upper jaw.

Indarctos (H.) arctoides Depéret, 1895

Hyænarctos arctoides DEPÉRET, 1895, Compte rendu Acad. Sci. (Paris), CXXI, p. 433; 1895, Compte rendu Assn. fr. Avanc. Sci., Paris, p. 12; 1896, Compte rendu Assn. fr. Avanc. Sci., Bordeaux, p. 541. STEHLIN, 1907, Bull. Géol. Soc. Fr., Ser. 4, VII, p. 221. PILGRIM, 1913, Rec. Geol. Surv. India, XLIII, p. 290; 1914, Rec. Geol. Surv. India, XLIV, p. 227.

(*Hyænarctos*) *arctoideus* DEPÉRET, SCHLOSSER, 1899, Palæontographica, XLVI, p. 106; 1900, Mittheil. Jahrb. K. Ungarn., Geol. Anstalt.

(*Ursus hyænarctoides*) DEPÉRET, SCHLOSSER, 1902, Geol. Pal. Abhandl., V, Part 3, p. 36.

TYPE.—Portions of maxilla with m^1-m^2, and of associated (?) mandible with p_4-m_2, from Montredon.

Depéret (1896) states that the upper molars are not square like those of *Hyænarctos*, but more elongate, and approaching the bears; that the talon of m^2 is shorter than in the bears; that m_2 is rather long and less developed posteriorly than anteriorly; and that m_3 is presumably small and round, with single root.

Schlosser and Pilgrim note the impossibility of determining the specimen on the meager description. Schlosser (1899) tentatively refers it to *Ursavus*, and (1902) remarks that in the posterior position and shortness of the metaconid and shortness of the talonid of m_2, and smallness of m_3, it is similar to *Hyænarctos* as well as to *Ursavus primævus*, and that he considers the species directly ancestral to *Ursavus depereti* from Melchingen. Pilgrim suggests the possibility of this form being connected with *Indarctos*. Stehlin (1907) notes that this type is also found in the lignites of Orignac and has been designated by various authors as a species of *Ursus*. He considers it represents a line between *Hyænarctos* and the true bear (p. 221).

Indarctos (H.) "punjabiensis," referred Lydekker

Figures 33 and 40

Indarctos (H.) "punjabiensis" LYDEKKER, 1878, Rec. Geol. Surv. India, X, p. 33; 1883, Pal. Indica, Ser. 10, II, p 229, Pl. XXXI, Fig. 1.

SPECIMEN.—Nearly complete mandible with c-m_3, from the Hasnot Siwaliks. Figured by Lydekker, 1883, Pl. XXXI, Fig. 1; this paper, Figs. 33 and 40.

REFERRED.—Tentatively referred by Lydekker (1883).—A second specimen, consisting of a fragment of the mandible showing a portion of the symphysis, the base of a canine and p_2, from the Sind, India Mus. Coll. Unfigured.

The portion of the mandible apparently exhibits a remnant of the upper section of the intermasseteric ridge, and there seems likewise to be present (in cast) a premasseteric constriction of the ramus inferior to m_2 (this constriction may have been responsible for Lydekker's statement that the mandible is shallower than that of *H. sivalensis*).

Teeth very slightly worn.

Canine moderately large, p_1 represented by an alveolus adjacent to the canine.

p_3 represented by single alveolus, separated by short diastema from p_1.

p_4 represented by broken base, moderately large, double-rooted.

m_1 heel tending to be unusually narrow as seen in inner border; the inner accessory cusplets are very slightly developed.

m_2 narrowed posteriorly.

m_3 relatively small and round.

Pilgrim, 1914, disagrees with Lydekker's reference (1883) of the specimen to *Hyænarctos punjabiensis*, stating that the specimen does not agree exactly either in color or amount of wear with the teeth of the type maxilla, was not found in the same season, and might as likely belong to the species *Indarctos salmontanus*.

The teeth superimpose moderately well over the type molars, but appear a trifle larger-proportioned.

Lydekkerion (H.) "palæindicus," referred Lydekker

Figures 32A and 39A

Hyænarctos "palæindicus" LYDEKKER, 1883, Pal. Indica, Ser. 10, II, p. 234. PILGRIM, 1914, Rec. Geol. Surv. India, XLIV, p. 228.

SPECIMEN.—Fragment of left mandible with p_3 alveolus, p_4, and m_1, from Siwaliks of Jabi, Punjab, India Mus., Calcutta. Figured by Lydekker, Pl. XXXI, Fig. 2. This paper, Figs. 32A and 39A.

p_3, indicated by double alveoli.

p_4, moderate-sized and typical appearance; anterior corner is broken.

m_1, protoconid is remarkably low, and the post-metaconid accessory cusplet remarkably large, approaching in size the well-developed and posteriorly-placed metaconid; the talonid valley is very broad; hypoconid ridge is relatively low; a cingulum is present on the outer border of the talonid (versus in referred *I. punjabiensis*).

Lydekker placed with this specimen the fragment of a right mandible containing m_2, which he stated may possibly have been associated with same; see following:

Figures 32B and 39B

Hyænarctos "palæindicus" LYDEKKER, 1883, Pal. Indica, Ser. 10, II, p. 234. PILGRIM, 1914, Rec. Geol. Surv. India, XLIV, p. 228.

SPECIMEN.—Right mandibular fragment with m_2. Figured in Pal. Indica, Pl. XXXI, Fig. 3; this paper, Figs. 32B and 39B.

The m_2 is unworn, deeply indented externally between the trigonid and talonid; cusplets of the inner and outer corners are well developed; the metaconid is unusually high and prominent (thereby suggesting that the tooth is not referable to the above low-crowned m_1). The tooth is much narrower than the m_2 referred to *Indarctos punjabiensis*.

The transverse narrowness of the mandibular fragment indicates the occurrence of a premasseteric fossa and explains Lydekker's statement that the mandible was much more slender and therefore dog-like than that of *Indarctos punjabiensis*. Lydekker further considered the fragment to show the loss of m_3 in this form, which loss he correlated with absence of a talonid in the m_2. There is, however, no reason to doubt the presence of m_3, which would have been placed in the missing base of the ascending ramus.

Hyænarctos laurillardi Meneghini

Figures 34 and 41

Amphicyon laurillardi Pomel, Meneghini, 1862, Atti, Soc. Ital. di Sci. Nat. Milan, IV (1863-2), p. 29, Pl. II. Forsyth Major, 1872, idem, p. 295.

Hyænarctos laurillardi Meneghini, Gervais, 1875, Zoologie et Paléontologie generales, Deuxième Ser., p. 22. Lydekker, 1883, Pal. Indica, Ser. 10, II, p. 248, footnote; 1885, Catalogue of the Fossil Mammalia in the British Museum, Part I, p. 156. Schlosser, 1887, Beiträge Pal. Österreich-Ungarn., VII, p. 87; 1888, Boll. Commit. Geol., p. 367 (lists only).

Hyænarctos anthracites Weithofer, 1888, Boll. R. Com. Geol. Ital., XIX, lists on p. 367; 1889, Jahrb. Geol. Reich., XXXIX, 1889, pp. 57 and 60. Depéret, 1906, Compte rendu heb. Acad. Sci. (Paris), CXLIII, p. 1122. Pilgrim, 1914, Rec. Geol. Surv. India, XLIV, p. 231.

Type.—Portion right mandible with canine to m_3 (p_{1-2} absent), from the Sarmatian of Monte Bamboli. Mus. Fisiocritici, Sienna. Figured by Meneghini, 1862, Pl. II. This paper, Figs. 34 and 41 by Miss Woodward, after Brit. Mus. cast.

Discussion.—(Based on casts of type seen in London and Paris.)

The presence of an intermasseteric ridge is indicated in the conformation of the remnant of the mandible posterior and inferior to m_3.

The teeth are very little worn; the main cusps are low.

p_1 and p_2 are absent; the cast, however, (?) suggests the possibility of the alveolus of p_1 being present in the original specimen, though not shown in Meneghini's figure.

p_3 is moderately small.

p_4 is enlarged, both the posterior and anterior accessory cusplets are present, the posterior base is less enlarged laterally than in *Hyænarctos gregori* (ref.), more enlarged than in *Lydekkerion palæindicus* (ref.).

m_1 is very low-crowned, paraconid-metaconid blade developed, metaconid prominent and placed widely inwardly and posteriorly; post-accessory metaconid cusp and a slight second accessory cusp present, endoconid prominent, and a very slight cusp present anterior to same, heel basin wide and open posteriorly.

Lycenarctos

MEASUREMENTS OF LOWER TEETH

	H. sp., Mexico (from type)	Ref. *H. gregori* (from material)	Ref. *H. insignis* (Stehlin illusts.)	Ref. from Aubignas (from material)	*I. oregonensis* (after Merriam)	Ref. *I. punjabiensis* (from cast)	*H.* sp., S. China (from type)	Ref. Red Crag. sp. (Newton illusts.)	*H. schneideri*, type (from cast)	Ref. *L.* (*H.*) *palæindicus* (from cast)	*H. maraghanus* (after figure)	Ref. *H. sivalensis* (from material)	*H. atticus*, type (Wheit. figure)	*H. laurillardi*, type (from cast)
p_3											13.5			8.5
p_4		25.5	23						23	21	24	23		18.5
m_1	46.5×24	43.5×23.5	41.5			42.5×21.5			41×23.5	39.5×21	44×23	(38×—)	(40)	33.2×16.5
m_2		(33)	32.5	32×21.8	32×((21))	31 ×23	30 2×22	29.5×22	(29)	29×21.5	32	28.5×18.5	(29)	23.7×15.5
m_3		—×(11.5)				18			(alv. 20)			(alv. single)		13

m_2 anteroposterior diameter is less than that of m_1, metaconid higher than protoconid, as in *Hyænarctos* and *Ursus*, versus *Canis* and *Hemicyon*, a slight paraconid present.

m_3 is oval, narrowed posteriorly and set at base of ascending ramus.

The specimen is definitely not amphicyonid. In the lowness of the cusps, the non-secant heel of m_1, and the absence of p_1-p_2, the specimen suggests *Hyænarctos*, particularly *H. palæindicus*. While the teeth somewhat resemble *Hemicyon*, the specimen definitely differs in the lower crowns, the reduction of the premolars, the less blade-like paraconid and more posterior position of the metaconid of m_1, the longer and hyænarctid proportion of m_2 relative to m_1 (74%, versus 60% in *Hemicyon*), and the greater prominence of the metaconid relative to the protoconid.

Gervais (1875) notes the great development of the premolars as compared to recent bear and suggests the reference of the specimen to *Hyænarctos*. Lydekker (1883) mentions in a footnote that Gervais has made a new species of *Hyænarctos* out of Meneghini's type specimen. Lydekker (1885) notes that the p_4 lacks the cusps which appear on the posterior tooth border in *Amphicyon* and *Canis*, and the small size of the specimen as compared to the three Indian species. He states the specimen may represent a new species of *Hyænarctos* or may possibly belong to *Dinocyon*, the molars being of a similar size to the upper molars figured by Gervais, 1859 (Pl. LXXXI, Figs. 8 and 9). Schlosser (1887) speaks of the p_4 as having become very small. Pilgrim (1914) suggests that *H. laurillardi* may be ancestral or near-ancestral to *Indarctos*.

Depéret correlates the Monte Bamboli deposit with the third stage of the Vindobonian or mid-Miocene. This would make the specimen contemporaneous with the *Hemicyon* of Stätzling and indicate an unexpected degree of specialization to have taken place in *Hyænarctos* even at that time.

(?) H. (Borophagus) diversidens (Cope), 1892

Borophagus diversidens Cope, 1892, Amer. Nat., p. 1028; 1893, Geol. Surv. Texas, p. 54, Pl. XIII, Figs. 4 and 4A.

TYPE.—A greatly reduced p_3 and enlarged p_4 (heel broken) in a fragment of a left ramus, which shows the (?) single alveolus of p_2 and trace of the alveolus of the canine; from the Blanco, Texas. Whereabouts of specimen unknown. Figured by Cope, 1893, Pl. XIII, Figs. 4 and 4A.

DISCUSSION.—The Cope sketch indicates an anteroposterior shortness of jaw and size of jaw and canine equaling that of *H. schneideri*, and a p_3 and p_4, which in the small size of the one and great size of the latter, are characteristic of the same and other species of *Hyænarctos*, as is the nearness of the p_1 ("p_2" of Cope) to the canine. The p_4, however, is so badly broken that the more exact reference of the specimen must remain in doubt.

URSAVUS Schlosser

A NON-URSID, AND MEMBER OF THE HEMICYONINÆ

Figures 42–45, 50 A-D

GENERAL DISCUSSION.—Specimens of dentition from some eight European localities of probable general Vindobonian age[1] have been referred to the genus under four named species as follows:

Ursavus brevirhinus HOFMANN-SCHLOSSER.

Upper and lower teeth, from Voitsberg, Steiermark.

m^1-m^2, from Kieferstädtel, Schlesien (type of *Hyænarctos minutus* of Schlosser and Koken).

m_1-m_2, from Steieregg.

Molars of both series, and a mandible from Oppeln, Upper Schlesien.

A premolar and incisor from Leoben (Redlich, 1906).

Ursavus primævus GAILLARD-SCHLOSSER.

Certain upper and lower teeth from La Grive St. Alban.

Ursavus depereti SCHLOSSER.

m_1 and m_2, from Melchingen.

m_1, from Neuhausen (*Galeotherium* Jäger, 1839).

Ursavus elmensis STEHLIN.

Mandible with dentition and an m^1 fragment, from Elm.

The material is all apparently of very similar general type, except perhaps for the genotypic species and the small-sized specimens representative of *U. elmensis* Stehlin, both of which species may prove worthy of subgeneric rank. A study of the illustrations shows the typically hyænarctid and non-ursid character of the teeth and mandibles. Certain characters, however, besides the small size, readily distinguish these little Miocene forms from the huge Pliocene forms grouped under *Hyænarctos*. They are, therefore, here retained in the genus *Ursavus*, though the inappropriateness of the name must be noted.[2]

In the closing pages of this section I discuss and tentatively describe, as representing a new species, (?) *U. pawniensis*, a fragmental mandible containing m_1-m_2, which I myself discovered some years ago in an exposure of the Pawnee Creek Miocene, Colorado.

Two years ago I had the pleasure of examining the type of *Ursavus primævus* Gaillard, and referred teeth from the Miocene of La Grive St. Alban in the Muséum des Sciences Naturelles, Lyons, as well as the two referred specimens from the type locality now in the British Museum.

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[1] According to Stehlin (1907), who considers the age of *U. elmensis* indefinitely Burdigalien or Vindobonian (i. e., Lower or Middle Miocene).

[2] *Loc. cit.*, under *Hyænarctos*.

Through the courtesy of Doctor Gaillard and of Dr. Smith Woodward, I am able to figure this material in the present paper. I base my discussion of the genus *Ursavus* mainly on the examination of this material, and on Wegner's (1913) fine figures of that from Oppeln. I learn from Doctor Gaillard that the m^2 (Fig. 43), heretofore illustrated with the p^4-m^1 (Fig. 42) of the La Grive type specimen, was not found associated with the same, and undoubtedly belonged to a second and evidently larger-toothed individual. A unique m_2 (Fig. 50B), collected at the type locality by Dr. Forsyth Major, and heretofore unfigured, adds to our knowledge of the La Grive St. Alban form.

Certain characters of this material are convincing evidence of the hyænarctid affinities of *Ursavus* and of its wide separation from the ancestral line of *Ursus*. The recent discovery of a typically developed ursid dentition in the Lower Pliocene of America further emphasizes the improbability of *Ursus* having been descended from a hyænarctid form, as discussed at greater length in the sequel. The resemblance of the upper molars of the Miocene *Ursavus* to those of *Helarctos* is not as striking as is their resemblance to those of *Indarctos*. *Anacodon ursidens* had developed in the Eocene low-crowned and "wrinkled" bear-like teeth.

Important among the characters that differentiate *Ursavus* from the ursids are those existing in the p^4, referred m_1 and m_2, and in the mandible itself. The p^4 in *Ursus*, *Helarctos*, and *Tremarctos* is extremely short relative to m^1; the paracone and metacone are low and cusp-like, versus blade-like, and the deuterocone is posterior and at the base of the metacone. The p^4 of *Ursavus* is definitely non-ursid; in its elongation relative to m^1, its sectorial development, and antero-medianly-placed deuterocone, it is hemicyonid. The vast difference in type between canid and ursid carnassials of the milk, and of the permanent dentitions, as discussed below, precludes (in my opinion) the possibility of the derivation of the carnassial of either from near-ancestral forms of the other. *Ursavus* m_2, referred, is markedly shorter than the m_1, and the trigonid is long relative to the talonid. The tooth thus resembles *Hyænarctos* and differs as absolutely from *Ursus* and *Helarctos*. The m_1 of *Ursavus* has a single undivided metaconid, resembling that of *Tremarctos*, *Hemicyon*, and *Canis*, and quite different from the "divided" metaconid of *Helarctos* and *Ursus*. Wegner's splendid cut of the Oppeln mandible (1913, Pl. XII, Fig. 20) shows a well-developed premasseteric fossa. Figures of *U. brevirhinus* Hofmann (1887, Pl. x, Fig. 1) and of *U. elmensis* Stehlin (1917, Fig. 5); Schlosser's remark as to the peculiar

character of the mandible, which he refers to the genotypic species; and the general similarity of the hyænarctid-like teeth, indicate that these mandibles were all of perhaps corresponding hemicyonid type (a type common to the faunas of Sansan and La Grive St. Alban). The hemicyonid rather than ursid proportions of the tooth series are well illustrated in figures 1A-1B where the p^4-m^2 of *Amphicyon*, *Hemicyon*, *Hyænarctos*, *Indarctos*, *Ursavus primævus*, *Tremarctos*, *Procyon*, and *Canis* are figured with the p^4s of each series brought to the same anteroposterior diameter.

History of the Genus.—Schlosser (1887) interprets a maxillary fragment with m^1-m^2 from Kieferstädtel, as representing a very typical *Hyænarctos*, describing it as a new species, *Hyænarctos minutus*. Koken (1888) discusses this specimen, noting the strong development of the inner posterior cingulum of m^1. Hofmann (1892) adds a palatal series to his previously described Voitsberg form (*Cephalogale brevirhinus*), and transfers the whole to *Hyænarctos*, as *H. brevirhinus*. Gaillard (1899) refers the La Grive St. Alban remains to *Ursus*. He considers *U. primævus* to be directly ancestral to *Ursus* and to represent a transitional stage between the carnivores and omnivores, thus to tie the living bears to the ancient canids, in each of which he notes that the volume of the upper molars is inversely proportional to that of p^4 (in the bears the carnassials being reduced relative to the upper molars, in the dogs the upper molars being reduced relative to the carnassials). Gaudry (*loc. cit*) believes Gaillard's discovery to show the bear not derivable from known *Hyænarctos*, and that the new form, in proving the great antiquity of the ancestry of the bear, suggests the antiquity of *Hyænarctos*. Schlosser (1899) decides, by comparison of originals and casts, of the material from Voitsberg, Steieregg, and Kieferstädtel, that all belong to one species. He considers that this can no longer be retained in the genus *Hyænarctos* or be referred directly to *Ursus*, and establishes for it a new genus, *Ursavus*. (It must be noted that the p^4, which Doctor Schlosser figures in with the Kieferstädtel m^1-m^2, belongs to the Voitsberg, a somewhat smaller form.) Schlosser refers to *Ursavus* as a separate species, *U. primævus* Gaillard. He suggests "*Lutra dubia*" Depéret to have been derived from *Ursavus*, and that *Ursavus* and *Helarctos* may have come from the same ancestral stem. Schlosser, however, mentions elsewhere (1900) that *Ursus* differs so widely from *Ursavus* and *Hyænarctos*, in the construction of the p^4s, that it is impossible to derive *Ursus* from *Hyænarctos*, which he finds in this the more specialized genus. Schlosser (1902) refers an m^1-m^2 from Melchingen to *Ursavus*,

Ursavus

COMPARATIVE MEASUREMENTS OF TEETH

	(?) *U. pawniensis*, new species, from Colorado	*U. depereti* Schlosser, 1902, from Melchingen (G)	*U. primævus* Gaillard, from La Grive St. Alban		*U. brevirhinus* Hofmann				*U. elmensis* Stehlin, from Elm
					From Oppeln, Schlesien, Wegner, 1913	"*U. depereti*," ref. Schlosser (*Galeotherium*) Jäger, 1839, from Neuhausen	From Voitsberg, Steiermark genotype	From Kieferstädtel, Schlesien, Berlin Mus. "*U. minutus*" Schlosser	
			Type p^4-m^1						
p^4			13 × 8		13.3×9.3(C)		12× 8(E)		Referred
m^1			13 ×12	14.5×13.5(A)	14.4×12		12×10.5	12 ×11(F)	(10.2 diam. toe)
m^2			16.5×12.6(B)	17×13(A)	15.6×12(D) 14.4×12(D)m^1		11.5×10	13 ×10.5	
				(*Lutra dubia* Depéret)			Referred	From Steieregg	Type
p_4					9.5× 5.1		8×4.5		6.5
m_1		22.5×10	20.6×10(A)	17×8.1 (versus 18×9 Schl. 1899, Pl. XIII, Figs. 14 and 20)	19.2× 9.2	18.5× 9	18×6.8	16×—	14× 6
m_2	16.5×11	16.8×10.8	14×9.2(B)		13.8×9.3		12× 8	11.8×7	10× 6
m_3	10. ×9.1						6.8×6.2		

(A) Larger of two m^1s and the m^2 of "type" as originally figured, and m_1 in Mus. Hist. Nat., Lyon.
(B) m^2 and m_2, No. 5318 in Brit. Mus. Coll. referred by F. Major.
(C) Wegner gives diameters of additional p^4s 10.4×10, and 12.8×—.
(D) m^1, and an m^2 of a second specimen.
(E) p^4 figured alone by Schlosser (1899), Pl. XIII, Figs. 13 and 19 (in part); measurements quoted by Schlosser for p^4–m^2 and m_1–m_3 after Hofmann; both series figured by Hofmann (1887, Pl. X, and 1892, Pl. II).
(F) Figured by Schlosser (1899), Pl. XIII, Figs. 12 and 19 (in part); measurements of Koken (1887) and Schlosser (1899, not 1887).
(G) Measurements given by Schlosser in text, versus those of his (and our) figures, 23.5×12.8 and 17.3×11.5.

as a new species, *U. depereti*, and places with this material the m_1 from Neuhausen described by Jäger (1839) as "*Galeotherium.*" He states that the Melchingen species is uncommonly like the somewhat smaller La Grive St. Alban form. He notes a certain similarity in the position and size of the metaconid and shortness of the talonid of m_1 between this material and *Hyænarctos*, but considers this not sufficient to classify the same with *Hyænarctos*, for he says that exactly the same characters are found in the geologically older *Ursavus primævus* from La Grive St. Alban. This, he argues, would also have to be classified with *Hyænarctos*, and the peculiarity of its upper molars show him most conclusively that it is an ursid (*Ursavus*). Stehlin (1907) describes the mandible of a small species from Elm, noting that a referred m^1 is somewhat distinct from the *Ursavus* type. Gidley (1923) notes that the p^4 of *U. primævus* is relatively larger and more definitely trenchant than in any of the living genera of bears, and that *U. primævus* is generically distinct from any of the living bears, but considers, on account of the similarity of the upper molars, that it ". . . probably represents a very closely related form if not an actual ancestor of the living *Helarctos*. . . ." Wegner, 1906, figures, under *Ursavus brevirhinus* Hofmann, a typical hemicyonid mandible, etc., from Oppeln.

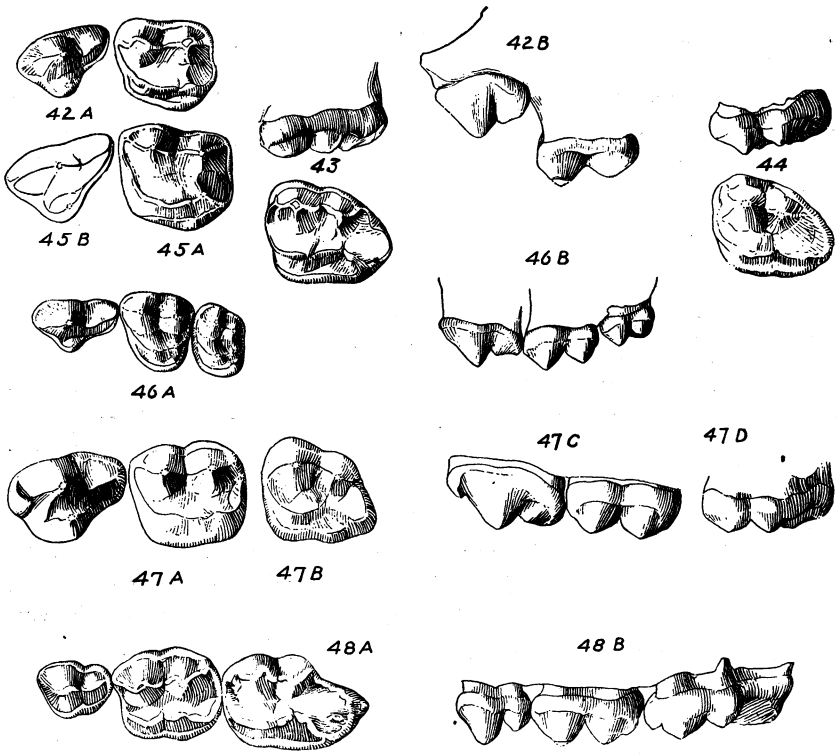
Characters of *Ursavus*

The characters of *Ursavus*, as seen in *Ursavus primævus* Gaillard, are as follows:

p^4 (only partially erupted), anteroposterior diameter equal to that of m^1; deuterocone placed widely inward and anteromedianly at posterior base of paracone, paracone and metacone blades developed, paracone directed sharply backward and angulated with respect to the metacone (versus non-sectorial in *Ursus*, where dp^3, unlike in the *megalocreodonts*, is a simple double-rooted cone).

m^1, and m^2 referred, moderately elongate, low-crowned, with reduced main cusps; in unworn state occlusal surface much wrinkled, inner cusps fused into a wedge-like ridge that lies well within and above the inner border. The area between the inner ridge and the outer cusps is high (the inner ridge shows no trace of a differentiated mid-cusplet). m^1, paracone bold antero-externally, metacone relatively smaller and tending to be connected by a cross-crest to hypocone, absence of cusplet median to protocone and hypocone, postero-inner cingulum prominent. m^2, external border of metacone considerably reduced relative to paracone border; talon somewhat developed. The upper molars thus differ in detail from the upper molars of *Helarctos malayanus*, to which they have a strong superficial resemblance.

m_1, referred, paraconid relatively large, paraconid-protoconid forming shear as in upper carnassial; metaconid single, not double as in *Helarctos* and *Ursus*; talonid broad, inner cusps much more prominent than hypoconid, as in *Hemicyon*. (In *Ursus* and *Helarctos* (Figs. 50A-54C), the protoconid is more anterior, resulting in



Figs. 42–45. *Ursavus primævus* Gaillard, from La Grive St. Alban, France, Mus. Hist. Nat., Lyon. Natural size.

Fig. 42. Type p^4–m^1, left. A, occlusal; B, outer view.

Fig. 43. Cotype, m^2, left (heretofore figured as of type specimen); occlusal and outer views.

Fig. 44. Referred m^2, left, Forsyth Major Coll., Brit. Mus., after Miss Woodward; occlusal and outer views.

Fig. 45A. Large m^1, left, referred.

Fig. 45B. Hypothetical p^4 drawn in same proportion to m^1 (Fig. 45A) as exists between p^4 and m^1 of type specimen. (Fig. 42.)

Fig. 46. *Hemicyon barstowensis*, new species, from Barstow Miocene, California, p^4–m^2. × ½. A, crown view; B, lateral view.

Fig. 47. *Indarctos*. 47 A–C, *I. punjabiensis* Lydekker, from Siwaliks, after Amer. Mus. cast and Lydekker's figures; × ½; A, occlusal view, p^4–m^1; B, referred m^2; C, outer view of p^4-m^1; 47 D, *I. salmontanus* Pilgrim, m^2 of type specimen, from Salt Range.

Fig. 48. *Helarctos malayanus*, p^4–m^2, Amer. Mus. No. 28254. Natural size; A, occlusal; B, outer view.

the paraconid-protoconid being relatively short; the talonid is long and narrow, the hypoconid more prominent than the single inner cusplet.)

The following additional *Ursavus* characters are seen in the better-represented material figured by Wegner (see below):

Mandible with well-developed intermasseteric ridge and premasseteric fossa.
m_2 short relative to m_1.
m_3 in base of strongly upright vertical ramus.

Ursavus brevirhinus Hofmann

(Genotypic Species)

Figure 50C

Cephalogale brevirhinus HOFMANN, 1887, Jahrb. K. K. Geol. Reich., XXXVII, p. 208, Pl. x, Figs. 1–6 (portions of crushed mand., n. sp., from Steiermark).

Hyænarctos minutus SCHLOSSER, 1887, Beiträge Pal. Österreich-Ungarn., VII, pt. 1, p. 311; VIII, p. 458. KOKEN, 1888, Sitzung. Ges. nat. Freunde, Berlin, p. 44, Figs. 1–2.

Hyænarctos brevirhinus HOFMANN, 1892, Jahrb. K. K. Geol. Reich., XLII, p. 64, Pl. II, Fig. 1 (dbl. maxillary series from Steiermark, figured); Pl. III, Figs. 5–7, limb elements.

Ursavus brevirhinus SCHLOSSER, 1899, Palæontographica, XLVI, pp. 103, 108, Pl. XIII, Figs. 12, 13, 18, 19, 23; 1900, Centralb. für Mineral., p. 261. HOFMANN-REDLICH, 1906, Verhandl. K. K. Geol. Reich., p. 170. HOFMANN-WEGNER, 1913, Palæontographica, LX, p. 228, Pl. XII, Figs. 17–21.

TYPE.—Portions of mandible with p_3-m_3, and c, from Voitsberg, Steiermark. Figured by Hofmann, 1887, Pl. x, Figs. 1–6; Schlosser, 1899, Pl. XIII, Figs. 13, 19. (m_1); Gaillard, 1899, Fig. 2.

MATERIAL REFERRED BY HOFMANN, FROM TYPE LOCALITY.—

Portion of palate with c, p^1-m^2, etc. incisors. Figured by Hofmann, 1892, Pl. II, Figs. 1-3.
p^4. Figured by Schlosser, 1899, Pl. XIII, Figs. 18, 23.
m_1. Figured by Gaillard, 1899, Fig. 9.
Portions of humerus, ulna, and femur. Figured by Hofmann, 1892, Pl. III, Figs. 5–7.

CHARACTERS:—

Premolars without accessory tubercles.
The p^4 typically sectorial, paracone large, deuterocone median and prominent.
Upper molars, prominence of antero-external corners of cingulum, and of cusp of postero-inner corner of m^1.
m^2, heel apparently not nearly as developed as in Kieferstädtel m^2.
m_1, post-external cusplet of talonid apparently absent as in *U. depereti* (extremely small in *U. primævus*).

The Voitsberg material, as noted above, on account of its small size and apparent lack of development of the heel of m^2, might well be retained as a species distinct from the following larger-sized material which might then be grouped under *U. "minutus"* Schlosser, 1887.

Fig. 49. (?)*Ursavus pawniensis*, new species, type mandible with m_2–m_3, from Pawnee Creek Miocene, Colorado, Amer. Mus. No. 20801, inner view; and occlusal view, reversed. Natural size.

Fig. 50A. *Ursavus depereti* Schlosser, type m_1 and referred m_2, from Melchingen; occlusal and outer views after Schlosser (1902). Natural size.

Fig. 50B. *Ursavus primævus* Gaillard, referred m_1; Gaillard Coll. after cast, and referred m_2, F. Major Coll., by Miss Woodward; occlusal and outer views. Natural size.

Fig. 50C. *Ursavus brevirhinus* Schlosser, m_3 of type, after Schlosser (1899). Natural size.

Fig. 50D. *Ursavus brevirhinus* Schlosser-Wegner, worn m_1–m_2 of Oppeln mandible, occlusal view, after Wegner. Natural size.

Fig. 51A. Referred *Lydekkerion* (*H.*) *palæindicus* Lydekker, non-associated m_1 (reversed), and m_2, after casts, occlusal and lateral views. × ½.

Fig. 51B. Referred *Indarctos* (*H.*) *punjabiensis* Lydekker, m_2 (of m_1–m_2), after cast; occlusal and lateral views. × ½.

Fig. 52. (?)*Ursus minutus* Gervais, m_3 of type, from Montpellier, after cast. Natural size.

Fig. 53. *Ursus böckhi* Schlosser, m_1–m_3, from Baroth-Köpecz, after cast. Natural size.

Fig. 54. Recent species, m_1–m_3, occlusal and lateral views. Natural size; A, *Tremarctos ornatus*, Amer. Mus. No. 35530; B, *Ursus americanus*, Amer. Mus. No. 41330; C, *Helarctos malayanus*, Amer. Mus. No. 16580.

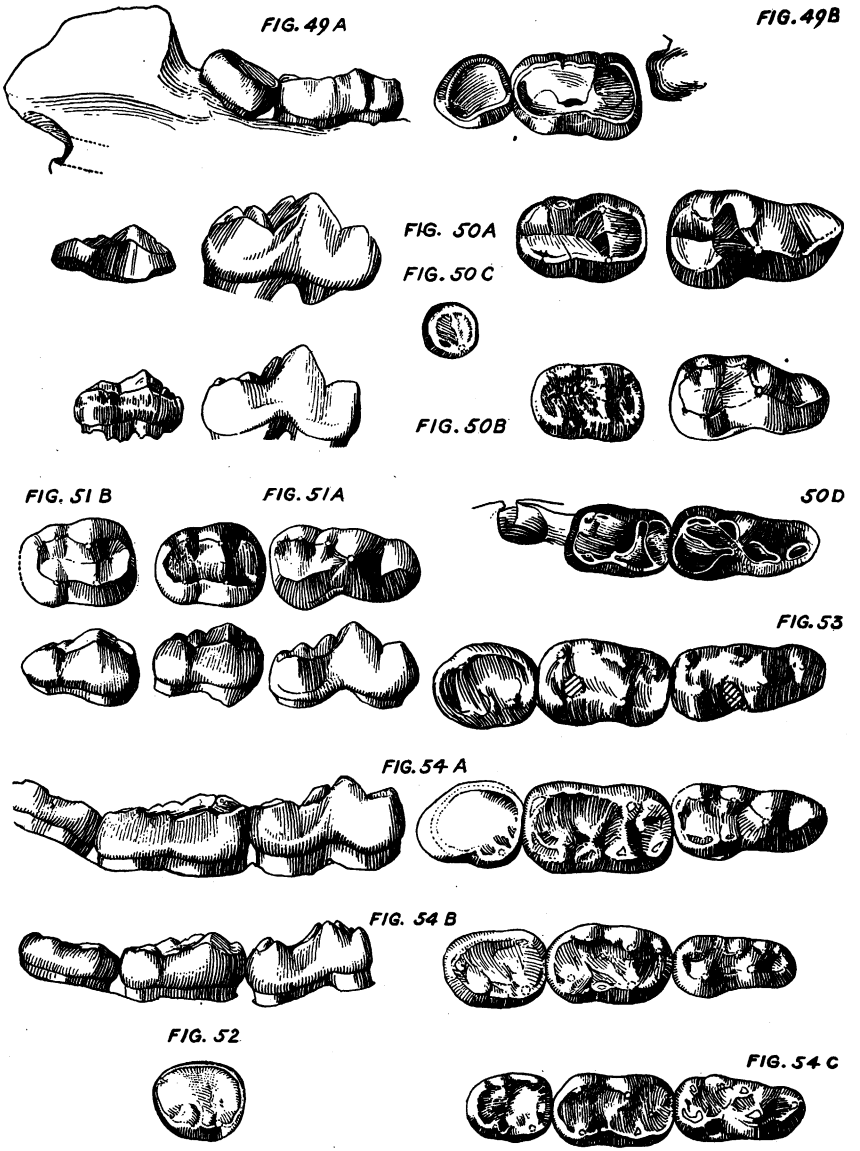


FIG. 49 A
FIG. 49B
FIG. 50A
FIG. 50 C
FIG. 50B
FIG. 51 B
FIG. 51A
50D
FIG. 53
FIG. 54 A
FIG. 54 B
FIG. 52
FIG. 54 C

MATERIAL REFERRED FROM FOUR LOCALITIES.—

(1) From Oppeln, Upper Schlesien, Univ. Breslau Coll. Referred by Wegner, 1913.

p^4, left (much worn). Figured by Wegner, 1913, Pl. XII, Fig. 22.

m^2, right, unworn. Figured by Wegner, 1913, Pl. XII, Fig. 17.

m^1, left, slightly worn. Figured by Wegner, 1913, Pl. XII, Fig. 18.

m^1, left, unworn. Figured by Wegner, 1913, Pl. XII, Fig. 19.

[(?) premolar].

Portion right mandible with p_4-m_2 and alveoli c-p_3 and m_3. Figured by Wegner, 1913, Pl. XII, Figs. 20, 21; Fig. 15. This paper, Fig. 50D.

CHARACTERS OF SPECIMEN:—

Mandible with well-developed intermasseteric ridge and premasseteric fossa.

m_3 in base of strongly upright vertical ramus.

m_2 elongate but shorter than m^1, which it exceeds in breadth.

p^4, much worn; outline suggests a diminutive *Hyænarctos sivalensis*.

m^1s, approximate size of larger specimen of *U. primævus*.

m^2, talonid moderately developed.

(2) From Kieferstädtel, Schlesien, Berlin Mus.

Left maxillary fragment with m^1-m^2 (type of *H. minutus* Schlosser, 1887). Figured by Schlosser, 1899, Pl. XIII, Figs. 12, 19. Gaillard, 1899, Fig. 8. Wegner, 1913, Pl. XII, Fig. 16 (*loc. cit.*, under Oppeln specimen). Koken (1888) notes that the anterior edge of m^2 lies opposite the anterior root of the zygomatic arch; the wide separation of the inner ridge from the outer cones in both molars, especially in m^2; and the strong development of the inner posterior cingulum of m^1.

(3) From Steieregg, referred by Schlosser.

m_1–m_2.

(4) From Leoben. Referred by Redlich, 1906.

An incisor and a premolar (ellipse, 10×7).

Ursavus primævus Gaillard

Figures 42–45, and 50B

Ursus primævus GAILLARD, 1898, Compte rendu heb. Acad. Sci. (Paris), December 26, p. 1237; 1899, Arch. Mus. Lyon, VII, p. 44, Figs. 24, 25.

Ursavus primævus SCHLOSSER, 1899, Palæontographica, XLVI, pp. 45, 104; 1900, Centralb. für Mineral., p. 261. GIDLEY, 1924, Journ. Mam., IV, No. 4, p. 240, Pl. XXVII.

Ursus primævus GAILLARD, 1899, 'A propos de l'Ours-miocène de La Grive St. Alban (Isère),' Figs. 1, 3 and 5.

TYPE.—Maxillary fragment with p^4–m^1, from La Grive St. Alban, France. Figured by Gaillard, 1899, Fig. 24; and Fig. 5, Coll. Mus. Lyon. Gidley, 1924, Pl. XXVII, Fig. 4; and this paper Fig. 42A and B.

REFERRED SPECIMENS FROM TYPE LOCALITY.—

m^2. Figured by Gaillard with type, 1899, Fig. 24; and Fig. 5. Gidley, 1924, Pl. XXVII, Fig. 4. This paper, Fig. 43, Coll. Mus. Lyon.

m^2. Figured this paper, Fig. 44, Brit. Mus. F. Major Coll.

m^1 (large). Figured this paper, Fig. 45A, Coll. Mus. Lyon.

m^1 (medium). Coll. Mus. Lyon.

m_1. Figured by Gaillard, 1899, Figs. 24 and 25. Schlosser, 1899, Pl. XIII, Figs. 14 and 20. This paper, Fig. 50B, Coll. Mus. Lyon.

m_2. Figured this paper, Fig. 50B, Brit. Mus., F. Major Coll.

CHARACTERS:—

p^4 equaling m^1 in anteroposterior diameter, blades sectorial, deuterocone anteromedian, approaching *Hemicyon*.

Upper molars elongate, low-crowned; occlusal surface multituberculate; inner cusps fused into wedge-like ridge, lying well inward of inner border, suggesting *Indarctos*, or to a less degree the bear.

m_1 referred, talonid moderately large and basin-shaped; inner cusps prominent, metaconid undivided, hyænarctid-like, and paraconid-metaconid shear developed.

m_2, right, referred, very short anteroposteriorly relative to referred m_1, trigonid broad relative to talonid (in the bear the m_2 is typically longer than the m_1, and the talonid is much longer-proportioned); the metaconid is more prominent than the protoconid; external and internal borders slightly constricted posteromedianly.

The figures (Figs. 42A and 45B) clearly evidence the strongly hemicyonid versus ursid proportions of the carnassial, and relative anteroposterior shortness of the m^1.

The referred m_1 of Gaillard[1] is as strongly hemicyonid as it is nonursid in its sectorial-tending paraconid-protoconid, undivided and markedly posterior metaconid, transversely widened talonid basin, strong post-metaconid and endoconid cusplets, and low outwardly curved hypoconid ridge with minute posterior cusplet. Its general similarity to the apparently larger m_1 of *U. depereti* is well shown by Figs. 50A and B. Except for the very slightly more anterior position of the protoconid and narrowness of the trigonid, the tooth strikingly approaches the m_1, referred by Lydekker to "*Lydekkerion* (*H.*) *palæindicus*" (Fig. 51A).

The m_2 referred (Fig. 50B), of the Forsyth Major collection, is generally similar to the *U. depereti* specimen and much suggests that referred by Lydekker to *L.* (*H.*) *palæindicus* (Fig. 51A). It agrees with the latter and differs from *Hemicyon* in the prominence of the metaconid relative to the protoconid, and its relative shortness anteroposteriorly. Approximately but one-half the size of the Lydekker tooth, it differs from this mainly in its greater anteroposterior elongation versus the relative shortness of the paraconid region, the poor definition to absence of

[1]The considerably smaller m_1 of *Lutra dubia* Depéret (figured by Depéret, 1892, Arch. Mus. Lyon, V, Pl. I, Fig. 7; Schlosser, 1899, Pl. XIII, Figs. 14, 20 ("after Depéret"); Gaillard, 1899, 'A propos de l'Ours-miocène de la Grive-Saint-Alban (Isère),' Fig. 3) is of somewhat different character from the above, in that: (a) the protoconid is situate slightly more anteriorly, resulting in slightly more bear-like proportions (the trigonid being very slightly shorter-proportioned, the paraconid-metaconid being thus less sectorial, the paraconid base fuller, the point of greatest indentation in the outer border more anterior, and the talonid being longer); (b) cusps of talonid rudimentary, the endoconid being much reduced (depicted too prominently as figured), versus well-developed in the former tooth, as it is in *Hemicyon*.

the cusplet anterior to the metaconid, the less-marked indentation of the outer margin, and the less reduction of the posterior inner border.

While *Ursavus primævus* cannot be considered to be related to the *Ursinæ*, the type and referred material have many characters in common with material referred to *Hemicyon* and to *Hyænarctos*:

The p^4 (Fig. 42) in its large size relative to the m^1, in its tall posteriorly directed paracone, anteroposteriorly elongated metacone, and anteromedianly placed and considerably developed deuterocone, agrees with the Hemicyoninæ.

The m^1 (Fig. 42) and referred larger m^1 (Fig. 45A) are of very similar construction to the m^1 of the greatly larger *Indarctos* (see Fig. 47A). The tooth is doubtfully *Helarctos*-like, differing in its greater relative transverse breadth, the wedge-like inner ridge, widely separated from the outer cusps, the definite metacone-hypocone cross crest, the diminutive but blade-like paracone and metacone, the prominence of the inner mid-border and antero-external tooth corner, the *Hemicyon*-like prominence of the post-cingulum cusplet, and considerable width of the trigon relative to the talon.

The m^2 (Figs. 43–44), heretofore figured as part of the type specimen (Fig. 42) as explained above, does not belong to the type. This m^2 very evidently represents a much larger-toothed individual, such as the large referred m^1 (Fig. 45A). Former figures of *U. primævus* have thus indicated an even greater degree of enlargement in the m^2 as compared to the p^4–m^1 than actually exists. Schlosser's figure (1887, as noted above) in the same way accentuates the proportions of both molars relative to p^4, in that in the same the relatively large molars of the Kieferstädtel specimen are illustrated with a p^4 of the smaller Voitsberg material. The m^2 (Fig. 44) in the British Museum collection is smaller though still large with reference to the p^4–m^1 of the type specimen. The larger of the two referred m^1s in the Lyon Museum would seem to be approximately proportionate to the m^2 formerly figured in with the type. I have figured along with these last two upper molars in outline the p^4 (Fig. 45B) of the type enlarged, so that the proportion between this hypothetical p^4 and the m^1 is identical with that existing in the type specimen. Though the m^2, when considered independently of the other teeth, in form considerably approximates that of *Helarctos*, it is seen to differ in detail in the angulation of the external cusps and the indentation of the mid-inner border. The tooth (excluding size) more resembles that of the much larger m^2 of *Indarctos* referred, in general proportions and cusp arrangement, prominence of the paraconid, and development of the talonid.

Ursavus depereti Schlosser, 1902

Figure 50A

Galeotherium Jäger, 1839, 'Über die fossile Säugethiere im Württemberg,' p. 71, Pl. x, Figs. 43–47. Lignites of Neuhausen m^1, left.

Ursavus depereti Schlosser, 1902, Geol. Pal. Abhandl., N. F., V, pt. 3, p. 35, Pl. II, Figs. 19, 20, 22, 23. Zittel, 1923, Grundzüge der Paläontologie, p. 471.

(?) *Hyænarctos arctoideus* Depéret, 1895 (Compte rendu heb. Acad. Sci. Paris, LXXI, p. 432), Schlosser, 1902.

Type.—m_1–m_2, left, from Melchingen, Tübingen Museum Coll. Figured by Schlosser, 1902, Pl. II, Figs. 19, 20, 22, 23.

TENTATIVELY REFERRED.—

m_1, fragment of talonid of left side, and

3d incisor and phalanx from Neuhausen; material on which Jäger in 1835 based *Galeotherium*.

and "a canine from Russberghof."

Schlosser notes that the m_1 is uncommonly like that of *U. primævus*, though the latter is rather smaller and its talonid has an indentation near the hypoconid which is lacking in this tooth; that the m_1 differs from *Ursus* in the extraordinarily strong metaconid which is set very far back, and in the shortness of the talonid and cusplets of its inner margin; that Jäger's m_1, apart from its small dimensions, corresponds with the Melchingen m_1; and that the m_2 differs from *Ursus* in the comparatively shorter talonid as well as the more posterior metaconid, which is higher than the other portions of the tooth. He states that he suspects *Hyænarctos arctoideus* Depéret, from Montredon, may be identical with the bear from Melchingen, since an *Hipparion* fauna also occurs in this locality. As remarked above, Schlosser considers *U. primævus* by all characters to be a direct ancestor of the Melchingen form.

The m_1 and m_2 are larger, but very similar, so far as may be judged by the figures, to *U. primævus*, and are typically hyænarctid.

Ursavus elmensis Stehlin, 1907

Ursavus elmensis STEHLIN, 1907, Verhandl. naturf. Gesell. Bâsel, 1917, XXVIII, pt. 2, p. 198, Figs. 5–7.

TYPE.—Left mandible with posterior root p_2, p_3–m_2, and alveolus m_3 from lignite mine of Elm. Figured by Stehlin, 1907, Fig. 5.

Referred m^1 (broken, outer cusps missing) of older individual than type; and c. Figured by Stehlin, 1907, Figs. 6 and 7.

CHARACTERS, AFTER STEHLIN'S DESCRIPTION:—

Much smaller than *U. primævus* Gaillard.

p_4, moderately large relative to m_1.

Lower molars with sharp cusps, enamel surface not wrinkled (probably an age character). m_1, blades tending to be sectorial, metaconid undivided, paraconid outer base slightly swollen; protoconid tending to be central; heel basin-shaped, with hypoconid and two inner cusps. m_2, heel set off from trigonid, short, and narrowed posteriorly as in *Hyænarctos*, versus *Ursus*.

m^1, fragment, referred, broad-proportioned transversely and short anteroposteriorly, anteroposterior diameter of lingual portion relative to anteroposterior diameter of m_1 being approximately 10% less than in *U. primævus*, and thereby suggesting the condition in *Hemicyon*. The alveolar edge, according to Stehlin, begins to rise into the vertical ramus at m_3, as in the Oppeln species.

Stehlin considers this form to be specifically distinct, but more nearly related to *Ursavus* than to *Hemicyon* and *Hyænarctos*.

(?) **Ursavus pawniensis**, new species

Figures 49 and 55B

In the summer of 1922[1] I had the fortune to discover lying in the wash of a small gully, within a restricted exposure of the Pawnee Creek Miocene, that outcrops to the northeast of the Pawnee Buttes, Colorado, the posterior portion of a mandible containing the last two molars. The close agreement in state of preservation between my find and the associated material of typical Miocene facies[2] seemed at the time to be contravened by the recent bear-like aspect of the two teeth as well as the fact that pre-Pleistocene bear was unrecorded in North America. A detailed study and comparison of the specimen, however, substantiates the presence of very unusual characters. These characters definitely distinguish it from the recent bear. The tooth characters themselves are suggestive to a most interesting degree of the European genus *Ursavus*, to which I here refer the specimen. For, as in the case of (?) *D. aurelianensis*, I prefer to temporarily refer the present unusual and fragmentary specimen as a new species to an already established genus, rather than to make the same the type of a new and perforce indefinitely characterized one.

The mid-Miocene beds of Pawnee Creek proper have been examined and extensively collected in years past by several expeditions from the American Museum of Natural History, the results of which have appeared in successive reports and memoirs of Osborn, Matthew, Gidley, and Granger.[3]

TYPE.—Posterior portion of left ramus with m_2-m_3 and remnant of the alveolus of m_1, from the Pawnee Creek Miocene, Tapir Hill, Pawnee Buttes, Northeast Colorado, Amer. Mus. No. 20801. Figured this paper, Figs. 49, and 55B.

CHARACTERS:—

The mandible is characterized by a peculiar heaviness of the external contour of the horizontal ramus throughout the area below m_3 (see ab, Fig. 55B), apparent considerable dorsoventral depth, and by a marked hollowing out of the anterosuperior corner of the masseteric fossa.

The teeth as seen in m_2-m_3 are moderate-sized, small relative to the weight of the mandible, the crowns low, cusps evidently reduced and confined to the periphery.

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[1]On the occasion of the visit to the Pawnee Buttes region, of Mrs. Childs Frick, Dr. W. D. Matthew, Mr. Harold Cook, and self, during the course of a brief reconnaissance of the Tertiary localities of western Nebraska and northeastern Colorado, a palæontologic tour kindly arranged by Professor Henry Fairfield Osborn.

[2]The same exposure has yielded in addition material representative of *Merychippus*, *Merycodus*, *Rhinoceros*, and *Tapirus*. The first intimation of the presence of the last was discovered by Dr. Matthew at the time of our visit, *Tapirus* being heretofore unreported from the Pawnee Creek (*loc. cit.*, Matthew, 1900).

[3]Matthew, 1907, Mem. Amer. Mus. Nat. Hist., I, Part 7.

Subsequent to my above discovery the particular restricted exposure was worked for several weeks by a party under Messrs. Markham and Figgins, Jr., through the coöperation of the authorities of the Colorado Museum, without, however, the location of further material referable to the new find.

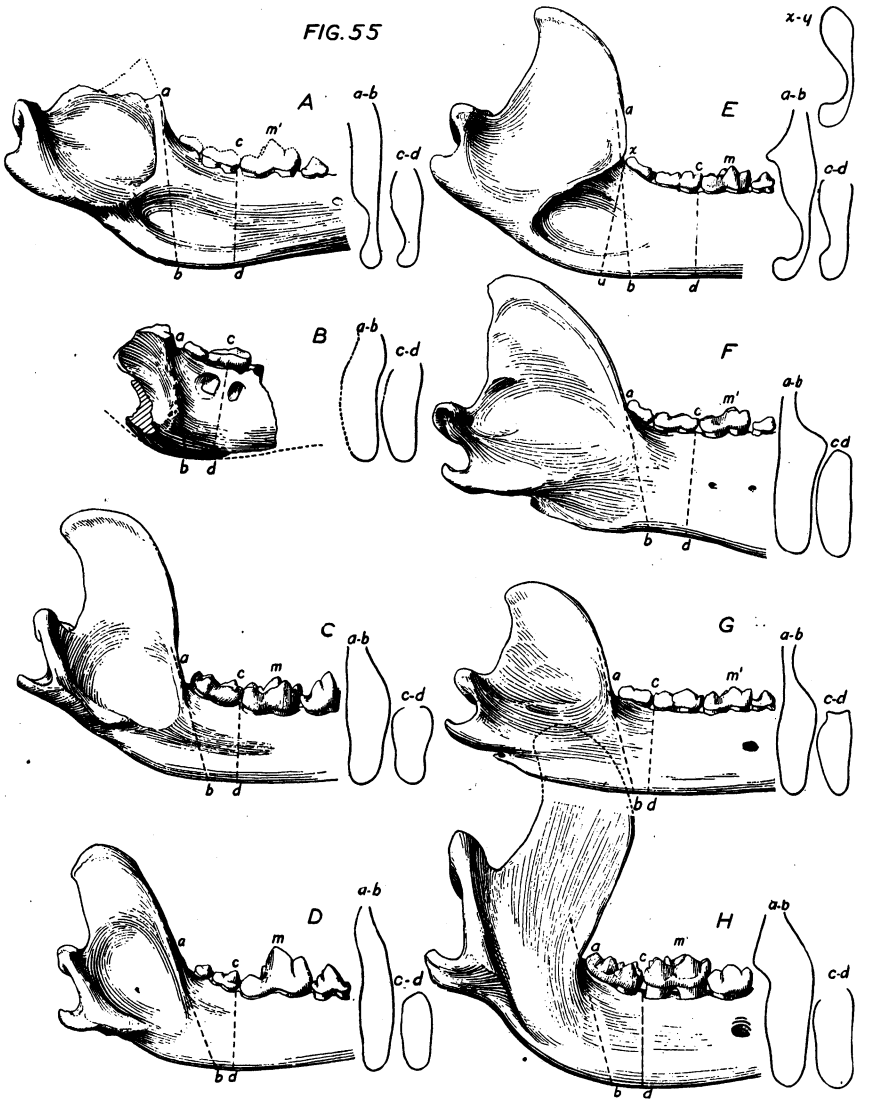


Fig. 55. Lateral views of the postero-external area of the mandible of:

A, *Hemicyon ursinus*, No. 21101, No. 20801; B, (?) *U. pawniensis;* C, *Procyon lotor;* D, *Canis latrans*; E, *Tremarctos ornatus;* F, *Helarctos malayanus;* G, *Ursus americanus;* H, *Ælurus fulgens.*

All drawings, except that of (?) *Ursavus pawniensis*, new species, which is of natural size, brought to approximately unit scale (the distance from incisive border to condyle being taken as unity). a, b, c, d, etc. cross-sections as shown.

m_2, elongate, antero-external corner of trigonid noticeably prominent and trigonid markedly broadened transversely; talonid narrowed, and of only moderate length; metaconid prominent and situated well posterior of the antero-inner corner (distance from posterior edge of post-metaconid accessory cusplet to anterior greater than to posterior border); the breadth of the anterior tooth border, and the prominence of the antero-external corner and of the metaconid afford sufficient indication of the considerable breadth and probable hemicyonid character of the talonid of m_1 and reduction of the lingual border of m^1. (In the bear the typical narrowness and the symmetry of the anterior end of m_2 are accompanied with marked narrowness of the heel of the weak m_1 and unreduced narrowness of anterior portion of m^1). The external postero-mid-base is slightly constricted opposite the junction of the anterior and posterior roots, is very slightly indented anterior to the hypoconid, and the border lying between these two indentations has been abraded by the action of the paracone of m^2. The anterior is much lighter than the posterior root. The inner border is indented anterior to the metaconid, this indentation appearing unduly prominent in the specimen through a slight fracture; the inner border is again slightly indented posterior to the diminutive post-metaconid accessory cusplet. (See cross-section, Fig. 55B).

m_3 is small relative to m_2 (see comparative schedule of percentages of m_2-m_3 in *Ursavus*, *Plionarctos*, *Ursus*, and *Tremarctos*, p. 110). The tooth is inserted within the base of the vertical ramus and is pitched slightly forward and inward with respect to m_2, all contrary to the bear, but similar to *Hyænarctos*. The outline of the occlusal surface tends to be circular save for a slight flattening of the outer side and slight narrowing of the postero-inner side.

DISCUSSION.—The teeth are considerably worn, the enamel of the outer line of the cusps of m_2 being cut through and the central and slightly concave triturating surfaces of both teeth being polished smooth. The aspect of the teeth suggests that in the unworn state the crowns were low, that the tubercles were generally confined to the periphery, and that the occlusal surface may have been "wrinkled" as in such other low-crowned forms as *Arctocyon*, the recent bear, certain mustelines, and *Ursavus*.

The fragmental condition of the mandible prevents a definite interpretation. The very unusual thickening of the lateral contour taking place over the area midway between the alveolar and (present) inferior borders, however, is highly suggestive of the swollen condition of the same area seen in Stehlin's figure of *U. elmensis*, in which this area is bounded inferiorly by the anterior masseteric depression, the same evidently representing but a slight modification of the *Hyænarctos-Hemicyon* adaptation. The comparative elevations and cross-sections shown on page 107 (Fig. 55A-H) and the following résumé illustrate the unusual character of this peculiar specimen and the impracticability of a direct reference of the same to any present known genus, such as *Ursus*, *Helarctos*, *Tremarctos*, or the new genus, *Plionarctos*.

The specimen differs from *Ursus* in the unusual heaviness of the external face, the apparent dorsoventral depth of the mandible inferior to m_3, the high position of the inner dental foramen, the form and relative proportions of m_2 and m_3 (the peripheral cusps being less elevated than in the grizzly or black bear), and in the small size of the teeth relative to the size of the mandible. The specimen, moreover, markedly differs from the bear in the m_2, in that the anterior is much broader than the posterior extremity, the antero-external corner being broadly produced; and again in the m_3 through its small size relative to m_2 (see table p. 110), and its position in the vertical ramus, and angulation in respect to m_2.

The specimen suggests *Helarctos* in the relative heaviness of the jaw and the tendency to roundness of m_3, but the teeth are much larger-proportioned (the m_2 being actually larger than that of any specimen of *Helarctos* in the American Museum collection); also the m_2 metacone lies definitely anterior to the protocone as in *Ursus* and the hemicyonids, versus its unusual posterior position in *Helarctos*.

The specimen is slightly more approached by *Tremarctos* in the deep hollowing-out of the anterosuperior corner of the main masseteric fossa, in the slightly more elevated and angulated position of the m_3 in relation to m_2, and in the greater anteroposterior length, and unnarrowed anterior border of m_2. The m_2 of *Tremarctos*, however, differs widely from that of the specimen in lacking the typical production of the antero-external border, and the reduction of the talonid and postero-external border; as does the m_3 in its elongation and the difference of proportion between it and the m_2.

The specimen definitely differs from the somewhat tremarctid-like *Plionarctos* m_2 in the production of the antero-external tooth border (which is non-produced and rounded in *Plionarctos*), and in the broadness of the trigonid in relation to the talonid (the crown being of nearly uniform width and longer-proportioned in *Plionarctos*), etc.

The specimen has the following characters in common with the Hemicyoninæ in the:

MANDIBLE.—The mid-external thickening at the produced base of vertical ramus, the deep hollowing out of the anterosuperior corner of the masseteric fossa, and the sculpturing of the inner face of the ramus posterior and inferior to m_3.

TEETH.—The location and angulated position of m_3 in the base of the ascending ramus; the prominence and breadth of the anterior border of m_2, which indicates a correspondingly broad talon in m_1; and the circular form of m_3, and its small size compared to m_2, as noted in comparison with Oppeln, Voitsberg, and Stehlin specimens of *Ursavus*.

The Pawnee Creek material nevertheless differs from typical *Ursavus* in the apparent absence of the premasseteric fossa, and in the greater elongation of the area posterior to the protoconid-metaconid of m_2. (The relative proportions of this area, however, have been noted to be extremely variable in *Hyænarctos*.)

ANTEROPOSTERIOR DIAMETER RELATIVE TO TRANSVERSE DIAMETER OF M_2; AND ANTEROPOSTERIOR DIAMETER OF M_2 RELATIVE TO THAT OF M_3 IN (?) *U. pawniensis*, *Ursavus*, AND PLIOCENE AND RECENT BEARS

	m_2 $\frac{\text{trans. diam.}}{\text{ant. post. diam.}}$		$\frac{\text{ant. post. diam. } m_3}{\text{ant. post. diam } m_2}$	
	mm.	%	mm.	%
Ursavus depereti	10.8 / 16.8	64		
Ursavus primævus	9.2 / 14	66		
Ursavus brevirhinus (Steiermark)	8 / 12	67	6.8 / 12	57
(?) *U. pawniensis*	11 / 16.5	67	10 / 16.5	61
Plionarctos edensis, new species	11 / 20.5	54		
Tremarctos ornatus, Amer. Mus. No. 35539	11.5 / 20	58	13.6 / 20	68
Helarctos malayanus, Amer. Mus. No. 16580	9 / 15.6	58	11 / 15.6	70
Ursus americanus Amer. Mus. No. 5044	11 / 18.5	60	14.5 / 18.5	78
Ursus species, from Red Crag	(12) / (20)	(60)		
Ursus böckhi Schlosser	11 / 18	61	14 / 18	78

AN AMERICAN TERTIARY BEAR

PLIONARCTOS, new genus

Figures 56–57 and 61–62

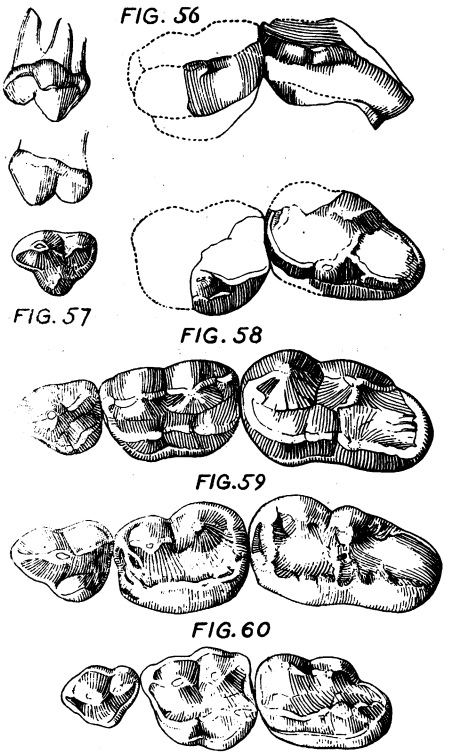
GENERAL DISCUSSION.—Recent work in the Eden Pliocene[1] of southern California has added largely to our previous collections and knowledge of that important phase of Pliocene life. Among the more interesting of the new material are four dental fragments, which, considered either individually or collectively, are bear-like and so generally approach *Tremarctos* that it is believed they represent a single Eden species. This material was secured by my indefatigable assistant, Mr. Joseph Rak. The contemporaneity of these specimens, blasted out of the heavily consolidated, though considerably faulted, deposit, with the Eden fauna, including *Hyænarctos*, is believed to be beyond question.

While the antiquity of the *megalocreodontic* canid type of dentition has been long and generally recognized, through the presence in collections from the Miocene and earlier periods of much dental material highly characteristic of recent *Canis*, the total absence from American collections of Miocene as even of Pliocene remains indicative of a *meionocreodontic* bear has long suggested that the bear must have been derived from some one of the more primitive canids via *Ursavus*, of the European Miocene, a form, as noted above, with somewhat bear-like molars, but large sectorial carnassials. In America itself this total absence from the formations of pre-Pleistocene age of ursid remains has been responsible for the generally held opinion that *Ursus* reached these shores only as a late European immigrant.

The Eden specimens are, therefore, not only of particular interest as representing the first intimation of the occurrence of a *meionocreodont* bear in the American Pliocene, but as supporting the long-doubted evidence of the parallel coexistence of a modern ursid and primitive *Hyænarctos* in the Pliocene deposits of Montpellier and of the Red Crag.[2] Our discovery thus tends to confirm the antiquity of the ursid tpye, and thereby to negate the possibility of the descent of recent *Ursus* from a Miocene *Ursavus*. The dentitions of the bear and of *Hyænarctos*, as discussed in the previous sections of this paper, are very highly specialized

[1]The Eden ledges were discovered by the writer in the winter of 1917, during the course of an investigation of the Badlands of San Timoteo Canyon and Bautista Creek, which were then supposed in entirety to represent accumulations of Pleistocene time. The investigation was undertaken in coöperation with Dr. John C. Merriam of the University of California, as a part of his broad and comprehensive plan for the study of the geologic and faunal history of the Pacific coast. The immediate results of the early field work at Eden have appeared in a publication of the University, 'Extinct Vertebrate Fauna of the Badlands of Bautista Creek and San Timoteo Canyon, Southern California,' Frick, C., 1921, Univ. Cal. Pub. Dept. Geol., XII, No. 5, pp. 335–424.

[2]The deposits of the Kangara district of the Indian Siwaliks, which are of supposed Pliocene age, and the Pontian of Baroth-Kopecz have likewise yielded specimens as noted below.



Figs. 56–57. *Plionarctos edensis*, new genus and species, from Eden Pliocene, California. Natural size.

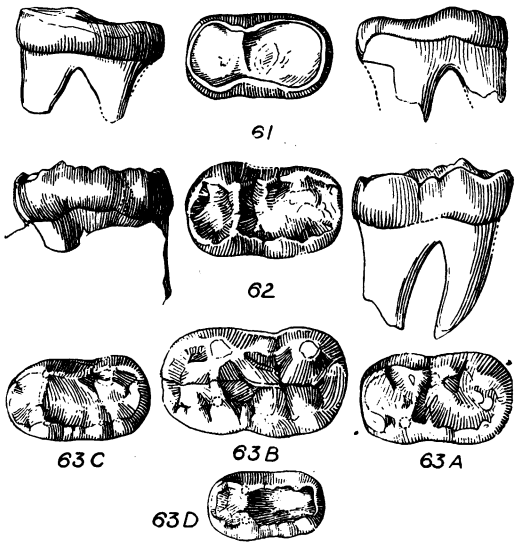
Fig. 56. m^1-m^2, left, of type specimen, Amer. Mus. Coll. No. 18115; inner and occlusal views.

Fig. 57. p^4, left, of cotype, Amer. Mus. Coll. No. 18117, inner, outer, and occlusal views.

Figs. 58-60. Comparison of p^4-m^2 of various species of recent bears. Natural size. 58. *Ursus kermodei*, from Gribbell Island, British Columbia. Amer. Mus. No. 34993; 59, *Tremarctos ornatus* (N. Y. Zool. Park specimen), Amer. Mus. No. 35539; 60, *Helarctos malayanus* (N. Y. Zool. Park specimen), Amer. Mus. No. 16580.

in contrary directions. Therefore, the evidence that points to the ancestry of Pliocene *Hyænarctos* lying in the Miocene near *Ursavus*, a type already highly developed in the direction of *Hyænarctos*, may be considered as emphatic proof that the ancestry of our Pliocene ursid was not represented in the Miocene by an ursavid form, but by a definitely *meionocreodontic* ursid. As noted above and as shown in the sequel, the early Eden bear in certain characters more resembles recent *Tremarctos*

than *Ursus* or *Helarctos;* the degree of similarity, however, must remain in doubt for lack of sufficient material. Whether the particular characters in which the specimen resembles *Tremarctos* and differs from *Ursus* may be merely primitive characters natural to an early bear form, and present in the Pleistocene arctotheres, and today surviving in *Tremarctos* but lost in the, in some ways, more specialized *Ursus,* or whether the ancestral lines of *Tremarctos* and the more tremarctid-like arctotheres were distinct since the pre-Miocene from the ancestral line of *Ursus,* may not be decided on the evidence now at hand.



Figs. 61–62. *Plionarctos edensis,* new genus and species, Eden Pliocene, California. Natural size.

Fig. 61. m_2, left, worn, Amer. Mus. No. 18116B; outer, occlusal, and inner views.

Fig. 62. m_2 right, slightly worn, Amer. Mus. No. 18115C.

Fig. 63. m_2s of recent bear, for comparison, occlusal views. Natural size. A, *Tremarctos,* Amer. Mus. No. 35539; B, *Ursus danis* (Colorado specimen), Amer. Mus. No. 24413; C, *Ursus americanus,* Amer. Mus. No. 5044; D, *Helarctos,* Amer. Mus. No. 28254.

The following paragraphs are devoted to the description of the new American evidence, and a summary of the European data, as to the existence of Tertiary *meionocreodontic* bear. The statement made by Owen in 1846 in regard to the history of the bear in Great Britain is believed to be as applicable to the past history, as it is perhaps prophetic of the future, of the bear in North America: "In conclusion, it may be

stated on the evidence at present acquired, that the period of the existence of the Ursine genus in this island has extended from the middle, or miocene tertiary formations, through the older and newer pliocene, and . . . has been continued . . . until the multiplication and advancement of the human race introduced a new cause of extermination, under the powerful influence of which the bear was finally swept away from the indigenous Fauna. . ."

Characters of *Plionarctos*, new genus

p^4, meionocreodontic, and

Upper molars and m_2 elongate, suggesting recent bear.

Teeth differing from recent bear in the anteroposterior shortness of m^1 in relation to m_2, and the shortness of the talon of m^2.

Plionarctos edensis, new species

Figures 56, 57, 61, 62

(For comparison, Figures 54, 58–60)

TYPE.—Fragment left maxilla with m^2 and a portion of m^1, from Eden Lower Pliocene, California, Amer. Mus. No. 18115, Figure 56.

REFERRED MATERIAL.—Collected with the type by Mr. Joseph Rak at the type locality.

p^4, left, Amer. Mus. No. 18117, Fig. 57.

m_2, left, Amer. Mus. No. 18115B, Fig. 61.

m_2, right, Amer. Mus. No. 18115C, Fig. 62.

CHARACTERS.—General ursid aspect of teeth.

Molars, the reduction and confinement of the main cusps to the periphery, the minute multituberculate character of the unworn occlusal surface, and the particular proportions of the teeth relative to one another.

m^2, talon considerably developed and deflected.

m_2, elongate, the anterior and the posterior extremities of subequal breadth.

p^4, small size relative to m^1, deuterocone at base of paracone and supported on separate or at least partially separate root.

The specimens differ from the recent bear mainly, as noted above, in the anteroposterior shortness of the m^1 in relation to m_2, and the shortness of the talon of m^2.

DESCRIPTION.—The type (Amer. Mus. No. 18115, Fig. 56) specimen exhibits a fragment of the left jugal and maxilla, including portions of the alveolar border and of m^1 and m^2. The anterior half of the crown of m^1 is missing, as is a section of the anterior external wall of m^2. The crowns of the teeth are very moderately worn, abrasion having removed only the more minute of the accessory tubercles that crowd the occlusal surface. In the characteristically-produced and deflected heel of m^2 (reaching posteriorly of the zygomatic root), the lowness of the tooth crowns, the general arrangement and reduction of the cusps, and the elongate proportions of m^1 and m^2, the specimen approaches the modern bear. The teeth are somewhat smaller

than those of an average-sized specimen of *Ursus americanus*, though the skull fragment suggests a skull of relatively stouter proportions.

m^1 (Fig. 56) is considerably broken; the general former outline of the crown is indicated by the tooth base. The form of the tooth was apparently more like *Tremarctos* than *Ursus*, except for the accessory conule of the mid-inner border, which is more as in *Ursus* than in *Tremarctos* (where the inner cusps are low and more or less fused into a single ridge).

m^2 (Fig. 56), save for the missing antero-external corner, is very well preserved. The protocone, as apparently the parastyle and paracone, were but moderately elevated. The inner tooth border is divided into two subequal portions by a slight constriction posterior to the accessory mid-conule. The metacone lies directly opposite to this constriction, as is usual in the bears. The heel is moderately well developed, and is considerably depressed or deflected outwardly and dorsally. The low inner cones (as noted in the case of m^1) are less fused than in *Tremarctos*, where the mid-accessory cusp as such is invisible; this cusp is variably developed in *Ursus*. In m_2, as apparently also in the m^1, the line of the inner cusps lies near the inner tooth border and the inner cingula are but slightly developed, as is usual in *Ursus americanus*. In *Tremarctos* the inner cingula are absent, in *Helarctos* they are characteristically developed, and the line of the fused inner cusps lies well inward of the inner tooth border.

p^4, referred (Amer. Mus. No. 18117, Fig. 57), is well preserved, and is but very slightly worn. While it is small in size relative to m^1-m^2 of the type specimen, it is not unusually small when compared to the smaller (Fig. 61) of the two m^2s from the same horizon (see below). The paracone and metacone are cusp-like (versus blade-like), the metacone being very small, and the paracone only moderately developed. The deuterocone is well proportioned and placed medianly to anteromedianly opposite the junction of the paracone and metacone, resulting in a concavity of the postero-inner border (versus the usual convexity occurring in recent *Ursus* and *Tremarctos*, through the more posterior position of the deuterocone). The deuterocone root was evidently separate, or partially distinct, and not as fused with the main posterior root as in the recent bears.

m_2, left, referred (Amer. Mus. No. 18115B, Fig. 61), is much worn, the parastylid and protoconid alone remaining of the original tooth pattern.

m_2, right, referred (Amer. Mus. No. 18115C, Fig. 62), held in a fragment of the mandible, is noticeably larger than the above (individual variation). The specimen is newly erupted, and the unabraded surface indicates the minute multituberculate character of the unworn teeth of the Eden form (versus the general smoothness of the crown of aged teeth, as shown in the worn specimen). The crown is rectilinear in shape, very elongate, practically as broad posteriorly as anteriorly, and but very slightly rounded at the corners; the main cusps are less well-developed than in the average specimen of *Ursus americanus*, and not nearly as prominently developed as in the Alaskan brown or the American grizzly bears. The metaconid is higher than the protoconid and lies opposite to slightly anterior to the protoconid as in *Tremarctos* and *Ursus*. The general form of the tooth, the fullness of the trigonid, the lowness of the main cusps, the presence of the typical accessory cusplet on the mid-external border, and the strongly multituberculate character of the occlusal surface suggest *Tremarctos* rather than *Ursus*.

The Eden specimens differ from modern *Ursus* in relative proportions (see table) and in a certain lack of specialization in:

The upper molars, the considerable relative length of m^1 compared to m^2, associated with lack of extreme development of the heel of m^2.

The p^4 referred, the median versus median posterior position of the deuterocone, and the presence of a separate (or at least partially separate) inner root, etc.

The m_2 referred, the anterior border, tending to be slightly broader than the posterior, the anterior edge higher, the cusps slightly less prominent, and the mid-external border less indented, and furnished with a prominent accessory cusplet as in *Tremarctos*.

The specimen differs even more from *Helarctos*:

In the upper molars of *Helarctos*, the fusion of the inner cusps is even more prominent than in *Tremarctos*; the fused line of the cusps lies well within the strong cingulum of the inner tooth border.

In still further contradistinction, the m_1 is shorter and narrower-proportioned, and the metaconid lies slightly posterior to the protoconid versus more anterior as in the specimen and in *Ursus* and *Tremarctos*.

The specimens more nearly approach *Tremarctos* than either of the two above genera in:

The general apparent slight elevation and development of the main cusps of the type and of the referred material, more particularly the apparent lowness of the main external cusps of the upper molars.

The relative size of m^1 and m^2, m^1 apparently approaching m^2 in anteroposterior diameter. In *Tremarctos* m^2 is relatively longer than m^1, though the talon is here but moderately developed. In *Ursus* the m^2 talon may be greatly extended.

Anteroposterior length of the trigon and talon of m^2 is approximately equal, versus in *Tremarctos*, where there is a tendency, as to some extent in *Helarctos*, for the talon of m^2 to be but little longer than the trigon, though in the latter the trigon may actually considerably exceed the talon. In *Ursus* the talon may equal or greatly exceed the trigon in length.

p^4, referred, the more median position of the deuterocone is approached in *Tremarctos* (and to some degree in *Helarctos*), versus always more posterior in *Ursus*. The deuterocone root is separate to partially separate, as is the case in *Arctotherium haplodon*, versus fused to main posterior root in *Tremarctos* and *Ursus*.

The development of the typical accessory cusp of the mid-external border, and prominence of the anterior border of m_2 approaches the condition in *Tremarctos*. In the grizzly bear there may be a slight tendency to development of such an accessory cusp.

(?) **Ursus minutus** Gervais

Figure 52

(?) *Ursus minutus* Gervais, 1848–1852, Zoologie et Paléontologie français, p. 7; 1853, Annales Sci. Nat., Ser. 3, XVI, p. 152; 1859, Zoologie et Paléontologie français, p. 206, Pl. viii, Figs. 1 and 1A; 1865–67, Mem. Acad. Sci. Montpellier, p. 142. Lydekker, 1883, Pal. Indica, Ser. 10, II, pp. 208 and 209. Osborn, 1910, 'Age of Mammals,' p. 315.

Type.—m_3, from Montpellier, Jeanjeau collector. Figured by Gervais, 1859, Pl. viii, Fig. 1. This paper, Fig. 52.

Characters.—Tendency towards circular outline, low crown, raised periphery,

wrinkled occlusal surface, single root, slight prominence of antero-external edge, slight indentation of mid-external border, and restriction of postero-external border.

DISCUSSION.—Gervais (1852) describes the specimen as representing a new species of *Ursus*, *U. minutus*. Gervais (1859) remarks that a last lower molar, which he figures (Pl. VIII, fig. 1), seems to indicate that there was present in the Pliocene deposits a species of bear differing from, but resembling, *Ursus ornatus* and *Helarctos malayanus*, and of approximately the same size as the latter; but that the presence of *Hyænarctos*, of which the lower dentition is not well known, in the same deposits makes the determination doubtful.

The tooth crown (Fig. 52) is apparently quite different from that of *Hyænarctos*, *Hemicyon*, or *Ursavus* (compare Fig. 50C), more resembling that of the recent bear, particularly *Helarctos* (Fig. 54C), in which occasionally the m_3 is even more circular in outline (see Amer. Mus. specimens).

(?) Ursus species, Owen and Newton, from Red Crag

Ursus species, OWEN, 1846, 'A History of British Fossil Mammals,' p. 105; 1856, Quart. Journ. Geol. Soc., XII, p. 227.

Ursus arvernensis (?) NEWTON, E. T., 1891, 'The Vertebrata of the Pliocene Deposits of Britain,' (Pal.) Mem. Geol. Surv. United Kingdom, p. 15, Pl. I, Figs. 12A and B. Woodward, 1898, Vert. Pal., p. 395.

TYPE.—m_2, left, from Newbourn, Red Crag (Woodbridge), Reed Coll. York Mus. Figured by Newton, 1891, Figs. 12A and B.

CHARACTERS.—Specimen as roughly figured by Newton is very typical of the m_2 of the recent bear.

HORIZON.—Red Crag or derived from the earlier Coralline Crag deposits.

DISCUSSION.—Owen (1846) states, "The ursine genus is represented by an ante-penultimate grinder of the right side, upper jaw, of a Bear, somewhat smaller than the corresponding tooth of *Ursus spelæus*."

Newton says of the specimen that he figures that the upper surface is unworn, the tubercles and wrinkles are not strongly marked, and that the fangs are much broken. He notes that this specimen, so far as he is aware, is the only one which can be taken as possible evidence for the occurrence of *U. arvernensis* in the English crags, or, indeed, in England, and this does not seem to him to be altogether free from doubt. Newton is unable to positively identify the tooth spoken of by Owen in the Moor Collection. He considers the only bear-like tooth in that collection to have more resemblance to *Sus*, and possibly that it may represent *S. palæochærus*. He lists the former specimen under *U. arvernensis*, the same species to which Lydekker (1864) referred a slender canine tooth of rough texture from the Red Crag of Newbourn (which Dawkins considered might prove to represent *Squalodon*).

Ursus theobaldi Lydekker, 1883

Ursus species, LYDEKKER, Rec. Geol. Surv. India, IX, p. 104.

Ursus theobaldi LYDEKKER, 1883, Pal. Indica, p. 211.

TYPE.—Cranium with roots of teeth, collected by Theobald in Kangara Siwaliks, 1875. Figured by Lydekker, 1883, Pl. XXVIII, Figs. 1 and 2. "Uppermost Pliocene."

CHARACTERS ACCORDING TO LYDEKKER.—Palate deflected upward in the vicinity of canines, and hinder border extended far behind m^2 (m^2 not extending posterior to root of zygoma as in all other bears), much as in *Melursus labiatus*, but palate more deeply concave posteriorly than in latter. Lydekker believed that the fossil must have been on the direct line of ancestry of *U. labiatus*.

(?) **Ursus böckhi** Schlosser, 1900

Figure 53

Ursus böckhi SCHLOSSER, 1900, Mittheil. Jahrb. K. Ungarn. Geol. Anstalt, XIII, p. 23, Pl. XII, Figs. 4–6; 1902, Geol. Pal. Abhandl., N. F., IX, pt. 3, p. 36. PILGRIM, 1913, Rec. Geol. Surv. India, XLIII, p. 290; 1914, Rec. Geol. Surv. India, XLIV, p. 231.

TYPE.—Mandible with p_4-m_3, from the Pontian of Baroth-Köpecz. Figured by Schlosser, 1900, Pl. XII, Figs. 4–6 (Pl. XII, Figs. 3, 7, 8, referred canine); this paper, Fig. 53, from Brit. Mus. cast No. 10592.

CHARACTERS:—

m_1, the slender proportions, weak middle region, and narrowness of the heel.

m_2, the noticeable narrowness of the anterior in relation to the posterior extremity and the great relative length of the talonid.

m_3, the large size.

DISCUSSION.—The specimen definitely differs in the presence of the above characters from *Hyænarctos*, *Hemicyon*, and *Ursavus*, and in the same way resembles the recent bear. The manner in which m_1 slightly exceeds m_2 in length, together with there being some indication of a premasseteric fossa in the mandible (as seen in cast), at least suggests that the represented form may have been more tremarctid than ursid-like (see comparative Figs. 54A-C). The South American bear, as well as the arctothere, however, have been unrecognized as yet in European deposits, and the characters may be only primitive.

Schlosser (1902) considers the species to lie midway between *Ursavus* (more particularly *U. primævus*) and *Ursus etruscus*. He holds that the latter is the ancestor of *U. arctus* and *U. spelæus*, that *U. americanus*, *Thalassarctos*, *Tremarctos*, and the still more different *Helarctos* and *Melursus*, had independent ancestors (the latter being derived from *U. theobaldi* Lydekker). He notes that the specimen has advanced in regard to the size and construction of its teeth to almost the true ursid condition.

Tertiary and Recent Bears and Oppeln *Ursavus*

COMPARATIVE MEASUREMENTS OF TEETH

	p^4	m^1	m^2	m_2	m_3	$\frac{m^2}{m_2}$ %	$\frac{m^1}{m^2}$ %
**Plionarctos edensis*, new species (p^4 and m_2 not associated)	10.7×7.5	(18)	21.8×(13.5)	19 ×11.5(lt.) 20.5×11.6(rt.)		(106–115)	82
U. böckhi Schlosser		(m_1)20.5×10		18 ×11	14 ×10.8		
U. species from Red Crag				20 ×12			
U. minutus Gervais					13.4×10.8		
Tremarctos, Amer. Mus. No. 35539	13.5	17.6×13.3	25 ×13.2	20 ×11.5	14 ×11	125	70
Tremarctos, Nat. Mus. No. 194,309	12 × 8.3	16 ×12.5	21 ×12.5	17 ×10	11.5× 9	124	76
Helarctos, Amer. Mus. No. 28254	9.5× 7	14 ×11.5	19 ×12	14.5× 8.5	10.3× 8.3	131	74
Helarctos, Amer. Mus. No. 35364	10.5× 9.5	15.5×14	20.5×13.6	16 ×10.5		128	75
Ursus perniger, Amer. Mus. No. 17794	11 × 8	16 ×12.5	24 ×14	18 ×11	14 ×11	133	67
U. danis, Amer. Mus. No. 24413	16 ×12.5	22.5×16.5	38 ×18	24 ×14.5	20.5×14.5	137	68
U. americanus, Amer. Mus. No. 41330	10.5× 7	17 ×11.5	22 ×12.5	16.5× 9.5	13.6×10	133	77
**U. brevirhinus* from Oppeln	14.4×10	14 ×12.2	15.6×12	13.8× 9.3			92

***Upper teeth not associated with lower.**

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