ART. XLIX.—The Extinct Felidæ of North America; by GEO. I. ADAMS, Fellow of Princeton College. (With Plates X, XI, XII.)

THE following paper is a result of studies by the author in the Department of Palæontology of Princeton. It is an attempt to summarize the literature on the extinct Felidæ, to add such new points of knowledge as it has been possible to discover and to propose a classification for the family. I wish here to express my thanks for privileges of study kindly extended by Prof. H. F. Osborn and Dr. J. L. Wortman of the American Museum, to Prof. Cope for suggestions and use of material, and to Mr. Dixon and Dr. Nolan of the Philadelphia Academy for assistance in examining specimens and literature in that institution. I wish also to acknowledge my special indebtedness to Prof. W. B. Scott, whose valuable criticism and kindly interest have been an inspiration to me in my work, and to Mr. J. B. Hatcher, from whom I have received much information and assistance. The illustrations are by Mr. Rudolph Weber and their excellence is due to his care and skill.

## Osteology of Hoplophoneus Primævus.

Hoplophoneus primævus is at present known from a short description of the type skull by Leidy (Geol. Sur. Wis., Iowa, Minn. and Neb. 1852), and later from a description of a specimen nearly agreeing with the type along with a second larger skull which belongs to a different species (Extinct Fauna of Dak. and Neb.) A restoration and brief description has been published by Scott (Bull. Mus. Comp. Zoology, Harvard, 1887). The material here described consists of a nearly complete skeleton, which is well preserved (No. 10741, Princeton Collection) and a skull somewhat crushed (No. 11013). In addition there is in the same collection a skeleton (No. 10934) not very complete but having associated with it the anterior and posterior portions of the skull which agree very closely with the above mentioned specimen and is supplemented by another lacking the occiput (No. 10540.) This latter specimen is slightly smaller but is a young skull just losing the deciduous canines. The principal material is that which was referred by the writer to H. primævus in the American Naturalist for January, '96, and corresponds with the original type.

This species of *Hoplophoneus* is of special interest inasmuch as it agrees very closely in size with *Dinicitis felina*, the osteology of which is known from the description by Dr.

Scott (Proc. Phila. Acad., 1889). In describing it I shall make comparisons with the lynx (Lynx canadensis) and occasionally with the lion, since the bones of the lynx, although they are nearly the same size, do not express the feline characters so well as do those of the lion. I shall not attempt to quote from previous descriptions or give minute descriptions where the characters agree with those of recent felines. The osteology is illustrated by Plate X.

In general Hoplophoneus primævus is comparable in size with the lynx, although having a longer head, the distal portions of the limbs relatively much shorter and the tail long.

The skull.—The skull is one fourth longer from the condyles to the premaxillary border than that of the lynx. This is due to a greater proportionate length of the face and palate. In H. primævus the distance from the condyles to the line of the upper molars is nearly the same as from that line to the premaxillary border. While in the lynx the first measurement is about the same as that of H. primævus, the latter is only about one-half as great. The brain case is not quite so large as that of the lynx and the post-orbital constriction is much more marked. The face is not only proportionately longer but wider, the width at the canines being as great as the width of the brain case at the parieto-temporal suture. The zygomata are expanded about as much as in the lynx in proportion to the length of the skull, but the space enclosed is proportionately longer and much wider because of the constriction of the brain case and the smaller size of the orbit. The orbit is considerably smaller than that of the lynx and is horizontally oval. The post orbital processes of the frontals and malar are short and rather stout.

The face is strongly arched transversely; seen from the side the angle it makes with the posterior portion of the skull is about the same as in the panther or lion, but it is straighter

and the frontal region not so full.

The bones of the skull are much thicker than those of the lynx and the processes and borders much more massive. is seen in the inion and post-tympanic process. The latter is trihedral and truncated distally. It is directed slightly towards the post-glenoid as if tending to approach it. The zygomatic process is strong and drooping with its glenoid portion looking slightly inward. The lambdoidal and sagittal crests are rather high and thick. The fronto-temporal ridges diverge at the fronto-parietal suture.

The sutures of the skull are very similar to those of recent The nasal processes of the frontals do not extend so far anteriorly, being separated by a considerable space from the ascending rami of the premaxillaries. The nasals are long

and inserted well into the anterior border of the frontals, their posterior borders being broadly rounded. The bullæ are seldom preserved, but judging from a cast of one they are

moderately expanded.

The foramina of the skull present peculiarly primitive characters, as has already been recognized. The condylar and carotid are distinct from the foramen lacerum posterius. There is a post glenoid foramen. The foramen ovale enters the outer end of a deep transverse groove situated in the base of the zygomatic process. There is an ali-sphenoid canal, the posterior opening of which is in the inner portion of the above mentioned groove and its anterior opening is just back of the anterior lacerated foramen. The opening of the foramen rotundum is concealed within the alisphenoid canal. optic foramen is in the same relation to the anterior lacerated as in the cats. There is also an ethmoidal foramen present. The palatal foramina need no special description. There is a post-parietal foramen and sometimes two. The infra-orbital is

large and vertically oval.

The mandible.—The mandible is quite characteristic of the Machærodonts. Its anterior portion consists of two vertical nearly plane surfaces meeting at a wide angle at the symphysis. The lateral face of the mandible is separated from the anterior by nearly a right angle marked by a distinct ridge, posterior to which is a shallow fossa for the superior canine. At this place the lower border of the mandible is produced into a moderate flange on the surface of which the fossa is continued. The symphysis is lower than the ramus and abuts against the flange on its inner side. The ramus is long and quite straight, being heaviest at the sectorial. The condyle is on a line with the alveolar border and is semi-conical. The coronoid is small and evenly rounded. The masseteric fossa is deep, the angle being well out from the plane of the coronoid. The dental and mental foramina are as in the modern cats. On the anterior or symphysial surface there are two foramina on either ramus.

Dentition.—There are three stout subconical incisors which are slightly recurved and are placed in nearly a semicircle. Their posterior surface, which is a little over one-third the circumference of the tooth, is slightly flattened and separated from the anterior by a sharp line which is slightly denticulate in an unworn tooth. They increase in size outward, the external being largest. The superior canines are long, compressed and slightly recurved. They are implanted by a strong fang which reaches well up to the frontal bone. Their anterior and posterior cutting borders are denticulate. When the mouth is closed the canines rest in the fossæ of the mandible, extending nearly as low as the flange. There is a small space

anterior to the canine and one about twice as great posterior to There are three superior premolars; the anterior one (p<sup>2</sup>) is considerably the smallest and may lack distinct anterior and posterior cusps. The second (p³) is well developed but may not have a distinct anterior cusp. The third (p4) is the sectorial. This tooth is different from that of the lynx or lion in not possessing an internal cusp; the inner root, however, supports a convex buttress which descends from the principal cusp. There is also an anterior basal cusp which is rather incipient and situated high on the principal cusp. The posterior cusp is a long cutting heel. The upper molar is rather better developed than in the modern cats and is inserted as in the lion by two roots in a transverse line. The incisors of the lower jaw along with the canines form a regularly curved series, the canines being not much larger than the external incisors. The internal incisors are much compressed and in some specimens are hardly more than rudiments. They are slightly divergent and have the same general structure as the The canine is curved slightly backward and has upper ones. a rather stronger posterior border. Its greatest diameter is nearly in an antero-posterior line. It is also denticulate when unworn, but the border soon becomes smooth. Back of the canine there is a diastema about twice as great as in the upper There are two well developed premolars, the anterior being, however, considerably the smaller. The inferior molar is a sectorial and differs from that of the modern cats in having a low heel and a somewhat variable postero-internal cusp. The teeth of the molar series differ from those of the modern cats in being more compressed and in having sharper borders which when unworn are feebly crenulated.

The vertebræ.—There are sixteen presacral vertebræ of one specimen, all of which are considerably mutilated so that it is possible to judge only of the relative size and length of the centra. They indicate a much stronger vertebral column than that of the lynx and one which is proportionately shorter in the lumbar region. Five lumbar vertebræ measure considerably less than any five of same region of the lynx. On the other hand, the cervicals are longer than those of the lynx and the axis particularly so. The thoracic vertebræ are, as near as can be judged from comparison with those at hand, a little longer and, proportionately to the other vertebræ, also more massive. From what I know of other representatives of the genus I think it safe to say that the processes were stout and well developed. The sacrum, as would be expected, is heavier and wider than that of the lynx and its centrum is not so much depressed. The caudals are not preserved in the specimens of this species, but from the other species it is evident that the tail was long like that of the recent cats.

The pelvis.—I have only fragments of the pelvis, but they give an idea of its relative size and strength. The acetabulum is one-fifth greater in diameter than that of the lynx. As a whole the pelvis is more massive and considerably longer. At the sciatic notch, however, the ischium has about the same diameter as that of the lynx.

The scapula.—The distal portion of the scapula is considerably larger than in the lynx, the glenoid cavity being about one-fifth larger. There is a short stout coracoid much the same as in the modern cats. No other features are pre-

served in the specimens which are at hand.

The fore-limb.—The humerus of H. primævus is the same length as that of the lynx, but fully one-half more massive. The head presents a large articular surface which is very similar in shape to that of the cats. The great tuberosity is particularly prominent and rises considerably above the head and is well set off from it. The smaller tuberosity is low but rugose and the bicipital groove quite broad. The prominent character of the bone is the bold deltoid ridge which has a straight sharp border on the internal side extending to the

great tuberosity.

On the outer side, the lower portion has a similar border which runs slightly divergent from the inner border, but farther up curves toward the smaller tuberosity and becomes a mere line on the convex surface. The prominence of the deltoid ridge makes the antero-posterior diameter of the humerus at its middle portion twice as great as the lateral diameter, a feature which is not met with in the Felidæ even in the lion. Below the deltoid ridge the anterior surface retreats rapidly as it descends, becoming an even convex surface. The supinator ridge is also very bold and is in fact a thin prominent border as far up as the lower portion of the deltoid ridge. Above it, extending in the same line but not connected with it, is a line for muscular attachment, extending to the base of the head. The ent-epi-condylar foramen is large and formed by a free arch, being but slightly depressed into the body of the bone. The trochlea is very similar to that of the lynx but slightly The anconeal fossa is deep and large, but not more oblique. perforated.

The ulna is practically of the same length as the humerus. Its olecranon is proportionately much longer than in the lynx and lion, being one-fifth the entire length, while in the lynx it is not quite one-eighth, and in the lion a little over one-seventh. The sigmoid cavity is long and defined much as in the cats. Except as to proportions, the ulna presents no especial pecu-

liarities.

The radius is three-fourths the length of the humerus and is a short bone compared with that of the modern cats. Its head presents a distinct notch on the dorsal margin. The bone has sharp lines and the lower portion is quite rugose. The styloid portion is heavy and the process short. The scapho-lunar articular surface is rather smaller than would be expected.

The manus.—The manus is particularly short and the digits divergent. The scapho-lunar, although not much different from that of the lynx in general structure, is wider and has a better developed tubercle. The line of union of its two elements is visible on its distal surface in the facet for the mag-The pyramidal is very seldom preserved with a specimen, but is fortunately retained in this case. It presents a concave surface for articulation with the unciform. On its external surface are two facets, the proximal for the pisiform and the other for the styloid process of the ulna. It also articulates slightly with the fifth metacarpal. The pisiform is well developed, articulating as in the Felidæ with the pyramidal and ulna. The unciform and magnum need no special description. In the specimen which I have the trapezium and trapezoid are absent. They are present in specimens of Hoplophoneus insolens. The trapezoid in them nearly excludes the second metacarpal from lateral contact with the magnum. In the specimen which I am describing the relation of the metacarpals is such as to indicate the same position. In this respect the carpus differs from that of the modern cats, in the lion the articulation being very large. The metacarpals are surprisingly short, being only about two-thirds as long as those of the lynx. The first metacarpal is about as much reduced as in the lynx or lion. The phalanges are large and the unguals have well developed hoods which are usually preserved.

The hind-limb.—The femur is the same in length as that of the lynx, but of course much heavier, and its extremities are rather larger in proportion to the strength of the shaft. The head is presented slightly more inward and forward. It presents about the same relative articular surface as the lynx and has a deep pit for the round ligament. The great trochanter is separated from the head by a more distinct notch, which is deepest at the neck. The digital fossa is deep and the posterior border of the great trochanter is reflected over it fully as much as in the lynx. The second trochanter is very prominent and its position is quite different from what it is in the modern cats. It is relatively farther below the head and not as much removed from the inner border of the femur. When the bone is viewed directly from in front a considerable portion of it is seen, while in the recent cats it is concealed by the shaft. The femur also differs from that of the recent cats in having a

distinct third trochanter which is connected above by a ridge with the great trochanter and is continuous below with the linea aspera externa. The shaft is more rugose than in the lynx and is not quite as straight. The patellar surface is broad

and shallow and the condyles large.

The tibia is absolutely and relatively shorter than in the lynx, being not quite four-fifths as long as the femur, while in the lynx they are of the same length. In the lion the tibia is five-sixths the length of the femur. The condylar surfaces are large and are separated only by a low spine. The shaft of the tibia is compressed laterally and the enemial crest is high. The anterior tuberosity is rather far from the condyles. The distal portion is quite different from that of the lynx or lion, inasmuch as the articular surface is very oblique and the astragalar groove only slightly indicated. The malleolus is heavy and straight. A distinct ridge rises on its anterior surface and extends a short distance up the shaft.

The fibula needs no special description. It is quite stout and has sharp lines for muscular attachment and is free the whole length of the shaft. Its distal end presents a large

articular surface for the calcaneum.

The pes.—The calcaneum is slightly shorter than that of the lynx owing to its tubercle being not quite so long. The sustentacular portion is situated rather farther distally and the facet is presented more nearly upward. There is no facet to support the head of the astragalus as in the lynx. This last mentioned bone extends much farther distally than in the lynx although the neck is not proportionately longer. The astragalus of *Hoplophoneus* is larger, particularly the body portion. Its trochlear surface is only slightly grooved and its outer border very oblique. It is in these two respects very primitive. The cuboid is somewhat larger than that of the lynx, while the navicular is considerably wider and the tubercle not so much reflected upon the head of the astragalus. Its distal surface presents three distinct facets for the cuneiforms. In these bones the relationship as regards the articulation with the metatarsals is similar to that of the trapezoid and magnum in the manus, the second metatarsal being nearly excluded from any lateral articulation with the ectocuneiform. In the modern cats this wedging in of the second metatarsal is a very great element of strength. The ento-cuneiform is not so much reduced as in the lynx since the first metatarsal is not so rudimental. The length of the metatarsals is proportionately even shorter than the metacarpals, being only four-sevenths as long as those of the lynx. The first digit is not much reduced and carries an ungual.

### Summary.

H. primævus differs from the recent Felidæ and the lynx in particular, in the following points:

The skull is Machærodont, is large in proportion to the body

and long anteriorly.

The brain case is relatively much less expanded and the post orbital constriction is very marked.

The mandible has a distinct vertical anterior face and a

moderate flange.

The post-tympanic is large, sub-cylindrical and shows a tendency to approach the post-glenoid process. The zygomatic processes are drooping.

There are distinct carotid, condyloid, post-glenoid and post-

parietal foramina and an alisphenoid canal.

The dentition is  $I_3^2C_1^4Pm_2^{\frac{1}{2}}M_1^4$ . The superior canine is very long, recurved, compressed and when the mouth is closed extends nearly as low as the flange of the mandible, resting in a slight fossa. The superior sectorial has an anterior basal cusp but no internal, the internal root supporting instead a convex buttress which descends from the principal cusp. The inferior sectorial has a small postero-internal cusp and a low heel. The incisors are subconical and slightly divergent. The inferior canine is not much larger than the external incisor. All the teeth when unworn are denticulated or feebly crenulated and the superior canines are permanently so.

The skeleton is about the size of the lynx but more massive as in the lion. The cervical region is rather long and the lumbar short as compared with the lynx. The tail is long as in

the lion.

The humerus has a strong massive deltoid ridge, the femur a third trochanter.

The ulna and radius and the tibia are proportionately much

shorter than in the recent Felidæ.

The pes and manus are very short and broad. The astragalus is only slightly grooved and its tibial surface is oblique. The scapho-lunar shows the line of union of its two elements. The second metacarpal is nearly excluded from lateral articulation with the magnum and the second metatarsal from lateral articulation with the ecto-cuneiform.

The unguals have heavy hoods and were retractile. The position of the feet was as in the modern cats.

# A comparison with Dinictis felina.

The osteology of this species of *Dinictis*, as has already been stated, has been described by Scott. In addition to the material

which was known at that time, the Princeton Museum contains besides duplicate portions of the skeleton, a humerus and a few bones of the carpus. These need no special description for my purpose here. The genus Dinictis stands ancestral to the genus Hoplophoneus and the species felina agreeing so closely in size with H. primævus makes a comparison very interesting. I shall state here the points in which D. felina differs, although many minor points which would be apparent to the eye are necessarily omitted.

The skull is slightly larger and is higher in the frontal region.

The mandible has a smaller flange.

The glenoid process is not so low and the post-tympanic

does not show a tendency to approach the post glenoid.

The dentition is  $I_3^*\check{C}_1^*Pm_3^*\dot{M}_2$ . The incisors are small, spatulate and in an even transverse row. The outer one is considerably larger than the others. The canine is larger at the base and not quite so long. The superior sectorial has an inner cusp but no anterior basal. The inferior sectorial has a better developed heel. The second lower molar is much reduced but constant.

The foramina are the same.

The skeleton is of nearly the same size but not so massive.

The limb bones have more slender shafts and not quite so large extremities.

The ulna and radius and the tibia are not so short in proportion to the lengths of the humerus and femur, which are almost identical in length with those of *H. primævus*.

The manus and pes are narrower and longer.

The unguals have weak hoods but were retractile, although

perhaps not perfectly so.

The generic distinctions are to be found in the structure of the sectorials, the character of the incisors and the unguals, although in distinguishing the two the other points above mentioned can be relied upon.

#### Measurements.

H. •	primævus.	D. felina.
Length of skull condyles to premaxillary	-	
	148	$154^{\mathrm{mm}}$
Length of cranium to anterior rim of orbit	99	108
Length of bony palate	79	72
Breadth of bony palate at sectorials	61	69
Breadth of skull at canines	47	50
Breadth of skull at post-orbital constriction,	<b>3</b> 5	33
Length of mandible from condyle to lateral		
incisor	112	119

	H. primævus.	D. felina.
Length of humerus	160	172
ulna		
radius	122	
femur	185	190
tibia		168
calcaneum	43	43
metatarsal IV	37	53
metacarpal IV	38	

The Hoplophoneus Series.

### Hoplophoneus primævus Leidy and Owen.

This species was the first Machærodont found in North America and was described as  $Machærodus\ primævus$  and later as  $Drepanodon\ primævus$ . The establishment of the genus Hoplophoneus Cope, removed it to that group. In Leidy's description in the Ancient Fauna of Dakota and Nebraska a skull is referred to this species which is considerably larger than the original type and quite different from it. The species as here used is as limited by the writer in the American Naturalist, January, 1896. The description of the osteology preceding this makes further mention of it here unnecessary. Dental formula  $I_3^2C_1^4Pm_2^3M_1^4$ .

# Hoplophoneus robustus Adams.

This species was proposed as representative of the larger skull, which was referred by Leidy to H. primævus. As compared with that species, it shows an increase in size and the skeleton is more massive. The skull is relatively large and the first superior premolar (pm²) more reduced and in old specimens may be absent. To this species should be referred the specimen determined by Osborn and Wortman as H. primævus (Bull. Amer. Mus., 1894, p. 228). The figure of the skull and the measurements here given are from that specimen.  $I_3^*C_1^*P^{m^2-\frac{2}{3}}M_1^*$ .

Length of	skull, condyles to premaxillary border,	180 <sup>mm</sup>
	humerus	
"	ulna	163
"	femuri	195
"	tibia	160

### Hoplophoneus occidentalis Leidy.

This is the largest species of the series. It was first proposed by Leidy on a fragment of a mandible (Extinct Fauna of Dakota and Nebraska). It is best known from a fine skull and nearly complete skeleton described by Williston (Kansas University Quarterly, June, '95), as Dinotomius atrox, which name, as has been shown by the writer, is a synonym (Amer. Nat., January, '96). The dentition is  $1\frac{3}{3}C_{\frac{1}{4}}Pm_{\frac{9}{2}}M_{\frac{1}{4}}$ . The inferior sectorial is very strong and thick at the base, the postero-internal cusp is wanting and the heel is reduced.

Length of	the skull, inion to premaxillary border,	$260^{mm}$
"	humerus	240
"	tibia	237

### Hoplophoneus insolens Adams.

The determination of the skeletal characters of H. occidentalis made it apparent that the specimen determined as such by Osborn and Wortman (Bull. Amer. Mus., 1894) is a quite distinct species, and it together with material in the Princeton collection was the basis of this species intermediate between H. robustus and H. occidentalis. As compared with H. robustus the skeleton is much larger, the limb bones being longer but not much heavier, the extremities being relatively smaller. The dental formula is  $I_3^*C_4^*Pm_3^*M_4^*$ .

Length	of skull, condyles to premaxillary border,	190 <sup>mm</sup>
.,,	humerus	200
"	ulna	212
"	femur	250
"	tibia	188

### Hoplophoneus oreodontis Cope.

This species is the type of the genus. It was first described by Cope under the genus Mach xrodus, but better material enabled him to separate from that genus. The specimen figured in the series is interesting as supplementing the material already known. This skull (number 10515 in the Princeton collection) differs from that described by Cope in showing the roots of a much reduced pm², thus changing the dental formula of the species  $I_3^3C_1^4P^{n\frac{2-3}{2}}M._1$ . It is the smallest species known from the White River.

Length of skull, condyles to premaxillary border, 135mm

# Hoplophoneus cerebralis Cope.

This is the smallest species and the most peculiar. It is the only representative of the genus thus far found in the John Day. It is peculiar in showing a short temporal space, a very convex profile, and a nearly vertical and abrupt occiput. The superior sectorial has a better developed anterior basal cusp than the other species; in this respect it approaches *Machærodus*, as has been noted by Cope. Dentition I<sup>2</sup>/C<sup>1</sup>/Pm<sup>2</sup>M<sup>1</sup>/. The species is known only from a skull.

Length of skull, condyles to premaxillary border, 120mm

There are thus six species of *Hoplophoneus* disregarding, *H. strigidens* Cope, which being known only from a fragment of a canine which presents an unusual form, is not characterized by any features which refer it to that genus rather than any other. The series of skulls figured in Plate XI show a great variation in size and a study of the skeletons shows a like variation.

#### The Dinictis Series.

Dinictis felina Leidy.

This is the type species of the genus and is well known from the original description by Leidy, and the osteology by Scott. A summary of its essential differences from *Hoplophoneus* is given in this paper, consequently no further discussion will be given here. The skull figured is a well preserved specimen in the Princeton Museum (number 10972). Dental formulæ  $I_3^2C_1^4$   $Pm_3^3M_2^4$ .

Length of	skull, condyles to premaxillary border,	$163^{mm}$
-66	humerus	172
"	femur	190
"	tibia	168

### Dinictis squalidens Cope.

This species was first described from a portion of a deciduous superior canine and a fragment of a mandible supporting the deciduous dentition. Later a mandible containing the permanent dentition was referred to it. The skull figured in the series (number 11379 in the Princeton Museum) contains the permanent dentition except the superior canines, which are just on the point of being replaced. Its reference to D. squalidens from the character of the mandible is not to be doubted. The specimen although immature is considerably smaller than D. felina and differs from it sufficiently to warrant its reference to a distinct species.

Length of skull, condyles to premaxillary border, 140mm

### Dinictis fortis Adams.

This species was described principally from a skeleton. *D. bombifrons*, which, was described from a skull, has since been determined to be a synonym of the former (Amer. Nat., January, '96, p. 50, foot-note). Further material has shown *D. fortis* to be quite distinct from *D. felina*, and now that the skull is known the species may be considered as established. The skull here figured is the one originally described as *D. bombifrons*.

Length	of skull, condyles to premaxillary border,	$185^{mn}$
-"	humerus	192
"	ulna	191
"	femur	205
"	tibia	186

#### D. cyclops Cope.

With this species we take up the John Day forms. The outline drawing here given is from the type skull figured by Cope. The striking features of it are its convex profile, the round orbit and the short temporal space. In a general way it is comparable with Hoplophoneus cerebralis, also from the John Day.

Length of the skull condyles to premaxillary border, 150mm

Dinictis brachyops (Pogonodon brachyops Cope).

As will be further pointed out in this paper, Pogonodon must be considered as a synonym of Dinictis. The tooth structure is identical and the dentition differs only in the absence of the second inferior molar, the reduction of which is indicated in other species of Dinictis. The figure given in the series is from the fragments of the skull described by Cope. The posterior portion of the skull is reversed and the restoration of the outline is conjectural. The skeleton is in part known and is very Dinictislike. This species is from the John Day.

Dinictis platycopis (Pogonodon platycopis Cope).

This is the largest of the series and with it is probably reached the culmination of the *Dinictis* type as regards size. The profile of the skull was probably more convex than is indicated in the figure, which is taken from Cope's Tertiary Vertebrates, since the specimen is slightly crushed. It is comparable with *H. occidentalis* although exceeding it in size. The skeleton is not known. The type specimen is from the John Day.

Length of skull, condyles to premaxillary border, 235mm

The foregoing series of *Dinictis* species, of which the skulls are figured in Plate XII, although less perfectly known than the *Hoplophoneus* series, is comparable with it. The genus *Dinictis* stands ancestral to the genus *Hoplophoneus* and, from what we know, seems to have been more conservative. In both there is a striking gradation in size. *Hoplophoneus* is greatly diversified in the White River. *Dinictis* remains are not so abundant and three of the six species are known only from the John Day, while only one species of *Hoplophoneus* is known from that formation. The range of the species in so far as I can report them is expressed in the following table.

	WHITE RIVER.			JOHN DAY.
	Titanotherium Beds.	Oreodon Beds.	Protoceras Beds.	
Dinictis fortis  '' felina  '' squalidens  '' brachyops  '' platycopis  '' cyclops	×	× × ×	×	× ×
Hoplophoneus primævus  oreodontis  robustus  insolens  cerebralis		× × × ×	×	×

### Nomenclature and Synonyms.

The following short account of the history of the genus *Machærodus* may not be out of place here, since this genus gives its name to a subfamily and its priority seems to be some-

what questioned.

Isolated teeth were first noticed by Cuvier in 1824, to whom specimens discovered in the Vald' Arno were exhibited by From evidence relative to their association with remains of Ursus, Cuvier was induced to refer them to that genus under the name Ursus cultridens (Supplement to Ossamens Fossiles, vol. v, Pt. ii, p. 517). The first description is due to Nesti, according to M. de Blainville, who cites his "Lettera terza dei alcune ossa fossile non peranco descritte al Sogn. Prof. Pali Savi, Pisa, 1826," in which the name Ursus trepanodon is used, whence later the genus Drepanodon, from the species name trepanodon, was evidently made. Later M. Bravard described Felis meganteron (now known as Macharodus meganteron) and conjecturally restored a portion of a skull by adding to it a canine of the character previously described as Ursus cultridens, referring it to the genus Felis under the specific name cultridens proposed by Cuvier (Monograph de deux Felis, p. 143, 1828). Kaup in Description d'Ossemens fossiles der Muséum de Darmstadt, 1833, laid stress on the differences which the falciform canines present as compared with known bears and felines, pointing out their differences from the teeth of other carnivores in the curved form and denticulate margins and proposed a distinct genus, Machærodus. An associated incisor he referred to a new genus Agnotherium, not recognizing that it probably belonged to the same individual. The real affinities had been recognized by Bravard, but Kaup was the first to propose a generic name for this type of dentition.

In De Blainville's Osteographie, under a description of Felis meganteron (Machærodus meganteron), a very full discussion is given in which he presses Bravard's claims. Pomel has also sought to substitute the species name meganteron for Kaup's Machærodus. Finally Bronn in Lethea Geonostica has attempted to combine Smilodon Lund, and Machærodus Kaup under the generic name Drepanodon, using Nestis' species

name.

The first Machærodont fossil found in North America was described by Leidy and Owen as *Machærodus primævus*. Later Leidy used for this species the generic name *Drepanodon*. Likewise Cope first described species under this genus *Machærodus*. Later, however, he removed them all to new genera. In referring to European species he used the genus *Drepanodon* 

with *Machærodus* as a synonym, but retained *Smilodon* as a distinct genus (Extinct Cats of North America, Amer. Nat., 1880).

It has not been definitely shown as yet that there are any representatives of the genus Macharodus in North America. In the American Naturalist, 1887, Cope proposed M. catacopis on the anterior portion of a mandible having a moderate flange and containing the roots of the incisors and a canine with a posterior denticulate border. It is not distinguishable from Hoplophoneus however. Cragin in Science, 1892, proposed M. crassidens on feline remains from the same beds and Williston has since (Kansas University Quarterly, 1895) referred other bones from the same locality to this species. None of the species can be said to be established as belonging to the genus Macharodus since the generic characters of dental formula, structure of the molar series and the basi-cranial foramina are not determinable in the specimens thus far found in the Loup Fork.

Smilodon is distinctively an American genus. It was established by Lund, 1842, on a specimen from Brazil (S. neogaeus K. Danske Vid. Selsk. Copenhagen). Leidy described a fragment of a maxilla containing a sectorial under the name Trucifelis fatalis. In structure the tooth agrees with Smilodon and a second specimen induced Cope to refer it to that genus. Smilodon floridanus Leidy is known from a well preserved skull from which the teeth have been lost.

The genus Eusmilus was established by Gervais (E. perarmatus, Journal de Zoologie, 1875). Previously Filhol had described M. bidentatus, which is synonymous, consequently

Gervais genus and Filhols species are accepted.

Dinobastis Cope, although founded on very limited material, will probably prove to represent the latest development of the Machærodont type in North America. The genus is based upon the absence of the internal root of the superior sectorial.

The genus Dinictis has remained well defined since first proposed by Leidy. To it, however, should be referred the two species of Pogonodon described by Cope. The genus Pogonodon as proposed by Cope does not differ from Dinictis as regards tooth structure, and the absence of the second inferior molar, which in Dinictis is much reduced, is not sufficient grounds for retaining it as a distinct genus, since in several specimens of Dinictis it is variable in size and in one is absent from one side. The genus Dinictis as thus constituted shows the reduction of this tooth, just as Hoplophoneus shows the reduction of the superior premolar.

The genus *Hoplophoneus* proposed by Cope embraces, besides new species, others previously described under the generic

names Macharodus and Drepanodon. Dinotomius atrox Williston is a synonym of H. occidentalis, as has been shown by the writer (Amer. Nat., January, 1896).

The genera Archælurus and Nimravus have remained as

first defined.

Our knowledge of North American fossil forms of the true Felinæ is very limited. Leidy has described Pseudælurus intrepidus, referring it to the European genus established by Gervais. There are several imperfectly known species of Felis. Leidy has described F. atrox and F. augustus. Felis imperialis Leidy is not sufficiently characterized to be retained. Scott has described ? F. maxima from a humerus found in the Loup Fork of Kansas. It will be remembered that remains from that deposit have been described under the genus Machærodus, and it is not probable that this humerus belongs to a different genus although further material must be found before the affinities of these forms can be determined. The genus Uncia Gray cannot be distinguished with certainty in fossil forms and is here included in Felis.

## The Dentition of the Felidæ.

The modifications of the dentition of the Felidæ consist, on the whole, of the reduction of the number of teeth until almost the entire function of the molar series is performed by a single large sectorial in each jaw and, accompanying the reduction in number, an increase in size and complexity of structure whereby the individual teeth become more perfectcutting instruments.\*

The specialization of one tooth as a sectorial to the exclusion of the others appears to be due to the following causes. It is to be observed that when a cat devours a carcass it cuts off masses by a shearing action of the jaws. In so doing the part to be divided is brought to the canthus or angle of the soft wall of the mouth, which is just at the front of the masseter muscle, at which point the greatest amount of force is gained, since the weight is brought immediately to the power. The first inferior molar situated at this point can be most effectively used and has developed into a sectorial. asmuch as the inferior and superior teeth do not directly oppose each other but form an alternate series, the first inferior molar more nearly opposes the last upper premolar and this tooth has become the superior sectorial. The shortening of the jaw which accompanied the reduction of the molar series has brought the canines nearer to the powerful muscles of mastication and they are as a result more effective weapons in the Felidæ than in other carnivores.

<sup>\*</sup> Origin of Specialized Teeth of the Carnivora, Cope, Amer. Nat., p. 171, 1879; Mechanical Genesis of Tooth-forms, Ryder, Proc. Acad. Nat. Sci., 1878.

The cause of the reduction of the molar series seems to lie in the following facts. If the jaws of one of the primitive Felidæ are examined it will be found that when they are closed the teeth which first come in contact are the sectorials, because of their elevated crowns. The premolars being further from the condyles are the last to come in contact. The function of seizing and holding is performed by the greatly developed canines and the function of cutting by the sectorials, hence no important function devolves upon the anterior pre-molars and posterior molars. Inasmuch as the lower series bite in front of the upper, it will be seen that the last inferior molar and the first superior premolar are only partially opposed by the teeth of the opposite series, consequently they are less functional and are the first to disappear.

The most primitive form of superior sectorial among the Felidæ consists of a principal, posterior, and antero-internal cusps, as is seen in *Dinictis*. To this form there is added in *Hoplophoneus* an incipient anterior basal cusp which in *Machærodus* is well developed. In *Smilodon* there is a second anterior basal cusp. The internal cusp present in *Dinictis* disappears in later genera, where it is represented only by a convex buttress, which descends from the principal cusp, and, as a more perfect shearing action is developed, this becomes less prominent until in *Dinobastis* it is absent and the internal root which supported it is lost.

The inferior sectorial in the most primitive genera consists of a principal, anterior, posterior and postero-internal cusps. The fate of the internal cusp is similar to that of the internal of the superior sectorial. Since it meets with no opposing cusp it is soon lost. The posterior cusp or heel is reduced in genera in which the superior molar is rudimental and does not oppose it. In Eusmilus dakotensis, it becomes a mere sharp line on the posterior border of the principal cusp. The function of the inferior sectorial devolves chiefly upon the principal and anterior cusps, which are well developed.

As the number of teeth was reduced the individual teeth become larger and the premolars developed posterior basal cusps by the elevation of the cingulum, as is seen in Felis. The incisors also became more robust in the Machærodont genera. In Dinictis they are small and form an even series. In Hoplophoneus they are more robust, and in Dinobastis we see their most specialized form. In this genus they have minute basal cusps and their margins are crenulated.

The development of saber-like canines characteristic of the Machærodont type is easily traced in Archælurus, in which the inferior and superior canines are sub-equal; in Ælurogale, where the posterior border is denticulate, and then in Dinictis, where both the anterior and posterior borders are denticulate.

With the higher genera they attained an enormous development, such as would seem to have been a positive hindrance in biting and seizing. In the true cats the canines remained

sub-equal although developing to a great size.

The development of a flange on the anterior inferior portion of the mandible is to be correlated with the lengthening of the superior canines. Its function seems to have been to protect these teeth, but in the latter genera the length of the flange evidently was not as great and the canines extending below the mandible were effective weapons when the mouth was closed. The most primitive forms probably possessed no flange since the canines were short and sub-equal. In *Archælurus* we see the first indication of a developing flange in the obtuse angle of the mandible and the shallow fossa in which the superior canine rests.

The evolution of the Felidæ is best indicated in the characters of the dentition. It is upon the dental formulæ and dental structure that generic distinctions rest, and a careful study of these points will reveal the genetic and phylogenetic relation-

ships of the family.

## The Succession of Genera.

There are two distinct types of development among the Felidæ. Of these the Machærodont type seems to have had its origin in America, since with the exception of Ælurogale and possibly Machærodus all the genera have been found here. The Old World was probably the home of the true cats, as it seems to be to-day. The only representative of them in America previous to Pliocene times was Pseudælurus, of which genus only one specimen has thus far been found. This genus may have been acquired through Oligocene intermigration, and the genera Ælurogale and Machairodus are probably European descendants of American forms.

Any attempt at a phylogenetic arrangement of the Felidæ must coincide with the occurrence in time, the order of reduction of the dental series, and the development of the individual teeth, particularly the sectorials. It is proposed herein to show that there is a succession of genera of the two types above mentioned which meets these requirements.

Of the Machærodont type the somewhat problematical form from the Bridger described by Wortman as ? Patriofelis leidyanus is the most primitive. From it Dinictis\* is derivable, through the reduction of the size of the postero-internal

<sup>\*</sup> D. fortis has been described as having the second lower molar very rudimental. In a specimen in the American Museum this tooth is absent from one side. In D. paucidens described by Mr. Riggs in the Kansas University Quarterly, April, 1896, it is absent from both sides. The dental formula of D. fortis is thus  $M = \frac{1}{2-1}$ , D. paucidens probably being a synonym.

cusp of the inferior sectorial and a modification of the heel. Thus is reached the most primitive species of the genus. Within the limits we can trace the reduction of the second inferior molar from a small two-rooted tooth to a mere tubercle and finally find it entirely absent in D. platycopis. The genus Hoplophoneus is well separated from Dinictis through the development of an anterior basal cusp on the superior sectorial and the loss of the internal cusp. The internal cusp had already shown some signs of reduction in certain specimens of Dinictis in that it had become lower and less distinct. Moreover, Hoplophoneus has lost the second inferior premolar and within the genus we can trace the reduction and final disappearance of the second superior premolar. postero-internal cusp of the inferior sectorial, which had shown signs of variation in *Dinictis*, is absent in the higher species of *Hoplophoneus*. The rapidly diminishing dental series reaches its maximum reduction in *Eusmilus*. Of this only the inferior dentition is known. It differs from Hoplophoneus occidentalis in the loss of an incisor, the reduction of the heel of the sectorial in E. bidentatus and its absence in E. dakotensis. This is the only genus in which the incisors have suffered a reduction in number, although in some specimens of *Hoplophoneus* the internal ones are much reduced.

With the formula  $I_{\frac{3}{2}}C_{\frac{1}{2}}Pm_{\frac{3}{2}}M_{\frac{1}{4}}$  the most stable form of Machærodont dentition seems to have been reached, since it has given rise through the addition of basal cutting lobes to genera which persisted until Pleistocene times. The genus Macharodus differs from the genus Smilodon in having a second basal lobe developed on the molar series. They are further distinguished by the fact that in Smilodon the post-glenoid and posttympanic are coössified. The absence of the entepicondylar foramen in the specimen of S. necator figured by Cope\* cannot be considered of generic importance since Burmeister has shown that it is present in three specimens which he has described.† Its absence in the case above mentioned is probably due to individual variation. The most specialized genus as regards the structure of the teeth is *Dinobastis*. In *Hoplo*phoneus the internal cusp of the superior sectorial has disappeared and the root supports a convex buttress. This is also the case in Macharodus and Smilodon, but in Dinobastis even the internal root has disappeared. The incisors also present a peculiarity, which is seen in some specimens of Macharodus and Smilodon, in the possession of minute basal cusps and crenulate margins. With this genus the Machærodonts culminated in specialization of tooth structure as they did in

<sup>\*</sup> Amer. Nat., 1880, p. 857.

<sup>†</sup> Description physique de la Republique Argentine, Text in Atlas, p. 106.

Am. Jour. Sci.—Fourth Series, Vol. I, No. 6.—June, 1896.

Eusmilus in the reduction of the dental series, and with this form they become extinct although it is probable, judging from fossil remains, that the dominant genus in Pleistocene times was Smilodon.

The genera Archælurus, Ælurogale and Nimravus seem to represent specialized forms of more primitive genera, forming a side line of development. Of these Archaelurus is most primitive. It is not directly derivable from any known form nor does it stand ancestral to the genera of Machærodonts previously discussed. The superior sectorial consists of a principal and a posterior cusp. There is a slight convexity in the position occupied by the anterior basal cusp in Hoplophoneus. The same thing is seen in Nimravus, but it does not develop into a true cusp. The principal cusp has a convex internal buttress as in *Hoplophoneus*. The inferior sectorial consists of an anterior, principal and posterior cusp or heel. From this genus Ælurogale could be derived by the loss of the first superior premolar. There is also a different development of the canine, the tooth becoming longer, recurved and acquiring a posterior denticulate margin. Nimravus differs in dental formula from Ælurogale in the loss of the second inferior premolar. The canine, however, is the most striking feature of this genus: it is nearly straight and spike-shaped, a form which is seemingly not derivable from Ælurogale but rather from Archælurus. Ælurogale is a European genus and although indicative of the order of reduction of the teeth in this small and seemingly aberrant group, it cannot be said to occupy an intermediate position between the other two genera. These three genera differ from other Machærodonts in the order of reduction of the teeth, all having retained the second inferior molar. This tooth is, however, on the point of disappearing in Nimravus, as is indicated by its absence on one side in a second specimen of N. gomphodus. Archælurus exhibits a peculiarity which should not be overlooked, in the strange deflection or exostosis of the border of the mandible posterior to the molar series. Of this a trace is seen in Nimravus.

Of the true cats there is but one genus which is known only as an extinct form, namely Pseudælurus. Felis, Lynx and Cynælurus, however, are known as fossils. Pseudælurus presents the most primitive dental formula and one which can be compared with Dinictis as regards tooth structure, but it differs in the absence of the second inferior molar. Pseudælurus probably gave origin to Felis through the loss of the second inferior premolar. Cynælurus differs from Felis in the absence of the internal cusp of the superior sectorial and the somewhat imperfect retractility of the claws. It forms a side development from the main line of descent. In

the genus Felis there is a tendency to the loss of the second superior premolar, it frequently being absent in old individuals. and thus is indicated the probable derivation of the genus Lynx. This genus occasionally loses the superior molar and so in exceptional cases we arrive at a dentition comparable with that of Eusmilus, the extreme reduction, however, taking place in the other jaw. In several species of Felis posterior cutting lobes are added to the premolars and an anterior basal cusp is indicated on the superior sectorial. Comparing the dentition with that of Macharodus or Smilodon, it differs in the retention of the internal cusp of the superior sectorial and the presence of an additional superior premolar.

#### PHYLOGENY OF THE FELIDÆ.

# Present systems of classification.

Cope, in his publication on the "Extinct Cats of North America,"\* has based his classification upon the basi-cranial foramina, making two families, the Felidæ and Nimravidæ, according to the following definitions.

Felidæ.—No distinct carotid foramen nor alisphenoid canal, condylar foramen entering the foramen lacerum posterius. No post-parietal and generally no post-glenoid foramina.

Nimravidæ.—Carotid and condylar foramina entirely distinct from the foramen lacerum posterius; an ali-sphenoid

canal and post-glenoid and post-parietal foramina.

This classification includes Machærodont members in each family. *Proælurus* is considered as the genus from which the true Felidæ may have been derived through *Pseudælurus*, if indeed these two genera are not the primitive members of that family. The Machærodont members of the Nimravidæ are suggested as the ancestors of the Felidæ. It should be remarked here that Cope's classification, based upon structural characters, does not permit of a phyletic interpretation, since the families as constituted by him are of polyphyletic origin as I interpret his meaning.

Zittel† establishes three subfamilies, the Proælurinæ, Ma-

chærodinæ, and Felinæ, defining them as follows:

Proælurinæ.—Dental formula  $\frac{3}{3}$ ,  $\frac{1}{4}$ ,  $\frac{1}{4}$ , lower carnassial with strong cutting talon skull elongated. Lower jaw slender, small in front with curved lower border; long-legged, fore and hind feet semi-digitigrade and pentadactyl.

Machærodinæ.—Dental formula  $\frac{3}{3-2}$   $\frac{1}{1}$   $\frac{4-2}{3-1}$   $\frac{1}{1}$ . Upper canine large and powerful, saber-shaped, compressed with anterior and posterior cutting edges. Front pms more or less reduced.

<sup>\*</sup>Cope, Amer. Nat, 1880, p. 834. † Handbuch der Paleontologie, 1893.

Upper carnassial with or without anterior basal cusp. Lower carnassial with talon. Lower jaw flattened at symphysis and separated from the lateral face by an angle. Lower border straight, more or less flared down in front. Femur frequently with third trochanter.

Felinæ.—Dental formula  $\frac{3}{3}$   $\frac{1}{1}$   $\frac{2-3}{2-3} \cdot \frac{1}{1}$ . Canine conical, upper and lower of about the same size; the two anterior pms lost. Upper carnassial with strong anterior basal cusp. Lower carnassial without talon. Upper molar reduced, lower one lost. Lateral surface of mandible not separated from the symphysis by an angle.

The Proælurinæ include *Proælurus* Fil. and *Pseudælurus* Gerv., but some doubt is expressed concerning the relations of *Proælurus*. From the creodont *Palæonictis* he derives the Machærodinæ, using Wortman's\* suggestion in this respect, while from an independent source in the Creodontia he derives

the Cryptoprocta and Felinæ through Prowlurus.

Schlosser† in Affen Lemuren, n. s., in criticising Filhol, expresses the opinion that *Pseudælurus edwardsi* is a true cat, while *Proælurus*, *Pseudælurus intermedius* and the problematical Cryptoprocta belong to another line. He points out clearly the Viverine relationships of *Proælurus* and rejects it as a probable cat ancestor; otherwise he accepts Cope's classification of the Felidæ.

# Proposed phylogeny.

As will be seen, these authors mutually criticise each other. The determination of the relationships of Proælurus removes the possibility of its being the ancestor of Pseudælurus and the true cats, as has been suggested by Cope, and also destroys the subfamily Proailurinæ as established by Zittel. unusual method of classification employed by Cope and accepted by Schlosser in this family, whereby Machærodont genera are grouped with the true cats, is avoided by Zittel's subfamilies Machærodinæ and Felinæ. These two subfamilies are the equivalents of the Machærodontinæ and Felinæ proposed by Gill and his classification is here accepted, since it has the priority, however referring Cynælurus to the Felinæ, inasmuch as the separation into a distinct subfamily Guepardinæ cannot be maintained. The points upon which the Guepardinæ was established are the non-retractility of the claws and the absence of the inner cusp of the superior sectorial. The claws are retractile although less perfectly so than in other

<sup>\*</sup> Wortman, Ancestry of the Felidæ, Bull. Ann. Mus., vol. iv, p. 94.

<sup>†</sup> Schlosser, Affen Lemuren, u. s., 1887, p. 420.

<sup>†</sup> Theodore Gill, Smithsonian Miscellaneous Collection, 230, Arrangement of the Families of Mammals, 1872.

Felidæ, and the absence of the cusp is not of sufficient importance, as would be judged by the absence of the same character in certain of the Machærodontinæ.

The subfamilies may be defined as follows, slightly modify-

ing Gill's definitions:

Machærodontinæ; superior canines large and powerful, usually saber-shaped with posterior and anterior denticulate borders, the inferior canine not greatly exceeding the outer incisor. Symphysial portion of the mandible separated from the lateral surface by an angle, the anterior inferior border of the ramus produced into a flange or making an obtuse angle with the symphysial portion.

Felinæ.—Canines sub-conical and sub-equal, inferior and

lateral faces of ramus continuous with the symphysial.

The Machærodontinæ as thus constituted include a group which is in some respects intermediate between the two subfamilies but which do not stand ancestral to any genera of either of them and are not derivable from them. They are Archælurus, the European genus Ælurogale and the peculiar Nimravus. Archælurus and Nimravus have been called by Cope the "false-sabre-tooths." Archælurus in general appearance is very suggestive as to what was the probable ancestor of the Machærodontinæ, but its late appearance and specialized tooth structure show that it could not have given rise to any known form outside of the genera above mentioned. On the removal of the matrix from one of the specimens I found that the internal cusp of the superior sectorial is wanting in Archælurus. The same also proved to be true in Nimravus, although reported as present in each by Cope. Moreover the posterointernal cusp of the inferior sectorial is wanting in Nimravus and probably in Archælurus. Thus there is found to be the same tooth-structure in these two genera that is seen in Ælurogale. It is therefore demonstrated that although the dentitions of these genera are more primitive as regards numbers, they could not have given rise to other Machærodonts or to the Felinæ. These three genera are related in the order of the reduction of the dental series, the character of the mandible and the structure of the canines. The canines of Archælurus have a convex anterior border and a posterior cutting edge, but in its present state of preservation shows no signs of denticulations. The canine of *Elurogale* has the posterior The peculiar spike-shaped canine of Nimborder denticulate. ravus is very suggestive that this genus marks the end of an aberrant phylum.

The subfamilies stand entirely distinct from each other and well separated from the Creodonts. In the subfamily Machærodontinæ there is, as has just been shown, a small group which stands in a peculiarly isolated position. There is, how-

ever, a specimen which may be considered as a probable ancestral form of all the Machærodontinæ and brings them a step nearer the Creodonts. It is the jaw fragment from the Bridger Eocene (number 11375 in the Princeton Collections) which Wortman has described as ? Patriofelis leidyanus (Am. Mus. Nat. Hist. Bull., 1892) as a probable connecting link between the Creodont Paleonictis and the Felidæ. A further knowledge of *Patriofelis* induced him to remove it from that genus (ibid., 1894). For the sake of reference I propose the generic name Elurotherium. Elurotherium leidyanum, following the description given by Wortman, consists of a jaw fragment containing the third and fourth premolars and the first molar or sectorial. It also bears a distinct trace of the alveolus for the canine, the position of which is such as to preclude the possibility of there being more than three premolars. The sectorial, as will be seen from a comparison with *Dinictis*, presents the same elements as that genus but has a much better developed postero-internal cusp and heel, thus fulfilling the requirement of an ancestral form. From what can be judged from the wear of the cusps and the relation of the teeth in the Felidæ it seems probable that it possessed the dental formula P<sub>3</sub>M<sub>2</sub> as was inferred by Wortman, thus exceeding the dental formula of *Dinictis* by a premolar. It will be noted that the dental formula of *Ælurotherium* was probably more primitive than that of Archælurus, thus not precluding the possibility of its being ancestral to that genus also, although probably quite removed from it.

The following arrangement according to subfamilies expresses the probable line of descent of each as well as the occurrence in time of the various genera.

Eocene	OLIGOCENE	MIOCEN	vie.	PLIQUENE	PLEISTOCENE	RECENT
BRIDGER	WHITE RIVER	JOHN DAY	LOUP FORK			
					DINOBASTIS	)
	ļ			Smilodon /	Smilodon	,
	Eusmilus		Machærodus	Machærodus		MACHÆRODONTINÆ
	Hoplophoneus	Hoplophoneus				I.ER
	Dinictis	DINICTIS				NOGIC
ALUROTHERIUM		ÆLUROGALE		ļ		NA
CREODONTA	<b>1</b> \	Archælurus				"
TNOC		Nimravus .	•			IJ
×	<b>1</b> \	Pseudælurus		_	Lynx	LYNX )
			Felis	FELIS	Felis	FELIS FELINA
				Cynælurus	Cynælurus	CYNÆLURUS )
	PHOSPHORITES	St. GERAND LE PUV	SANSAN	VAL D'ARNO		

There is a point of difference among the two sub-families which should be discussed here. It is the character of the basi-cranial foramina which was made by Cope a basis of classification. The arrangement of the foramina and the presence of the alisphenoid canal as found in those genera which he made to constitute the Nimravidæ is such as is found in primitive forms. It is not unnatural that the higher forms should have paralleled each other in the loss of the alisphenoid canal and the disposition of the foramina, so that in Smilodon and Felis we find the same conditions although the two genera represent the most specialized forms of the phyla in which the basi-cranial characters are known. The two subfamilies exhibit a most remarkable parallelism in development. point of divergence from a common ancestor is quite removed from the position by the most primitive of the well known Indeed it is not impossible that the Felidæ may have had a separate origin from the Creodonts, but our knowledge of their early relationships is too meagre to justify any definite conclusions on this point. As we know them the phyla are distinct.

The following key for determining the genera of the Felidæ is submitted. *Ælurotherium* not being well known is contrasted with *Dinictis*, which it most resembles in the characters known. *Eusmilus*, being known only from the lower dentition, is contrasted with *Hoplophoneus*.

I. Superior canines large and powerful, usually saber-shaped with posterior and anterior denticulate borders. Inferior canine not greatly exceeding the outer incisor. Mandible with the symphysial portion separated from the lateral by an angle, the anterior inferior border of the ramus with a flange or making an obtuse angle with the symphysial portion.

#### Machærodontinæ.

- A. Anterior inferior border of mandible with an obtuse angle.

  a. Superior sectorial without internal cusp.
  - a.a. Superior canine recurved posterior border, not denticulate.
    - 1. Dentition I\(\frac{3}{4}\)C\(\frac{1}{4}\)Pm\(\frac{4}{3}\)M\(\frac{1}{2}\) Archælurus.
  - b.b. Superior canine recurved posterior border, denticulate.
    - 2. Dentition I&C1Pm3M2 Ælurogale.
  - c.c. Superior canine spike shaped.
    - 3. Dentition I3C1Pm3M2 Nimravus.
- B. Anterior inferior border of mandible with a flange.
  - b. Superior sectorial with internal cusp.
    - d.d. Inferior sectorial with strong postero-internal cusp and talon.
      - 4. Dentition ? I 3 C 1 Pm 4 M 2 Elurotherium.
    - e.e. Inferior sectorial with small postero-internal cusp, talon reduced.

- 5. Dentition  $I_{\frac{3}{3}}C_{\frac{1}{1}}Pm_{\frac{3}{3}}M_{\frac{1}{2-1}}$  Dinictis.
- c. Superior sectorial without internal cusp.
  - ff. Anterior basal cusp of superior sectorial, incipient premolars without basal cusps.
    - 6. Dentition  $I_{\frac{3}{4}}^{3}C_{\frac{1}{4}}^{4}Pm^{\frac{3-2}{2}}\dot{M}_{\frac{1}{4}}^{4}$  Hoplophoneus.
    - 7. Dentition I/2C/1Pm/1M/1 Eusmilus.
- d. Anterior basal cusp of superior sectorial well-developed, no internal cusp, premolars with basal lobes.
  - gg. Superior sectorial with single anterior basal cusp, postglenoid and post-tympanic processes distinct.
    - 8. Dentition I\(\frac{3}{3}\)C\(\frac{1}{1}\(\frac{2}{2}\)M\(\frac{1}{4}\) Machaerodus.
  - hh. Superior sectorial with a second anterior basal cusp, post-glenoid and post-tympanis processes coössified.
    - 9. Dentition  $I_{\frac{3}{3}}C_{\frac{1}{1}}Pm\frac{2}{2-1}M_{\frac{1}{1}}$  Smilodon.
  - ii. Superior sectorial without internal root.
    - 10. Dentition probably like Smilodon, Dinobastis.
- II. Canines sub-conical and sub-equal, inferior and lateral faces of ramus continuous with symphysial.

#### FELINÆ.

- B. Anterior and inferior borders of mandible continuous.
  - e. Superior sectorial with internal cusp.
    - 11. Dentition I3C1Pm3M1 Pseudælurus.

    - Dentition I<sup>3</sup>/<sub>3</sub>C<sup>1</sup>/<sub>1</sub>Pm<sup>3-2</sup>/<sub>3</sub>M<sup>1</sup>/<sub>1</sub> Felis.
       Dentition I<sup>3</sup>/<sub>3</sub>C<sup>1</sup>/<sub>1</sub>Pm<sup>2</sup>/<sub>2</sub>M<sup>1-1</sup>/<sub>1</sub> Lynx.
  - f. Superior sectorial without internal cusp.
    - 14. Dentition I3C1Pm3M1 Cynælurus.

#### EXPLANATION OF PLATES.

#### PLATE X.

#### Hoplophoneus primævus, all $\times \frac{1}{2}$ .

- FIGURE 1.—Skull (number 11013 Princeton Museum restored from number 10540.)
  FIGURE 2.—Manus (number 10741 Princeton Museum.)
- FIGURE 3.-Pes
- FIGURE 4.-Femur
- FIGURE 5.—Ulna and radius FIGURE 6.—Tibia and fibula
- FIGURE 7 .- Humerus

#### PLATE XI.

- Hoplophoneus series, all  $\times \frac{1}{2}$ .
- FIGURE 1.—Hoplophoneus cerebralis (after Cope.)
- oreodontis (10515 Princeton Museum.) FIGURE 2.-44

4.6

- primævus (11013 Princeton Museum.) FIGURE 3.— 4.6
- FIGURE 4.robustus (650 American Museum.) insolens (11022 Princeton Museum.) FIGURE 5.—
- ..
- FIGURE 6 .-occidentalis (after Williston.)

#### PLATE XII.

- Dinictis series, all  $\times \frac{1}{2}$ .
- FIGURE 1.—Dinictis squalidens (11379 Princeton Museum.)
- FIGURE 2.-" cyclops (after Cope.)
- .. felina (10972) Princeton Museum.) FIGURE 3.—
- FIGURE 4.-" fortis (10502 Princeton Museum.) [reversed.) brachyops (Cope's type, Amer. Mus., posterior portion FIGURE 5.-
- 44 platycopis (after Cope.) FIGURE 6 .-





