

Auditory Region in North
American Fossil Felidae:
Its Significance in
Phylogeny

GEOLOGICAL SURVEY PROFESSIONAL PAPER 243-G



Auditory Region in North American Fossil Felidae: Its Significance in Phylogeny

By JEAN HOUGH

SHORTER CONTRIBUTIONS TO GENERAL GEOLOGY, 1952, PAGES 95-115

GEOLOGICAL SURVEY PROFESSIONAL PAPER 243-G

*Detailed descriptions and illustrations of the
ear region in some fossil and recent genera,
and a proposed revision of superfamily
classification of the Carnivora*



UNITED STATES GOVERNMENT PRINTING OFFICE, WASHINGTON : 1953

UNITED STATES DEPARTMENT OF THE INTERIOR

Douglas McKay, *Secretary*

GEOLOGICAL SURVEY

W. E. Wrather, *Director*

For sale by the Superintendent of Documents, U. S. Government Printing Office
Washington 25, D. C. - Price 20 cents (paper cover)

CONTENTS

	Page		Page
Abstract.....	95	Generic descriptions—Continued	
Introduction.....	95	Subfamily Nimravinae.....	103
Acknowledgments.....	97	<i>Dinictis</i> (Oligocene species).....	103
General characters of the auditory region in Oligocene		External characters.....	103
Felidae.....	97	Internal structure of the bulla and middle ear.....	103
Auditory bulla.....	97	Basicranial foramina.....	103
Basicranial foramina.....	99	<i>Dinictis cyclops</i> Cope (John Day species).....	105
Generic descriptions.....	99	<i>Nimravus</i>	106
Subfamily Machaerodontinae.....	99	Subfamily Pseudaelurinae.....	106
<i>Hoplophoneus</i>	99	American genera.....	106
General characters.....	99	Asiatic and European genera.....	106
Auditory bulla.....	99	Summary and conclusions.....	106
Basicranial foramina.....	99	Homology of basicranial features of the Feloidea.....	107
<i>Eusmilis</i>	99	Septum bullae.....	107
General characters.....	99	Form and position of the septum.....	107
Middle and inner ear structure.....	100	Mode of development of the bulla.....	109
Basicranial foramina.....	100	Basicranial foramina.....	110
Pliocene machaerodonts.....	100	Summary and conclusions.....	112
<i>Smilodon</i>	101	Evolution of the intracranial circulation.....	112
General characters.....	101	Evolution of the auditory bulla.....	112
Internal structure of the auditory bulla.....	102	Proposed taxonomic changes.....	113
Structure of the middle and inner ear.....	102	Summary of superfamilies and families.....	113
Basicranial foramina.....	102	Selected references.....	115

ILLUSTRATIONS

	Page		Page
FIGURE 5. <i>Hoplophoneus primaevus oreodontis</i>	98	FIGURE 10. <i>Viverricula ind. rasse</i>	100
6. <i>Smilodon californicus</i>	100	11. <i>Felis catus</i>	100
7. <i>Smilodon californicus</i>	100	12. <i>Canis dingo</i>	110
8. <i>Dinictis felina</i>	104	13. <i>Vulpes velox</i>	111
9. <i>Dinictis cyclops</i>	105		



AUDITORY REGION IN NORTH AMERICAN FOSSIL FELIDAE: ITS SIGNIFICANCE IN PHYLOGENY

By JEAN HOUGH

ABSTRACT

The auditory region of the North American fossil Felidae is described in detail. In the Oligocene Felidae the characters of this region, especially the foramina associated with the veins and arteries of the head, are like those of the modern Canidae rather than the Felidae. On the contrary, all of the middle Miocene (post-John Day) and later genera have typical felid characters in this part of the skull. This has profound significance for the phylogeny and major taxonomy of the family. If any of the species of Oligocene felids are ancestral to the modern forms, an evolution of both the venous and arterial system of the head as well as the auditory bulla must have taken place. This is quite possible, for not only is there theoretical support for it in the ontogeny of modern genera, but there are species that have characters linking the Paleofelides to the Neofelides. Nevertheless, postulating such an evolution is a radical step as it throws doubt upon the validity of the current superfamilial classification of the Carnivora. This arrangement is based primarily on the homology of the two-chambered bulla, and the presence or absence of the postglenoid foramen. If, as this paper attempts to show, these structures are not homologous, but have evolved independently in the Viverridae and Felidae (and in other families), the categories Aeluroidea and Arctoidea of Flower (Feloidea and Canoidea of Simpson) have no phylogenetic significance, but are at best convenient divisions applicable to modern genera only.

INTRODUCTION

The threefold division of the Carnivora into Aeluroidea, Cynoidea and Arctoidea was based by Flower (1869) primarily on the characters of the auditory region, especially the presence or absence of a septum dividing the bulla into two chambers, and the arrangement of the basicranial foramina. In these features, the Aeluroidea (Viverridae, Felidae, Hyaenidae) represent one extreme, the typical arctoid Carnivora (Mustelidae, Procyonidae, Ursidae) another. The Cynoidea (Canidae) Flower thought intermediate between the two. In the Aeluroidea the interior of the bulla is divided into two chambers by a septum which completely closes off the chambers except for a small opening just below the fenestra cochleae; the postglenoid foramen is reduced or absent, the condyloid foramen concealed by the foramen lacerum posterius, the carotid canal reduced to a vestige and the posterior carotid foramen (where present at all) very inconspicuously placed in a

common fossa with the posterior lacerate foramen. The Arctoidea, on the other hand, have a simple, one-chambered bulla, a large postglenoid foramen, a large condyloid foramen quite distinct from the foramen lacerum posterius, a well-developed bony canal for the carotid artery and a large posterior carotid foramen also distinct from the posterior lacerate foramen. The Cynoidea have some features of each group. There is a partial septum, the postglenoid foramen is moderately large, the condyloid foramen is smaller than in the Arctoidea and the carotid canal less conspicuously developed. The posterior carotid foramen is a narrow slit opening into the common fossa with the foramen lacerum posterius.

These characters were probably considered by Flower, and certainly by Turner (1848) who originated the idea, as no more than morphological correspondences the use of which gave a more natural classification (*sensu* Dobzansky, 1941, p. 363) than the use of adaptive characters of the limbs and teeth. Mivart, however, in a series of papers (1882, 1885, 1890) elaborated on the idea extensively, giving it an archetypal significance by compiling long lists of features in the soft parts and skeleton linked, as he thought, with the key characters of the basicranium. With the rise of the evolutionary theory, this archetypal concept of homology gave way in turn to a phylogenetic one. Homology indicated common ancestry, proof of which was to be sought first in ontogeny, and later, as the fossil record became better known, in paleontological history.

The first result of this shift in zoological theory was the reduction of Flower's threefold classification to a twofold one. Flower had considered the partial septum found in many canids, and especially well developed in *Canis jubatus* homologous with the septum bullae of *Felis*, at least in the morphological sense. (It has the same position and where the bullae is well inflated appears to be an intermediate stage in the evolution of the typical felid septum.) Winge's studies (1895) seem to show that the septum of *Canis* was, in fact, homologous in mode of origin (not position) with the septae and rafters that radiate from the crista

tympani across the walls of the bulla in some mustelids. These are ossified from folds of the mucuous lining. In spite of the fact that this homology was disputed by Van Kampen (1905) who denied that the septum in *Canis* originated from mucous folds and considered it rather a part of the original wall become concave by bone apposition on the outer side and simultaneous resorption on the inner side, Winge's classification continued to be universally accepted for over half a century. This was in part due, however, to support given to the idea of the homology of the basicranial characters of the Cynoidea and Arctoidea by certain phylogenetic theories of Matthew (Wortman and Matthew, 1899). These theories, which derived the Procyonidae and Ursidae from Miocene canids, were based almost wholly on dentition and tended to make the Canidae the central stock of the arctoid Carnivora. Their influence was so great that except for a few minor shifts of certain problematical families and the substitution of the names Canoidea and Feloidea by Simpson, (1945), for the Arctoidea and Aeluroidea of Flower the resulting division of the Carnivora into two superfamilies (and the phylogeny derived from this) has, to the writer's knowledge, not been challenged until recently.

The increase in knowledge of the fossil Carnivora, however, has brought many new facts of morphology and phylogeny to light. Some of these were presented by the writer in an earlier paper (Hough, 1948), in which it was shown that the derivation of the Procyonidae and Ursidae from Miocene canids is untenable when characters other than those of the dentition are taken into consideration. The work of Scott and Jepsen (1937), Jepsen (1933, 1941) on the fossil Felidae has emphasized the antiquity of this family, and its separation from the Viverridae. These facts, together with much unpublished data known to specialists in the field, tend to cast doubt on the validity of the superfamily arrangement of the Carnivora and to pose many taxonomic problems for which to date no consistent solution has been offered. In fact, the general taxonomy of the order has blundered along in a curious kind of compromise by which one set of criteria are used for determining the systematic position of recent forms and quite another that of the fossil genera. The recent Canidae, for example, are included in the Canoidea because of the supposed homology of the septum present in some canids with that of such of the arctoid Carnivora as have septae, and because of a hypothetical relationship of fossil forms based on dentition. *Daphoenus*, which has a demi-bulla virtually identical with that of both the modern *Nandinia* and the fossil *Paleoprionodon* contemporary with *Daphoenus*, is also

included in the Canoidea but on the basis, presumably, of the dentition, or of an alleged canid ancestry.

Paleoprionodon and *Paradaphoenus*, whose basicranial characters are almost exactly alike, are placed in different superfamilies, one in the Feloidea and the other in the Canoidea presumably on the basis of dentition although the dental characters of *Paleoprionodon* differ from those of *Paradaphoenus* in the same way that those of *Poiana* differ from *Civettictis*—modern viverrines included by Gregory (1939) in the same subfamily. The basicranial foramina of the fossil Felidae have long been known to be canoid (Scott and Jepsen, 1937; Jepsen, 1933) but, although these features are considered of paramount importance in the classification of Modern carnivores, they have been entirely ignored in the superfamily allocation of the fossil Felidae. The writer feels that the inconsistencies are, in fact, so great that a paleontologist from Mars, with no inherited prejudices based on the magic of names would be hard put to understand our classification at all.

This confusion in taxonomy has arisen, of course, from a confusion as to the definition and significance of homology. As applied to modern carnivores, the concept, in practical usage at any rate, has largely an archetypal significance. Applied to fossil forms, homologies are used as a means of tracing phylogenies. The result, naturally, is extremely illogical. Zangerl (1949), impressed by some of these inconsistencies and the circular reasoning which is both a cause and a result, has argued recently for a return to a purely archetypal definition of homology. This, however, is clearly impossible under current evolutionary theory, the soundness of which seems, at least in the present state of knowledge, firmly established. Attempting to turn back the clock, zoologically speaking, would lead only to further confusion. A phylogenetic definition of homology is the only theoretically sound one. In any case, the dilemma is more apparent than real. The two concepts of homology, properly interpreted, support one another. True correspondence in structure can only be the result of similar ontogenetic development and this in turn depends ultimately on a common phylogenetic origin. General correspondence of structure, and even in some instances detailed similarities can, of course, be the result of parallelism and convergence. (For a full discussion of this see Haas and Simpson, 1946.) However, the writer believes that in mammals, at least, these processes can be distinguished if all lines of evidence are properly evaluated. It is the duty of a good phylogeneticist to do this, however difficult the task may be.

In fossil Felidae the difficulty is particularly great because of the large amount of parallelism and convergence, not only in the dentition, as is generally recognized but, as will be shown in this paper, in the basicranial structure as well. The studies here presented are an attempt to examine as thoroughly as possible the facts of the supposed homologies on which the major taxonomy of the Feloidae is based and to propose a theory of phylogeny supported by, or at least not inconsistent with, these facts.

ACKNOWLEDGMENTS

Some of the data on which the study is based were gathered from museums other than the U. S. National Museum under a grant from the Geological Society of America prior to the writer's employment with the U. S. Geological Survey. The writer wishes to thank the council of the Geological Society of America and the staffs of the various museums in which this preliminary work was done, for their valuable cooperation.

GENERAL CHARACTERS OF THE AUDITORY REGION IN FOSSIL FELIDS

AUDITORY BULLA

The structure of the bulla in the Oligocene Felidae is difficult to interpret. No known specimen has a complete bulla, and many have no remnants of it preserved. Some skulls, especially those more recently collected and carefully prepared, have a considerable portion remaining—in most specimens the antero-lateral wall, including the auditory meatus and the crista tympani. A few have traces of the posterior and medial walls. Moreover, a careful examination of the bones in contact with the roof of the bulla—the basioccipital, basisphenoid, exoccipital and petrosal—show unmistakable impressions of a bulla even in skulls where no remnant now remains in place. Piviteau has described this same condition in the skulls of the European species, *Eusmilis bidentatus* (Piviteau, 1931, p. 31, Pl. VI, fig. 1).

The anterolateral portions of the bulla, which are present in many specimens, have been interpreted as an anterior (tympanic) chamber similar to that of the living Viverridae or Felidae—interpretations differ as to which. Plausible as this idea is (and consistent with the accepted taxonomy of the Felidae) it is almost certainly not correct. Aside from the impressions on the roofing bones, mentioned above, there is evidence in the remnants of the bulla itself that that structure was complete, fully ossified and similar in shape and size to that of the Canidae.

Remnants of the bulla that remain intact in specimens of *Hoplophoneus* and *Dinictis* from the White River formation are not the same in size or shape in any two skulls, or even on both sides of the same skull. The edges are irregular and jagged. They are, therefore, quite unlike the regular, smoothly margined, horse-shoe shaped demi-bulla of such fossil forms as *Paleoprionodon* and *Daphoenus*, or the modern viverrid *Nandinia*. Moreover, a demi-bulla, in those forms in which it occurs, lies at a very low angle and covers only the antero-lateral portion of the auditory region. It does not touch the basisphenoid. The margins, which are incurved, are in contact with the promontorium except directly ventral to the fenestra cochleae. In *Hoplophoneus* and *Dinictis*, on the other hand, the circle of bone around the auditory meatus arches around the middle ear structures. It may be in contact with the basisphenoid by a broad strip of bone, if that much of the bulla is present, but it is never in contact at any point with the promontorium. It seems to correspond very closely to a portion of the antero-lateral wall of the normal one-chambered bulla of the Canidae.

Examination of a number of miscellaneous dog and wolf skulls that were collected after being exposed to weathering shows that the bulla is broken in nearly all such specimens. The portions remaining are exactly those found in the saber tooth carnivores—the anterior wall where it is re-enforced by its juncture with the postglenoid process, the basisphenoid, the crista tympani and in some cases the medial and posterior walls. The incomplete state of the bullae, therefore, in the fossil specimens in question, can be almost certainly attributed to the conditions of fossilization, that is, to exposure to weathering for a considerable length of time before burial, followed by rapid entombment under a heavy load of sediment. These are exactly the conditions known to exist in a flood-plain type of deposition, such as that of the White River formation.

The portions of the bulla could, of course, represent a part of the lateral wall of a two chambered bulla the anterior chamber of which was globular, as in the domestic cat. Opposed to this is the contact with the basisphenoid (which never occurs in the Felidae), and the absence of any trace of a septum bullae. This septum is an extremely strong structure. Attempts to break the bulla of a cat or viverrine will easily prove that this is so. Moreover, a complete septum like that of the Felidae leaves a strong impression on the periotic, as can be ascertained by examination of modern specimens, and no such imprint is present even in skulls whose preservation is almost perfect. It seems virtually impossible therefore, that a septum bullae

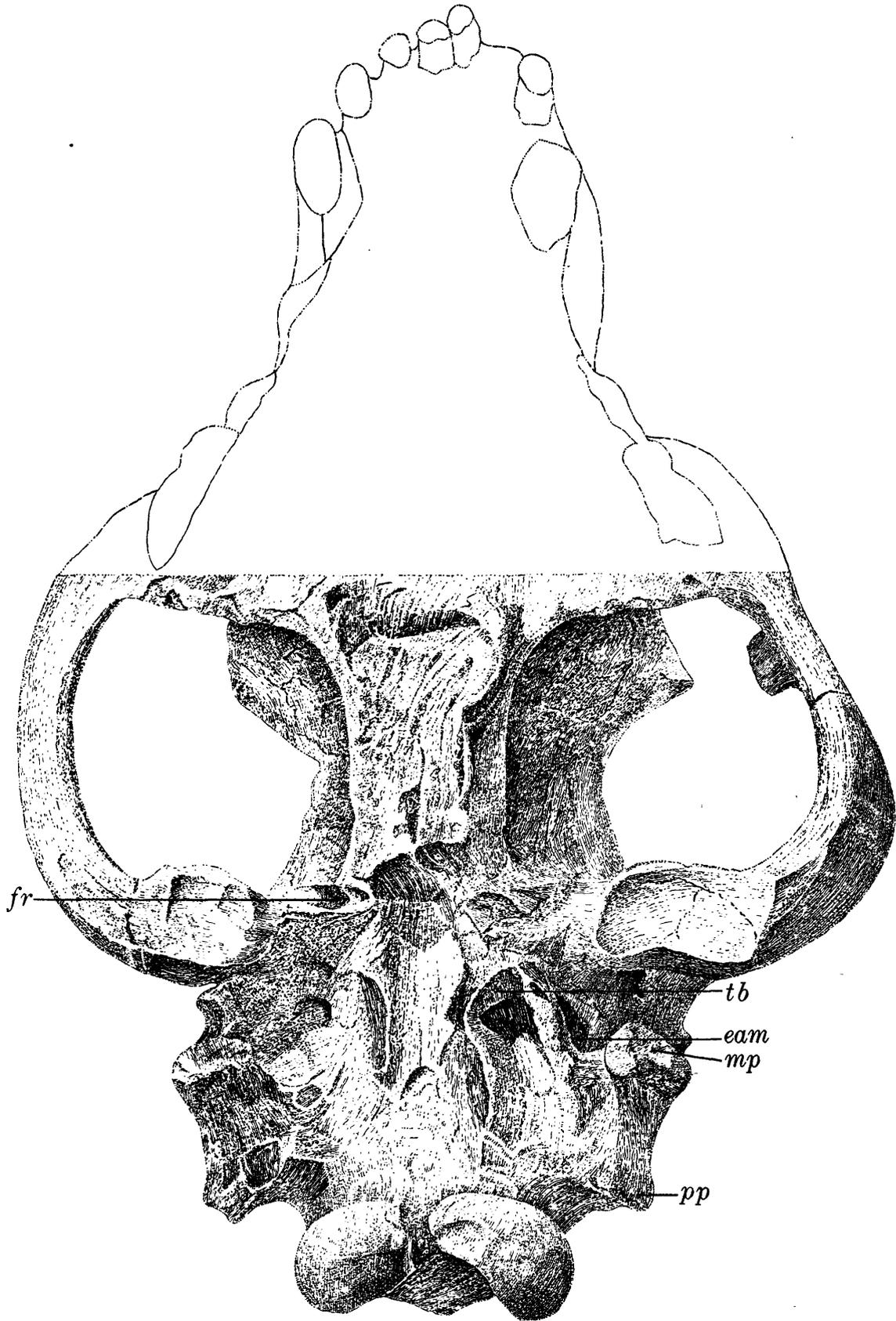


FIGURE 5.—*Hoplophoneus primaevus oreodontis* Cope, Princeton Museum 10515, $\times 1\frac{1}{2}$.

corresponding to that of the modern Felidae in form and position was present in the Oligocene genera.

BASICRANIAL FORAMINA

The basicranial foramina of the Oligocene Felidae are as anomalous as the structure of the auditory region. They are distinctly not feloid—(Scott and Jepsen, 1937, Piviteau, 1931, and others) in number or position. There is an alisphenoid canal, and a large postglenoid foramen. The condyloid foramen is large and well separated from the foramen lacerum posterius. The carotid canal is well defined and terminates either in a space between the alisphenoid and promontorium or a large foramen lacerum medium. The posterior carotid foramen is behind the foramen lacerum posterius and well separated from it. These characters are all canoid and point to a venous and arterial system of the head almost at the opposite extreme from that of the modern Felidae.

These characters as well as those of the bulla will be considered in more detail in the following descriptions.

GENERIC DESCRIPTIONS

SUBFAMILY MACHAERODONTINAE

HOPLOPHONEUS

GENERAL CHARACTERS

The space occupied by the auditory cavity is narrow. (See fig. 5.) This is due, in part, to the narrowness of the basicranium itself, and in part to the enormous development of the mastoid processes. These form short broad columns extending forward and downward well below the plane of the basicranium. The width is so great that the medial margin is on a line with the inner margin of the glenoid fossa. Comparison with *Canis* and *Felis* (where the mastoid hardly appears on the under surface of the skull) reveals that the space for the promontorium and structures of the middle ear is very restricted. The promontorium is large and rounded, but the depth of the cavity makes it appear buried in the basicranium. It is in fact, somewhat deeper below the level of the basioccipital than in modern carnivores, or in the contemporary *Dinictis*.

The paroccipital process projects backward from the base of the mastoid and forms a distinct leaflike process. The size of the process, and its distinction from the mastoid, vary from individual to individual in the species from the Brule formation. In all known specimens from the Chadron formation it is well developed and similar in shape and size to that of the contemporary daphoenids.

AUDITORY BULLA

Because the auditory cavity is so narrow, the bulla is almost triangular. This was determined by care-

ful preparation by G. L. Jepsen of the type specimen of *H. oreodontis*, Princeton Museum 10515 (fig. 5) which disclosed a considerable portion of the bulla including the rim around the external auditory meatus, and the anterior and medial wall broken off level with the basioccipital. This wall tapers almost to a point anteromedially and broadens posteriorly. The medial wall is curved and moderately inflated but the floor is flattened giving a pill box shape.

The lateral wall is in reality lateromedial so that the meatus faces obliquely forward, directly into the base of the postglenoid process. The mastoid and postglenoid processes together form a long passageway, open ventrally, through which a cartilaginous tuba auditiva undoubtedly passed. The connection between the exterior of the skull and the sound producing apparatus thus follows a very roundabout route. The resonating chamber also is extremely small and with no extension into the mastoid or paroccipital as in recent carnivores such as *Taxidea* or *Ursus* which have a small, flattened bulla.

THE BASICRANIAL FORAMINA

There is a long alisphenoid canal terminating in a foramen rotundum situated at one end of a common fossa with the foramen ovale. This relationship is precisely that of *Canis* except that, due to the relative shortness of the cranial portion of the skull in *Hoplophoneus* the fossa extends mediolaterally parallel to the base of the postglenoid fossa rather than anteroposteriorly as in *Canis*.

The postglenoid foramen is large. The posterior carotid foramen and the foramen lacerum posterius are separate but they are in the same relative position as in the Canidae and may have been enclosed in a common fossa. The condyloid foramen is in the same position as in *Canis*, but is larger.

EUSMILIS

GENERAL CHARACTERS

The U. S. National Museum specimens of this genus have no trace of an auditory bulla. The general aspect of the auditory region is like that of *Hoplophoneus*, differing only in the enormous size of the mastoid process. In older individuals this process reaches the proportions of that of *Smilodon*, but the difference from *Hoplophoneus* is more than a difference in size. The mastoid is falciform with a flattened posterior surface inclined obliquely forward. The exoccipital is flattened against the dorsal half of this surface and makes a sutural contact with it. There is no distinct paroccipital process. The appearance of the hinder part of the basicranial region resembles that of the bears, *Hemicyon*, the walrus, and the South American saber-

tooth marsupial *Thylacosmilis*, and strongly suggests that this exaggerated development of the mastoid auditory bulla is determined both by the size of the head and the canine teeth.

In a specimen at the South Dakota School of Mines (2815), are remnants of a bulla, including the antero-lateral wall, the crista tympani and the external auditory meatus. The last is a short tube whose sides are made up of the base of the postglenoid process anteriorly, and of the mastoid posteriorly. A flattened projection of the tympanic bridges the space between these two processes and forms the floor. The very large crista tympani is projected far into the auditory cavity. A very peculiar sort of septum is formed by what appears to be an extension of the base of the postglenoid process continuous with the roof of the meatus. The structures of the middle ear lie above this septum. The condition is somewhat similar to that found in *Amphicyon*, and also resembles *Smilodon*, where the bulla is divided into upper and lower chambers.

MIDDLE AND INNER EAR STRUCTURE

The promontorium is large and round, and situated almost in the center of the auditory cavity. The lateral and posterior surfaces are almost vertical. The fenestra cochleae lies about midway along the external face. The fenestra vestibuli is in the usual position just opposite the meatus, slightly anterior of the anterior margin of the mastoid process. Just above this opening is the minute aperture of the facial canal. The length and position of the external part of this canal is determined by the peculiar conformation of the mastoid. A deep groove extends from the base of this process to its tip. It is parallel to the anterior margin of the process and separated from it by only a thin ridge of bone. Apparently, the facial nerve and accompanying blood vessels leaving the apertura canalis facialis passed under the spur of bone from the base of the mastoid and from there followed along the groove to the tip of the process. This course does not differ in its position in relation to the mastoid from that of other carnivores but appears to do so because of the size and forward inclination of the mastoid process.

The carotid canal is clearly marked by a groove in the basioccipital extending anteriorly about to the midpoint of the medial margin of the promontorium. Apparently the internal carotid artery entered the cranium at that point.

BASICRANIAL FORAMINA

The basicranial foramina are essentially the same in number and size as those of *Hoplophoneus*. There is an alisphenoid canal. The foramen ovale and foramen rotundum occupy a large fossa lying obliquely along

the ridge leading to the base of the postglenoid peduncle. There is a large postglenoid foramen. The posterior carotid foramen is large and lies very far back. It is separate from the foramen lacerum posterius. The condyloid foramen is also separate and very large.

PLIOCENE MACHAERODONTS

Two specimens from the Ash Hollow formation of Nebraska (one of which is in the Nebraska State Museum and will be described in detail shortly by C. B. Schultz, the other in the Frick collection and also to be the subject of a detailed paper some time in the future), illustrate in an interesting way the further evolution of the auditory region in the Eumiloid group.

The specimens consist of two very complete and well-preserved skulls and lower jaws with some associated skeletal material. They are clearly machaerodonts but of a line divergent from the typical *Smilodon* of the Rancho la Brea tar pits. The dentition is of the hoplophonoid type with most of the characteristic features developed to a much greater degree than in *Smilodon*. As the writer pointed out in an earlier paper (Hough, 1950), weakness of the lower jaw in the latter seems to be a degenerate feature. These specimens not only have proportionally more alongate and recurved sabers but also strongly developed flanges to the lower jaw with flaring lobate margins which closely resemble those of the marsupial *Thylacosmilis*. The reduction of the premolars and the enlargement of the carnassial has proceeded to such an extent that P⁴ and M₁ are the only functional cheek teeth. They extend along the entire margin of both jaws and have the backward inclination characteristic of the hoplophonoid and eumiloid group. In youth the high crowns are trilobate and trenchant. Even in old age they remain efficient shearing instruments because the occlusal relations are such that the wear is oblique (almost a 45 degree angle, in fact), and the crowns may be worn to the gums on one margin while retaining a sharp cutting edge on the other.

As would be expected, the mastoid processes are strongly developed, almost covering the entire auditory region. The tympanic bulla is represented by only a small swelling on the extreme medial portion of the auditory cavity. This cavity is therefore largely excavated in the mastoid, the hypotympanic sinus extending far into the mastoid process as in many modern mustelids. The condition parallels that of *Smilodon*, to be described in detail later, but differs enough to emphasize the divergence of the lines of descent. (In the writer's opinion there were many lines of descent

from the widespread hoplophoneid population of the early Oligocene.)

The smaller skull, which is also younger geologically as it comes from the middle level of the Ash Hollow formation, has a shorter upper canine with less curvature and a moderately developed flange to the lower jaw. Morris Skinner, who collected the specimen, rec-

SMILODON

GENERAL CHARACTERS

The auditory region of the well-known Pleistocene saber tooth from the Rancho la Brea Tar pits has been fully described by Merriam and Stock. The basic structure is the same as in *Hoplophoneus*, but this similarity is masked by the enormous development of the

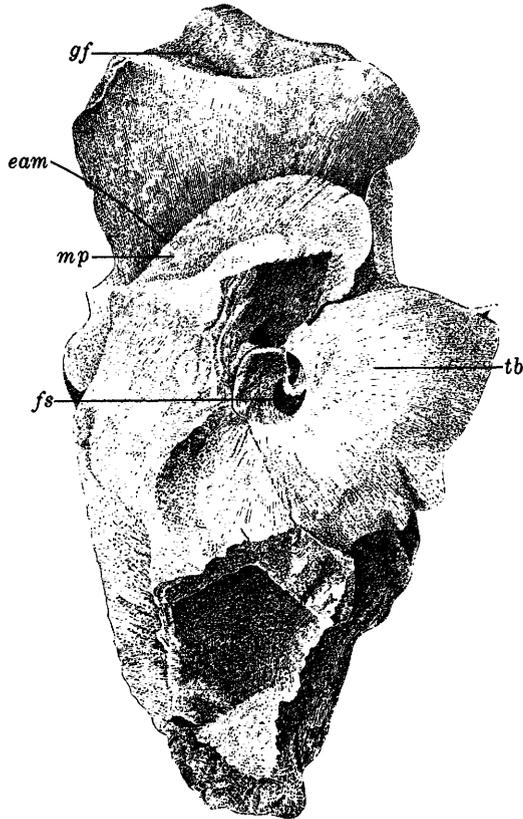


FIGURE 6.—*Smilodon californicus* Merriam, Chicago Natural History Museum 12409; ventral view of auditory bulla, $\times 1$. Anterior at top, median side at right.

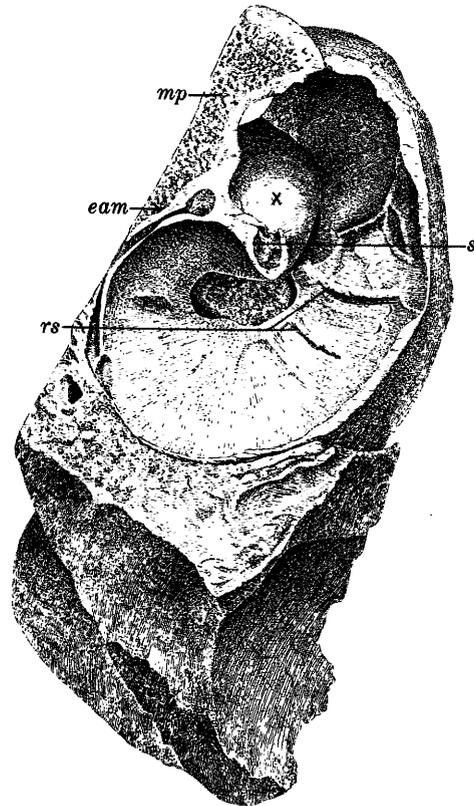


FIGURE 7.—*Smilodon californicus* Merriam, Chicago Natural History Museum 12563; section through auditory region to show horizontal septum, $\times 1$. Anterior at top, median side at right.

Symbols used on figures

<i>ao</i>	auditory ossicle	<i>fenr</i>	fenestra rotundum	<i>pp</i>	paroccipital process
<i>b</i>	bullae, remnant	<i>flm</i>	foramen lacerum medius	<i>p</i>	promontorium
<i>ce</i>	cartilaginous entotympanic	<i>flp</i>	foramen lacerum posterius	<i>rs</i>	radiating septae
<i>eam</i>	external auditory meatus	<i>fr</i>	foramen rotundum	<i>s</i>	major septum
<i>eb</i>	entotympanic part of bulla	<i>fs</i>	stylo-mastoid foramen	<i>tb</i>	tympanic bulla
<i>eo</i>	exoccipital	<i>gcc</i>	groove for carotid canal	<i>tm</i>	remnant of in-bent margin of
<i>fc</i>	condyloid foramen	<i>gf</i>	glenoid fossa		tympanic
<i>fenc</i>	fenestra cochlearae	<i>mp</i>	mastoid process	<i>tr</i>	tympanic ring

ognized its transitional nature. This is confirmed by the auditory region. The mastoid is less markedly developed along the posterior margin of the basicranial region and much less extended over the auditory cavity. The tympanic bulla is large for a machairodont and highly inflated, especially dorsoventrally. There is apparently little extension of the hypotympanic sinus into the mastoid process, although this point requires further investigation.

mastoid processes, which are the most conspicuous external features of the basicranium (figs. 6, 7). In some specimens this overgrowth of the mastoid process is so great that it completely bridges the external auditory meatus and is in contact with the base of the post-glenoid process. In almost all specimens the breadth anteromedially equals that of the auditory bulla. In fact, as Merriam and Stock point out (Merriam and Stock, 1932), in many skulls the bullae appear as slight

swellings on the inner side of the heavy mastoid. In only one specimen described by them (University of California, no. 11256) and a few immature skulls examined by the writer is the bulla larger than the mastoid.

The paroccipital forms a distinct leaflike process that projects backward much as in *Hoplophoneus* and not like that of *Eusmilis*.

INTERNAL STRUCTURE OF THE AUDITORY BULLA

The tympanic itself is flask shaped, with a long tubular meatus similar to that of *Hyaena*. In the majority of skulls it is highly inflated and has a steep medial wall. The auditory meatus is roofed by the squamosal, which also forms the anterior wall. The posterior wall is formed of the mastoid. In specimens in which the mastoid does not come in contact with the postglenoid process the floor is formed of a narrow wedge of the tympanic. This wedge becomes narrower but persists even if completely covered over by the mastoid.

The cavity of the bulla is divided by a septum which is not, however, in the same position as that of *Felis*, and in the writer's opinion is not a septum bullae. The septum in *Smilodon* is a horizontal sheet of bone dividing the bulla into dorsal and ventral parts. The dorsal or upper chamber is the smaller. The hypotympanic sinus is almost entirely dorsal of the cavum tympani and continues into the paroccipital. The much more extensive ventral chamber containing the acoustic portion of the ear extends from the foramen lacerum medium to the base of the paroccipital process and extends laterally into the mastoid process, which is hollowed out and lined with the tympanic. Merriam and Stock describe essentially the same condition. They term the two divisions the outer and inner chamber. The ventral chamber, however, is "outer" only anteriorly, where of course it communicates with the external auditory meatus. On the other hand, the "inner" chamber of Merriam and Stock extends forward, beyond the ectotympanic chamber not only medial to, but actually above that chamber. It is topographically more accurate, therefore, to term the two divisions upper and lower.

The lower or tympanic chamber extends medially to cover all of the petrosal except a small portion of the promontorium just around the fenestra cochleae. Just below the promontorium at this point a narrow slit-like aperture provides communication with the upper chamber. From the inner roof of the latter several ridges radiate to the lateral margins. In many specimens one of these is strongly enough developed virtually to divide the chamber into an outer and inner portion.

THE STRUCTURE OF THE MIDDLE AND INNER EAR

The external auditory meatus extends very far into the tympanic cavity. It is a narrow tube with a very thick floor formed, as stated before, of a thin wedge of the tympanic underlain by the mastoid. The external opening is very far forward. From this the meatus slants posteriorly and dorsally. The crista tympani is thus obliquely placed, the lowest part being just opposite the internal opening of the Eustachian tube. There is no extension of the hypotympanic sinus along the sides of the meatus. The dorsal chamber, however, extends above the meatus for almost its entire length.

The promontorium is large and broadly oval. It slopes gradually and equally in all directions. The fenestra cochleae is also large and round, and faces posterolaterally. Because the septum lies just above and anterior to the fenestra, it opens into the ventral chamber.

The fenestra vestibula faces anterolaterally. Lateral and anterior of it is the very large fossa for the tensor tympani. The epitympanic recess is deep, extending well under the roof of the meatus. A short sulcus facialis extends from the fenestra vestibuli to the base of the ridge leading downward and somewhat laterally to the stylomastoid foramen. This foramen lies far forward because of the extreme anterior extension of the mastoid process. A ridge along the anterior margin of the mastoid process is pierced by a canal that evidently formed the bony third part of the facial canal, which is thus almost vertical.

BASICRANIAL FORAMINA

There is no alisphenoid canal. The postglenoid foramen, which varies in size but is minute in some specimens, is entirely hidden by the coalescence of the mastoid and postglenoid processes. The condyloid foramen and the foramen lacerum posterius are somewhat separate, but connected by a common groove. The degree of separation is varied. In some skulls the two foramina are about as close together as those of the lion and tiger and may be said to have a common opening. In others they are as far apart as in the dog and the groove connecting them is shallow. It is interesting that in the true felid, *Panthera atrox* contemporary with *Smilodon*, the two are well separated. Merriam and Stock report that only 4 or 5 of a total of 20 specimens have a condition resembling that of *Felis*.

The carotid canal was not conspicuous in any of the skulls examined by the writer and Merriam and Stock do not describe it although the position is indicated in one of their illustrations (1934, pl. 15, fig. 1). The carotid artery was evidently minute in relation to the size of the size of the head in fact, possibly degenerated

beyond that of *Felis*. The posterior carotid foramen opens into a common fossa with the foramen lacerum posterius and is also inconspicuous.

SUBFAMILY NIMRAVINAE

DINICTIS (OLIGOCENE SPECIES)

EXTERNAL CHARACTERS

Many specimens of *Dinictis*, like those of *Hoplophoneus*, have no bulla. There are more, however, in which parts of the bulla are preserved, and in all cases these specimens are also more complete otherwise. In the skull of a young individual of *Dinictis*, U.S.N.M. 15889, collected from Niobrara County, Wyo., almost the entire anterior part of the bulla is intact (fig. 8). An American Museum specimen, figured by Matthew (1910) as *Dinictis squalidens* Cope also has a well-preserved auditory region with enough of the bulla to show clearly its shape and size.

The parts of the bulla that remain do not in any way correspond to the anterior chamber of the bulla of the recent Felidae. In the National Museum specimen, for example, the anterior portion of the bulla on the left side extends in contact with the basisphenoid about halfway along the medial margin of that bone. No flattening or differentiation distinguishes this medial portion of the bulla from that immediately surrounding the auditory meatus. On the right side only a circular rim of bone around the auditory meatus remains. The broken edge is irregular and there is no trace of a septum.

Impressions on the overlying bones, and also the portions which remain, show that the bulla in *Dinictis* must have been very large and well inflated. It extended from a point well beyond the base of the postglenoid process anteriorly, almost to the edge of the skull laterally and posteriorly to the base of the paroccipital process. The inflation was even, giving the bulla a globular shape similar to that of the modern Canidae.

The external auditory meatus faces laterally and only slightly forward differing markedly from *Hoplophoneus* in this respect. It is oval in outline and formed almost entirely of the tympanic. The two legs are almost in contact across the roof excluding the squamosal. The mastoid process, although more prominent than in the living Canidae and Felidae, is small compared to that of *Hoplophoneus*. It consists of a rugose knob of a size usual for *Procyon*.

The paroccipital process projects backward as a flattened, triangular lobe very like that of *Daphoneus*.

INTERNAL STRUCTURE OF THE BULLA AND MIDDLE EAR

The auditory cavity proper is shallow, as is usual in dinictids, and in contrast to *Hoplophoneus*. The an-

terior part is roofed by an extension of the alisphenoid that meets the basisphenoid laterally and is in contact with the promontorium by a narrow process. From the anteromedian corner a ridge runs parallel to the raised rim of the basisphenoid. Lateral to this, a groove marks the position of the Eustachian tube, and medially a similar groove leads into a large open space between the posterior margin of the alisphenoid and promontorium. This condition is unlike that of either the Canidae or Felidae where the alisphenoid meets the base of the promontorium and completely roofs the cavity, somewhat as in the Ursidae.

The epitympanic recess is relatively shallow and does not extend far under the meatus. There is a conspicuous fossa in the squamosal just anterior of the base of the mastoid process. This is somewhat similar to the suprameatal fossa of the Procyonidae but it is deeper, and more medial and posterior in position.

The promontorium is pear-shaped, much as in *Daphoneus*. The fenestra vestibuli is small and faces laterally. A narrow spur bridges the space between this and the mastoid. Along this a groove passes from the fenestra vestibuli to the large round foramen stylo-mastoideum primitivum. From this a wider groove deeply excavated in the knob like mastoid continues obliquely downward and slightly forward along the peduncle to its tip. This groove undoubtedly is the external part of the facial canal and marks the exit of the facial nerve from the skull.

The fenestra cochlaeae faces postero-laterally and is located very far back—again a similarity to *Daphoneus*.

BASICRANIAL FORAMINA

An alisphenoid canal, whose posterior opening is in a common fossa with the foramen ovale, is present. The position of this fossa is much as in *Hoplophoneus*, that is, just medial to, and on a line with, the anterior rim of the glenoid fossa. There is a large postglenoid foramen. The carotid canal lies in a distinct groove in the basioccipital extending from the foramen lacerum medium to the posterior medial corner of the bulla. The medial margin of the promontorium meets a process from the basioccipital which forms a roof for this canal for a short distance. The posterior carotid foramen is at the extreme postero-medial corner of the bulla. Just adjacent to it but entirely separate is the foramen lacerum posterius. The condyloid foramen is large and situated just behind and slightly medial to the depression in the rim of the auditory cavity, which, when the bulla was present, marked the common exit of the foramen lacerum posterius and the posterior carotid foramen.

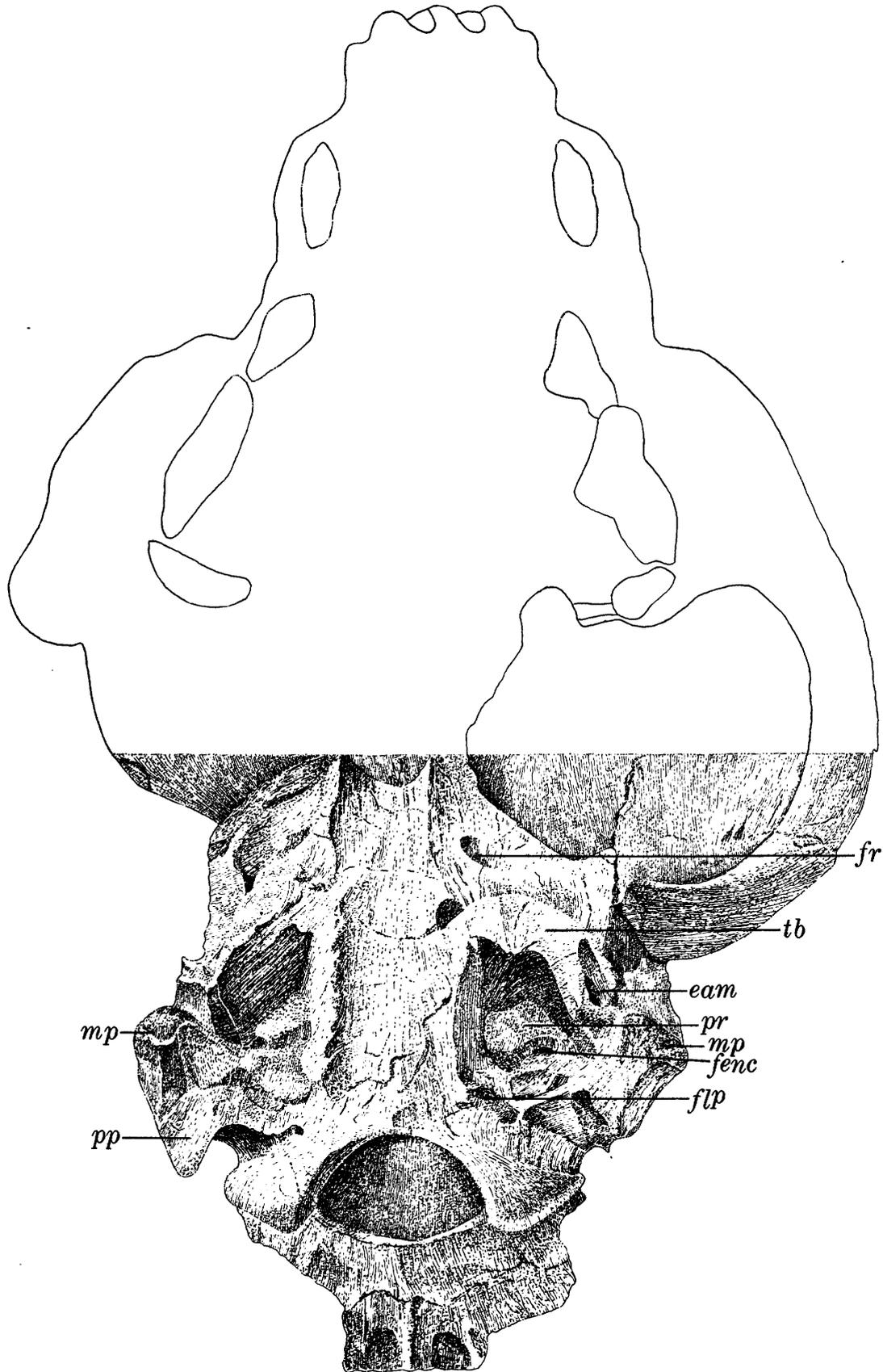


FIGURE 8.—*Dinetis felina* Leidy, U. S. National Museum 15889; a young individual, $\times 1\frac{1}{2}$.

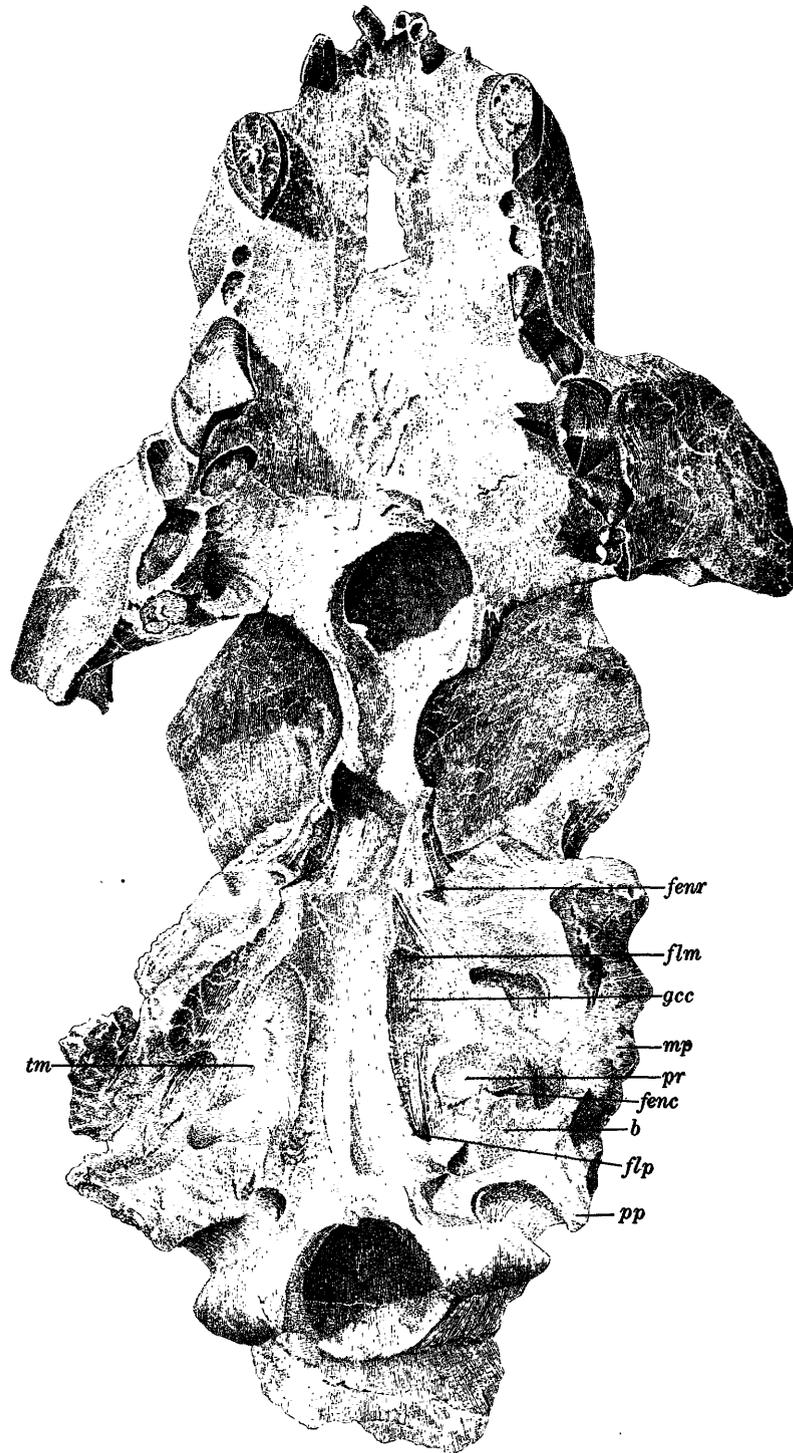


FIGURE 9.—*Dinictis cyclops* (Cope), U. S. National Museum 16558, $\times 1$.

***DINICTIS CYCLOPS* COPE (JOHN DAY SPECIES)**

The matrix has not been removed from the remnants of the large completely ossified bulla which was evidently present in the type specimen, American Museum of National History 6930. Further preparation, which would remove the cast of the interior of the bulla

formed by the matrix, did not seem necessary as a skull in the National Museum (16558) from the same locality also has the floor of the bulla broken away but with no hard matrix, so that the overlying well-preserved structure is exposed (fig. 9). This is closely similar to that of the White River dinictids, except in two

very significant respects. The roof is more completely ossified, with the alisphenoid meeting the base of the promontorium laterally and forming the anterior margin of the large foramen lacerum medium medially. More important still, there appears to be a trace of a septum bullae. This is actually represented by only a low broken ridge, but it is in the same position as that of *Felis* and the anteroexternal surface of the promontorium is flattened and grooved in such a way as to indicate strongly the presence of a well-developed anterior chamber. If this interpretation is correct, however, the chamber was relatively large and well inflated, similar to that of *Felis* rather than of *Panthera*.

The basicranial foramina present no significant change from the condition in the Oligocene genera. There is an alisphenoid canal with a large foramen rotundum transversely placed. The postglenoid foramen is unusually large. The condyloid foramen is also large and well separated from the foramen lacerum posterius.

The posterior carotid foramen is large and, although posterior in position, is separate from the foramen lacerum posterius. The carotid canal is represented by a deep groove extending directly forward from the posterior carotid foramen, along the medial margin of the promontorium, to the foramen lacerum medium.

NIMRAVUS

The auditory region of the White River species, *Nimravus bumpensis* does not differ in any important respect from that of *Dinictis* except that the bulla, judging from the portion which remains in the type specimen and the cast of the interior of the bulla present on one side, was smaller and less inflated. The basicranial foramina are the same in size, number and arrangement.

The John Day species *Nimravus gomphodus* and *Nimravus (Archaelurus) debilis* have remnants of a highly inflated, well rounded bulla. These remnants in *Nimravus debilis* consist of a broad circle of bone around each auditory meatus. In shape and symmetry they strongly suggest an anterior chamber. There is no trace of a septum so that if a division of the bulla existed in these early forms the septum must have been one that did not reach the roof of the auditory chamber. Moreover, if an anteroexternal chamber existed, it was relatively large and highly inflated as in most species of *Felis*. This is in contrast to the Pseudaelurinae.

SUBFAMILY PSEUDAEURINAE

AMERICAN GENERA

The auditory region of *Pseudaelurus intrepidus* has been admirably described by Stock (1934, pp. 1052-

1053). This description is summarized here, with a few notes for the sake of comparison.

The bulla, which although completely ossified is small, is divided into two externally visible chambers. The anterior chamber is much the smaller and very much flattened, as in *Panthera* and certain tropical species of *Felis*. The posterior portion is globular, very much higher than the anterior, and has a steeply sloping medial wall. The auditory meatus is triangular, with no lip or tubular prolongation. The anterior wall is in contact with the base of the postglenoid process. The posterior wall meets the mastoid process. The floor of the meatus appears to be composed only of the squamosal.

The mastoid process is but little developed and entirely separate from the paroccipital process. The latter is a triangular flattened lobe that is directed backward much as in *Daphoenus*.

Compared with the small size of the bullae, the basioccipital region between them appears very broad.

The cranial foramina are transitional. There is an alisphenoid canal. The postglenoid foramen seems to have been very minute. (This part of the skull is crushed so that the size and position could not be exactly ascertained.) The posterior lacerate foramen is large and well removed from the condyloid foramen. The carotid canal could not be traced but the posterior carotid foramen apparently opened into the foramen lacerum posterius.

ASIATIC AND EUROPEAN GENERA

Metailurus of the upper Miocene of China, as described by Teilhard de Chardin (1945) has an auditory region closely similar to that of *Pseudaelurus*. The bulla is two chambered, with the anterior external chamber much the smaller and flattened, and the posterior chamber globular much like that of *Felis*.

Therailurus from the Pliocene of France (Piviteau, 1931) also has a flattened anterior chamber to the bulla, but this is much smaller in relation to the highly inflated posterior chamber than in *Metailurus*.

In both *Metailurus* and *Therailurus*, however, the basicranial foramina show a notable advance in a feloid direction. There is no postglenoid foramen, no alisphenoid canal and the carotid and condylar foramina are closely connected with the foramen lacerum posterius.

SUMMARY AND CONCLUSIONS

Two facts stand out clearly from the foregoing descriptions:

1. The auditory region in the Oligocene Felidae is distinctly canoid both in the absence of a septum bullae

and in the form, number, and position of the basicranial foramina.

2. The auditory region in the post-Oligocene Felidae (Machaerodonts as well as true felines) has the diagnostic characters of the Feloidae.

So impressed was Teilhard de Chardin with this distinction that he based his classification upon it, but without any phylogenetic implications, as he expressly states. The Oligocene Felidae, the Paleofelidés of his classification, are sharply separated from the post-Oligocene Neofelidés. These two major categories are subdivided into normal and saber-tooth types. This arrangement, especially when presented in diagrammatic form, brings out forcibly the parallelism which is such an essential feature of the family, but leaves the phylogenetic relationships very much in doubt. (It also does not express the parallelism with entire correctness, since there are both saber-tooth and normal type canines in the Nimravinae and Pseudaelurinae.)

The Asiatic record, with which Teilhard's classification is primarily concerned, commences with the Miocene. As he points out no "primitive" Oligocene cats are found in China, even in otherwise richly fossiliferous beds of that age. The situation in North America is quite different. The Oligocene record of the family is well documented and, although few Miocene and Pliocene specimens are known at the present time, they provide a series of transitional forms linking the early Machaerodonts with the Pleistocene *Smilodon*, and the Nimravinae with the Felinae. It seems reasonable to suppose, therefore, if the currently accepted phylogeny of the Felidae first proposed by Matthew (1910) is correct, that an evolution of the auditory bulla toward increasing complexity took place in both subfamilies. In the Machaerodonts, a horizontal septum was formed, something like that of the Hyainidae, dividing the cavity of the bulla into a lower, anterior chamber and an upper, posterior chamber. In addition, radiating rafters and septae complicate the walls of the posterior chamber, much as in certain modern mustelines such as the wolverine.

In the Felinae, the septum was formed in the position of that of *Felis* but was at first an incomplete septum similar to that found in certain of the Canidae. Increasing ossification in this region produced a complete septum that divided the bulla into the typical anterolateral and posteromedial chambers.

The basicranial foramina underwent a transformation as the venous and arterial system of the head changed from a canoid to a feloid type. This evolution, like that of the septum bullae, was a gradual thing that first developed to different degrees in individuals and was only slowly fixed in the entire population.

It is possible, of course, to insist on the rigid homology of the two-chambered bulla and on this basis to exclude all of the Oligocene genera, *Nimravus* and *Dinictis* as well as *Hoplophoneus* and *Eusmilis*, from the ancestry of the Felinae. Under this hypothesis such ancestry must be sought in a series entirely independent of the North American fossil forms as we know them.

This view has not been without its defenders. Cope originally separated all of the fossil Felidae, including *Pseudaelurus* (which, of course, he did not know from complete North American specimens) from the modern family. The basis for his Nimravidae, as a later discussion made clear, was the nature of the basicranial foramina.

Gregory's classification (1939) follows a similar pattern. His section Machaerida apparently includes both the Machaerodontinae and the Nimravinae, and the evolutionary series he erects, on the basis of the auditory bulla, consists of *Paleoprionodon* → *Cryptoprocta* → *Felis*. Of course, he considered this sequence only a morphological series illustrating the postulated evolution of the auditory bulla. Nevertheless, if the auditory bullae did evolve in this way, the fossil Felidae are automatically excluded from the ancestry of *Felis*. No known fossil felid has an auditory bulla at all resembling that of *Cryptoprocta*.

Aside from the fact that phylogenies such as these do not correspond to the fossil record as we know it and ignore the transitional stages between the Nimravinae and Felinae, in the writer's opinion there is little in the morphology and embryology of recent forms to warrant such a rigid application of the principle of homology. Since, in any case, a transformation of the venous and arterial system of the head must have taken place (*Paleoprionodon*, like all Oligocene carnivores, has a canoid type of basicranial foramina) a review of the whole question seems in order.

HOMOLOGY OF BASICRANIAL FEATURES OF THE FELOIDEA

SEPTUM BULLAE

FORM AND POSITION OF THE SEPTUM IN THE FELOIDEA

It is well known that the form and position of the septum, and consequently of the two chambers into which it divides the bulla, differ very much in the Viverridae and Felidae, and even more widely in the other families usually included in the Feloidae. In the Viverridae the septum, which is really the posterior wall of the anterior chamber, is in contact with the basisphenoid medially for some distance so that the tympanic chamber is entirely anterior in position and

the entotympanic posterior. In the typical Viverridae the anterior chamber is always the smaller, and somewhat flattened. The size of the posterior chamber may vary, but these relationships remain the same. In the Felidae the septum, also the posterior wall of the anterior chamber, has no contact with the basisphenoid, but curves posteriorly and laterally from the anteromedial corner of the bulla and meets the crista tympani at a point just opposite the stylomastoid foramen. The tympanic takes no part, therefore, in the medial wall of the bulla which is formed throughout by the entotympanic in contact with the bones of the midline of the skull. The chambers formed are anterolateral and posteromedial. In the Felinae, as in the Viverridae, there is considerable variation in the proportions of the two chambers, but the anterior chamber (even if highly inflated, as in *Felis catus*) is always the smaller. In *Panthera* and some of the tropical species of *Felis* the anterior chamber is much flatter and very narrow antero-posteriorly.

In *Hyaena* the principal septum extends lateromedially from a point just opposite the stylomastoid foramen across the fenestra cochleae to the medial coner of the bulla as in *Felis* but, since it is a horizontal sheet of bone extending posteriorly almost the whole length of the auditory cavity, it divides the bulla into a very large anterior ventral chamber, and a much smaller posterior upper one. The former is the real bulla. The latter is not a separate chamber formed by an entotympanic, but a cavity in the base of the paroccipital process. Projecting from the horizontal septum there is a ridge somewhat in the position of the septum of *Canis*, but very much shorter in most specimens. It is the greater or lesser development of this ridge that gave rise to the various early statements, seemingly contradictory, as to the presence or absence of septae.

Pocock (1916) sought to homologize the septum in *Hyaena* with that of the Viverridae. No doubt it does represent the posterior wall of the tympanic chamber, but in this sense it is equally homologous with the posterior wall of the bulla in the Canidae. It is certainly not, so far as form and position are concerned, homologous with the septum in either *Felis* or *Viverra*.

The structure of the bulla in *Proteles* is unique, and unlike that of either *Hyaena* or the Felidae, but with some points of resemblance to that of the Viverridae. The anterior chamber of the bulla is flask-shaped and has a long tubular meatus resembling that of many of the Mustelidae. It appears complete in itself with a well-rounded convex posterior wall. This wall is paper-thin and composed entirely of the tympanic. The promontorium lies far forward and is completely

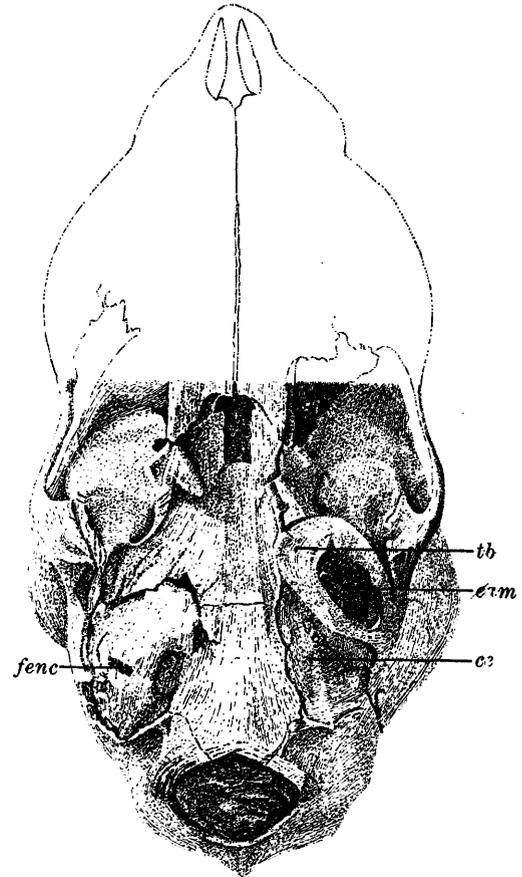


FIGURE 10.—*Viverricula indica rasse* (Horsfield), U. S. National Museum 154917; young individual, $\times 2$.

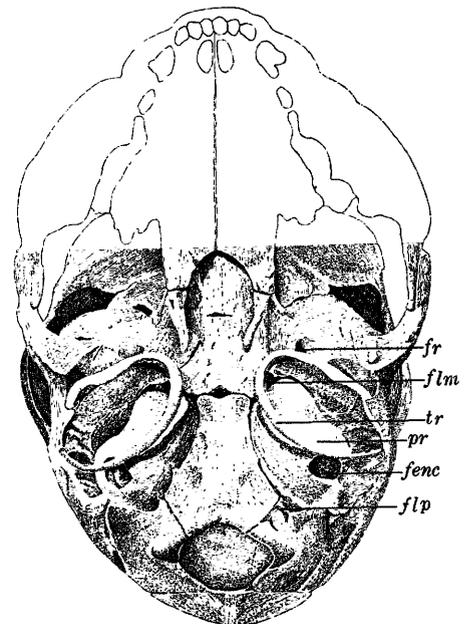


FIGURE 11.—*Felis catus* Linnaeus, U. S. National Museum 188652, young individual, $\times 2$.

enclosed by the anterior chamber, the posterior wall of the chamber lying posterior of the fenestra cochleae. A well-marked sulcus in the periotic, with a raised bony rim, extends past the fenestra cochleae and into a bony canal between the mastoid process and the posterior chamber. This chamber is an entotympanic ossification, but is not closely homologous with that of the Felidae and Viverridae. The anterior wall is applied to the under surface of the anterior chamber and united to it by suture. Laterally, there is a suture between the entotympanic and the mastoid which can be traced from the posterolateral corner of the auditory meatus downward and backward to the posterolateral corner of the posterior chamber. At this point it joins the paroccipital process—which is very large and leaf-like, and forms a deep cup which embraces the posterior wall of the bulla. A large part of the lateral wall of the bulla is thus formed by the mastoid rather than by the entotympanic. Dorsally, the mastoid process is hollowed out into a deep rounded cavity. At the antero-medial corner of the posterior chamber a shelf is pressed against the posteromedial wall of the anterior chamber. It extends about halfway across the cavity of the bulla, swinging around posteriorly to merge with the posterior wall. A narrow strip of entotympanic forms the lateral rim of the cavity in the mastoid process, but does not floor the cavity. In the ventral lateral wall of the posterior chamber a few septae radiate from the floor perpendicularly to the anterior wall.

MODE OF DEVELOPMENT OF THE BULLA

As would be expected, the differences in the form and position of the two chambers of the bulla in the adult "aeluroid" Carnivora are foreshadowed by the differences in the mode of development.

In the Viverridae the anterior (tympanic) chamber develops very early and is completely ossified in adult form before there is much ossification of the posterior (entotympanic) chamber. In a very young individual *Viverricula indica raase* (U.S.N.M. 154917, fig. 10), whose milk teeth were not erupted, the anterior chamber is completely ossified. It is a horseshoe-shaped demi-bulla precisely like that of the fossil forms *Daphoenus vetus* and *Paleoprionodon*, and of the adult *Nandinia* (a recent South American viverrid in which the entotympanic remains cartilaginous throughout life). Ossification of the entotympanic takes place first along the medial and posterior margins of the cartilaginous entotympanic, a strip between these ossifications and the anterior chamber remaining cartilaginous until very late in development. The form of the tympanic changes very little. In the earliest stages,

the margins of this chamber are curved upward in such a way as to be almost in contact with the promontorium. This incurved margin forms the septum bullae of the adult. As the strip dividing the tympanic and entotympanic ossifies, the latter coalesces at the point of contact with the septum. A real interior wall to the posterior chamber is thus not formed, and the septum bullae is not composed strictly (as is sometimes stated) by the fusion of two sheets of bone, but of one—the tympanic—with only a slight participation of the entotympanic at the extreme ventral border.

In a felid corresponding in age to the specimen of *Viverricula* mentioned above the only ossification of the bulla is the tympanic ring, a narrow rim of bone encircling the auditory region and lying parallel to and slightly above the promontorium. The space enclosed by this ring is very much greater than that enclosed by the anterior chamber in *Viverricula*. In a specimen of *Felis catus* that died at birth (fig. 11) only a very small part of the posteromedial border of the promontorium lies outside the tympanic ring. The upper margin of the ring is slightly incurved, but is not in contact with the basisphenoid or the petrosal. As ossification proceeds, the ring becomes filled in ventrally, leaving open the large oval external auditory meatus. Simultaneously with this ossification of the anterior chamber, ossification also commences from a tympanic center. This is at first entirely posterior, but the growing entotympanic appears to force the original tympanic ring downward and forward to an oblique position, leaving a wide space filled with cartilage between the medial margin of the tympanic chamber and the basisphenoid. This is gradually filled in by bone developed, possibly, from both centers to form the medial border of the posteromedial chamber. There is no stage in *Felis* where the tympanic forms a complete chamber as in *Viverricula*, with the entotympanic cartilaginous.

At birth the auditory region of *Canis* is strikingly similar to that of *Felis*—much more than the auditory region of *Felis* resembles that of any viverroid studied. There is an ossified ring present in *Canis* in essentially the same position as that of *Felis*, but it is flatter and crosses the promontorium dorsal and posterior to the ventral rim of the fenestra cochleae. In a specimen of *Canis dingo* which died at birth only the faintest rim of the posterior part of the auditory region is not encircled by the tympanic ring (fig. 12). In *Canis* as in *Felis* this ring shifts forward and downward as further ossification takes place. This shift is very much less in all cases than in *Felis*, but varies according to the size and degree of the inflation of the fully developed bulla. The part anterior and ventral to the tympanic

ring is formed by an outgrowth of ossification filling in the space enclosed by the ring—except the auditory meatus. Posteriorly, ossification takes place from cartilage as in the formation of the entotympanic in *Felis* (fig. 11). However, this proceeds simultaneously with the growth of the tympanic anteriorly and the two fuse indistinguishably without forming a complete septum or separate chambers.

Van der Klaauw (1931, p. 277) states that an entotympanic is developed in cartilage in *Canis*, but seems to ossify out of the tympanic ring making the bulla simple and seemingly formed by the tympanic alone.

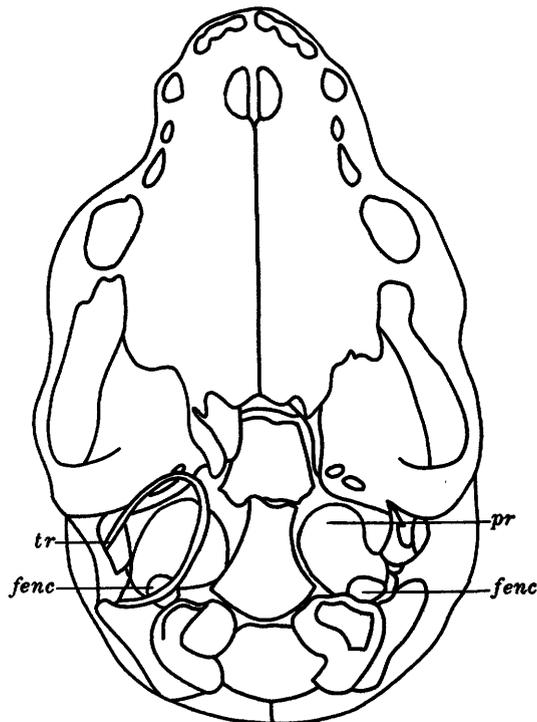


FIGURE 12.—*Canis dingo* Meyer, U. S. National Museum 8742, at birth, $\times 5$.

On a later page, however, he warns against homologizing the faint line which crosses the bulla in *Canis* in very much the same position as a similar one in *Felis* marking the division between the tympanic and entotympanic. The former he says marks the position of the septum in *Canis* and so has nothing to do with the similar line in *Felis* because the septum of *Canis* is not homologous with the septum in *Felis*. This seems a very confusing statement. The fact is that the line on the bulla in *Canis* does mark the division between the tympanic and entotympanic, that is, the position of the original tympanic ring, just as it does in *Felis*. The margins of this ring in *Canis*, however, are not incurved even originally to the same degree as in *Felis* and further ossification in that direction does not take place so

no septum is formed from the tympanic. The partial septum found in some Canidae is a later development formed entirely by the inner margin of the entotympanic. It is not homologous in the strict ontogenetic sense with that of *Felis*, since the septum in *Felis* is formed from both the tympanic and entotympanic, but neither does it correspond to the septae and rafter which radiate from the crista tympani in such mustelids as the wolverine. All of these forms, however, have this in common: The septae formed are neomorphs ossifying from membrane relatively late in ontogeny, and probably late phylogenetically as well. In the Viverridae, on the other hand, the posterior wall of the anterior chamber ossifies very early and a complete anterior chamber is formed before any ossification commences in the entotympanic cartilage. As will be shown, this also agrees well with the probable phylogenetic history of the bulla in the Viverridae.

BASICRANIAL FORAMINA

In all mammalian embryos, including that of man, there is a large postglenoid foramen. Intracranial blood is carried from the skull largely by the internal jugular. In some orders, notably the Artiodactyla, this is also true of the adult—the postglenoid foramen in the adult is enormous, and the external jugular the sole vein leading from the cranium. In man, an opposite development takes place; the postglenoid foramen closes shortly before birth, the external jugular atrophies, and the lateral cranial sinus is drained by the internal jugular, which leaves the skull through the large foramen lacerum posterius.

In all adult Carnivora there is some modification of the embryonic condition. This is relatively slight in the Arctoidea, somewhat greater in the Canidae, and in the Felidae and Viverridae parallels the condition in man.

Similarly, there are changes in the cranial arterial system from the embryo to the adult. These, however, are not inevitably linked with the venous changes, but can occur independently. In man, (where the venous system is extensively modified in the adult) the internal carotid, which is a large and important artery in the foetus, remains so throughout life. In the Arctoid Carnivora (Ursidae, Procyonidae, Mustelidae) also, the internal carotid artery is large and conspicuous in the adult (half the diameter of the external carotid) with a strongly developed bony canal and a large conspicuous posterior carotid foramen. Because the venous system in this group also retains much of the embryonic condition and the internal jugular is relatively small in size the foramen lacerum posterius is not

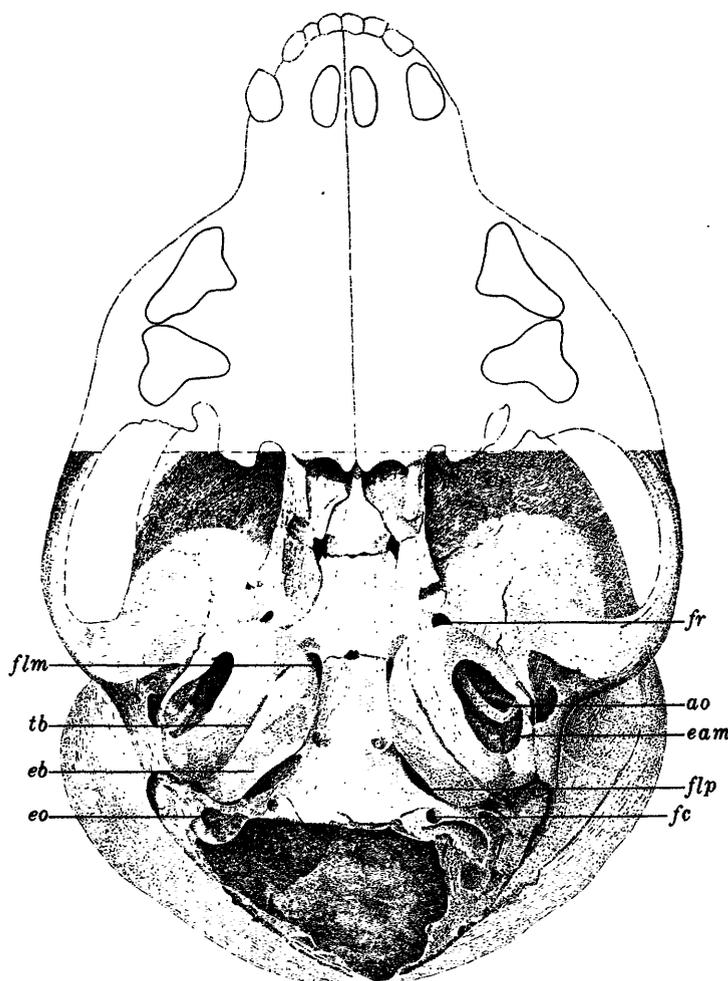


FIGURE 13.—*Vulpes velox* Frisch, U. S. National Museum 25425, young individual, $\times 2$.

exceptionally large and does not conceal the condyloid foramen.

In the Felidae, both the venous and arterial systems are profoundly modified in the adult. The internal carotid artery becomes vestigial, in the domestic cat imperforate throughout most of its length. The ascending pharyngeal (a branch of the external carotid) takes over the intracranial portion of the circulation. This degeneration of the internal carotid reaches its extreme in the domestic cat. In *Panthera*, however (Davis and Story, 1943), the internal carotid although minute in size, is perforate at least for some distance beyond its origin. It passes through the middle ear in the normal way, enters the foramen lacerum medium and anastomoses with the circle of Willis. This is in contrast with the condition in the domestic cat where the ascending pharyngeal is the dominant vessel beyond the foramen lacerum medium.

The Viverridae, although tending in the same direction as the Felidae (the reduction of the internal carotid), achieves this in a different manner, and to different

degrees in the various genera. In *Nandinia*, according to Davis and Story (1943) the internal carotid is a relatively slender vessel, and it is described by Tandler (1906) as considerably weaker than the external carotid. In *Herpestes* on the other hand, the caliber is about the same proportionally as in the Arctoid Carnivora, but the canal is extremely short. In all of the Viverridae (except *Nandinia*, where the bulla is incompletely ossified), there is a well-developed bony canal similar to that of the Mustelidae, and a conspicuous posterior carotid foramen situated very anteriorly.

The changes in the venous system in the Viverridae have proceeded much further. Virtually all of the genera usually included in this family even aberrant forms such as *Cryptoprocta* and *Hyaena* have a minute postglenoid foramen and a small concealed condyloid foramen.

The Canidae have some characteristics that ally them with the Arctoidea, some with the Feloidea. The venous system is entirely "arctoid," with a large postglenoid foramen and conspicuous condyloid foramen.

The internal carotid is also well developed, but the course of the artery and the structure of the canal resemble that of the Felidae rather than that of the Mustelidae, Procyonidae or Ursidae. There is no bony canal formed of the tympanic. Instead the artery runs forward to the foramen lacerum medium through a groove formed of the periotic and the inner margin of the tympanic. The posterior carotid foramen is concealed in a common fossa with the foramen lacerum posterius.

SUMMARY AND CONCLUSIONS

EVOLUTION OF THE INTRACRANIAL CIRCULATION

As is pointed out above, all Oligocene Carnivora have a "canoid" type of cranial circulation. Even such forms as *Paleoprionodon*, which have been considered ancestral "feloids" because of the demi-bulla and viverroid features of the dentition, have a postglenoid foramen and a large unconcealed condyloid foramen. A transformation of the cranial circulation from the "canoid" to the "feloid" type must therefore have taken place—unless one is to consider the Felidae to have been created at the beginning of the Miocene.

As a matter of fact, the stages in this transformation are well shown by the North American specimens of fossil Felidae. *Pseudaelurus* is a perfect intermediate form, in these respects, between *Nimravus* and the Felinae. When the basicranial region of various other American pseudaelurines becomes known, still other stages will probably be demonstrated. It is possible, for example, that *Adelphailurus* (now known only from an incomplete skull) had somewhat the same combination of features as *Metailurus* of China, or *Therailurus* of the Pliocene of France, that is, no postglenoid foramen and no alisphenoid canal, a large condyloid foramen, and well-defined carotid canal with the posterior carotid foramen distinct from the foramen lacerum posterius.

The machaerodonts show a similar evolution. As there is good evidence that this group was distinct from the Nimravinae as far back as the early Oligocene, these changes must have proceeded independently in the two lines. The degeneration of the carotid artery seems to have taken place at a faster rate than in the Felinae. The union of the posterior carotid foramen with the posterior lacerate foramen is more complete and more constant in *Smilodon* than in *Felis atrox*. It is important to note that in both these genera, known from hundreds of specimens, the extreme condition, either way, exists as an individual variation. It seems probable, therefore, that all of these changes began as individual differences and that evolution to the

modern type consisted in the gradual fixation of such random variations.

This is entirely in accord with the arrangement of the foramina as they actually occur in the living members of the Felioidea. There is not a feloid "type". The changes in the venous and arterial system occur in different combinations and to different degrees not only as between the Viverridae and Felidae, but among the genera that comprise the respective families. The similarity of arrangement, therefore, is far better interpreted as progressive evolution taking place independently in various vertical lines of descent, rather than a phenomenon linked with phyletic branching.

EVOLUTION OF THE AUDITORY BULLA

The evolution of the auditory bullae in the Felidae presents a more difficult problem than that of the basicranial foramina, partly because of the imperfect preservation of the bulla in all Oligocene felids and partly because of the universal belief, amounting almost to dogma, in the strict homology of the two-chambered bulla.

However, it is seen from the foregoing discussion that there is no close correspondence in detail in the form and position of the septum which divides the bulla into two chambers in the Viverridae and Felidae—to say nothing of the Hyaenidae and *Proteles*. Furthermore, the mode of formation of the two chambers in the Felidae differs as much from that of the Viverridae as from that of the Canidae. The similarity which exists (the formation in the adult of two complete chambers) is an end result rather than a step-by-step correspondence in detail. In fact, the early stages in the formation of the bulla in the Felidae resemble those of the Canidae more closely than those of the Viverridae do these of the Viverridae. The Canidae, in turn, differ from other "canoid" carnivores in having an entotympanic center of ossification.

A demi-bulla of the type found in the recent *Nandinia* was undoubtedly "primitive" for all of the Viverridae. Gregory's assumption that *Viverravus minutus* has such a bulla is based on an erroneous interpretation of a figure of Teilhard de Chardin (1914–1915, pl. 9, fig. 10). This figure and the description, and also an examination of the specimen of *Viverravus* in the American Museum collection show that the structure in question is the promontorium. The bulla in *Viverravus*, as in all miacids, was unossified. Nevertheless, the general idea is apparently correct. The Viverridae did originate from various miacid populations (probably in different places and at slightly different times) and, the writer believes, had a demi-bulla of

this type from the beginning. Possibly there never was a central type at any time, and such universally recognized genera as *Prionodon*, *Herpestes*, *Viverra*, *Arctictis* etc. are each the result of the separate development of a vertical cline.

There is absolutely no paleontological evidence that this kind of demi-bulla was primitive for the Felidae. Both the Machaerodontinae and the Nimravinae are as old, if not older, than the Viverridae. The earliest Oligocene representatives of both the former are highly specialized animals. Even supposing a common origin with the other Carnivora, from a miacid ancestry (which the writer considers doubtful, at least for the Machaerodontinae), a long period of progressive evolution separates *Hoplophoneus*, *Dinictis*, and *Nimravus* from *Viverravus* or *Paleoprionodon* or any form conceivably included in the Viverridae.

Incomplete though the bullae are in the known specimens of Oligocene felids, to anyone who has studied the auditory region in these forms the evidence is indisputable that the structure was simple and without a septum—certainly not a demi-bulla of the *Daphoenus* type. Therefore, it seems probable that the bullae evolved in the direction of increasing complexity, which improved the efficiency of hearing in both lines of descent, in various populations at various times, in various places. Since there was apparently more migration and consequent interchange of genes than in the Viverridae, this evolution was more universal and produced the uniformity of type so characteristic of later members of the phyla. This is in accord with the known fossil record and with the size, structure, and habits of the animals.

PROPOSED TAXONOMIC CHANGES

In accordance with the views expressed in this paper, the following modification and redefinition of the major taxonomic categories of the Carnivora are proposed. It is not supposed by the writer that this revision represents the final word on the subject. Criticism and suggestions are invited. An attempt has been made, however, to provide a basis for division into superfamilies that will be consistent with the morphology of the forms and their geologic history, in so far as that is known. The superfamily divisions in current use are especially objectionable because they cannot be properly defined, and also because, having been based originally on modern forms, they have an archetypal significance which, when extended to extinct forms readily lends itself to "proof" of erroneous theories of evolution.

SUMMARY OF SUPERFAMILIES AND FAMILIES

Machairodontoidea
Hoplophoneidae
Eusmilidae
Machairodontidae

Diagnosis—This superfamily would include all of the genera listed by Simpson for the Machairodontinae, as well as the new forms from the Ash Hollow formation which are mentioned in this paper. The evidence supporting the separation of this group from the Felidae seems to the writer indisputable. Numerous features of the skull, dentition, and skeleton reveal its unity and its divergence from other carnivore groups. Of these features the most important are:

1. The size and function of the incisors, which throughout the history of the group remain stout grasping teeth.

2. The tendency toward the reduction of the lower canine, which in its most extreme development becomes incisoriform and no longer shears against the upper canine.

3. The high degree of carnassialization. Even in the earliest representatives of the group this is more extreme than in any of the true Felidae, and is unique among the Carnivora in the part played by P³. This tooth never has the grasping function it has in the Felidae, but is a shearing tooth acting with the main carnassial, P⁴. In the Ash Hollow specimens P⁴ is enormously enlarged and elongate while P³ is lost altogether.

4. The backward inclination and peculiar growth pattern of the carnassials, which causes the wear of these teeth to be oblique and maintain a cutting edge even in old age.

5. The size, form, and function of the upper canine, which is not only always extremely long in proportion to the skull and has a broader basal diameter than in any felid, but is also more compressed and recurved.

6. The retention of primitive features, such as the small brain case and pronounced postorbital constriction, even in the Pleistocene members of the group.

7. The auditory region which, even in primitive members, differs in its narrowness, depth, and the position of the tympanic bulla from that of the contemporary *Dinictis*. Compare, for example, figures 5 and 6, where the remnants of the tympanic bulla clearly show a large inflated structure in *Dinictis* and a compressed one in *Hoplophoneus*. In later forms this is fused with, and overgrown by the mastoid. In *Dinictis* and *Hoplophoneus*, additional resonating chambers are produced, not by the development of a large inflated tympanic bulla as in the Felidae, but by excavation of the mastoid process. Septae, if formed, are radiating or horizon-

tal and do not truly divide the bulla into tympanic and entotympanic chambers.

These characters, together with features of the skeleton too numerous to mention here, but which have been described in an earlier paper (Hough, 1950), seem sufficient justification for separation from the Felidae. In addition, that there is no evidence—only purely hypothetical considerations—that the machairodonts had a common ancestry with the Felidae, and certainly no evidence that any genera of the group entered into the composition of the modern family. In popular terms, the early machairodonts were not cats, nor did their descendants become cats in the strict sense of the word. They were throughout their history pseudo-felines, a primitive group, evidently world-wide in distribution judging from the known occurrences, which paralleled the true Felidae—but very remotely—in some features and which successfully over some 22,000,000 years filled an ecological niche similar to that now occupied by the modern cat family.

It is the geological long range, and the ubiquity and diversity, which provide the justification for the superfamily rank. *Hoplophoneus*, *Eusmilis*, and *Smilodon* (to name only the typical North American genera), although possessing the common characters listed above, differ pronouncedly from each other in ways which make ancestral relationships difficult to trace, from the known forms at least. This diversity, which is a matter of combination of characters rather than a marked divergence of any one, points to a common ancestry either very remote or not very unified, that is, from different species or even different genera, rather than from one interbreeding population. It is also probably that the sample known is small in relation to the actual number of genera and species which at one time existed.

Aeluroidea (or Herpestoidea, if strict rules of nomenclature are followed)

Daphoenidae

Viverridae

? Hyaenidae

Diagnosis.—Bulla always two-chambered with the entotympanic cartilaginous in the early forms (Daphoenidae). Basicranial foramina canoid in Oligocene genera, postglenoid and condyloid foramina reduced in all later forms; carotid canal well-developed in all genera that have a completely ossified bulla; posterior carotid foramen large and anteriorly placed.

Discussion.—This is the most certain and stable of the categories. Known as early as the earliest Oligocene, or even perhaps latest Eocene of the Phosphorite beds of Quercy, France, the phylum has retained the same type of auditory bulla and the same trends in the evolution of the dentition throughout its history. The

inclusion of the Hyaenidae is questioned because of the lack of knowledge of the auditory region in *Ictitherium* and in other early representatives that could be transitional between *Hyaena* and the more typical Viverridae.

Cyno-feloidea

Canidae

Felidae

Nimravinae

Felinae

Diagnosis.—Canidae and Felidae representing two diverging branches, one retaining the primitive condition of the undivided bulla with at most a partial septum, the other early developing a rudimentary septum which in later forms becomes complete, dividing the cavity of the bulla into two chambers. Basicranial foramina but little modified from the embryonic condition in the Canidae and early Felidae (Nimravinae); in the later Felidae becoming highly specialized with the complete closure before birth of the postglenoid foramen and atrophy of the internal carotid artery.

Discussion.—This is the most radical change proposed and will seem at first thought to be without foundation. Modern Canidae and Felidae, however, have more characters in common than usually recognized. Neither have any close affinity with any other family—common opinion notwithstanding. Both families are highly specialized for their particular habits of life in all features of the dentition and skeleton. Carnassialization in both has been brought to a high degree of perfection, in the Canidae in conjunction with an equally effective crushing dentition, in the Felidae with all functions of the teeth sacrificed to that of shearing flesh. The Canidae are strictly cursorial; the Felidae semi-cursorial with an advanced type of foot mechanism adapted to their particular mode of attack. Traced backward, however, the characters of the two converge toward each other and also toward the primitive Viverridae. All writers on the subject have pointed out the viverrid characters of *Pseudocynodictis* and the numerous resemblances, in all part of the anatomy, between *Daphoerus* and *Dinictis*. The Oligocene canids and felids, however, agree with one another and differ sharply from the Oligocene Viverridae (the Daphoenidae of this classification) in the characters of the auditory region. Therefore, the earliest separation from closely similar contemporaries can be conceived to be on this basis. If only the Oligocene Carnivora were known, the writer believes that the major taxonomic grouping, if any were attempted, would certainly be on this basis. The Canidae and Felidae, nevertheless, must have diverged before the Oligocene and pursued a separate evolution in dental characters. After the Oligocene

this divergence became also marked in the basicranial region because of the more rapid evolution of the felid branch in this respect. The result was the convergence in the Felidae of characters of the bulla and the venous and arterial system of the head toward the viverrid condition.

Arctoidea

Procyonidae

Ursidae

?Mustelidae

Diagnosis—Bulla simple, without septae or rafters in all early forms and in most later ones. When septae and rafters do form, these are radiating ridges that do not bring about a bipartite division of the bulla. Increasing complexity of the bulla (which aids in resonance) takes the form of hollowing out of the mastoid, the formation of cancellous tissue in the mastoid and paroccipital, and extension of the hypotympanic sinus along the sides of the meatus. Basicranial foramina persistently primitive with little modification from the embryonic condition. Postglenoid foramen always large, the carotid canal a bony tube in the medial wall of the bulla, the posterior carotid foramen large and well separated from the foramen lacerum posterius.

Discussion—The earliest procyonids have a very typical auditory region indistinguishable in essential features from that of the modern representatives of the family. In fact, the earliest procyonids, except for the smaller braincase are almost identical with *Bassariscus*. The evolution of *Procyon* and *Nasua* from these primitive forms presents no difficulty.

The relationship of the Ursidae is more obscure. However, their affinities as far as they are known seem closer to the Procyonidae than to the Canidae.

The early Mustelidae are clearly closely related to the early Procyonidae. There is a persistent tendency for the late Oligocene and Miocene carnivores with a procyonid type of bulla, such as *Plesictis genetoides*, to develop mustelid characters in the dentition. The more complex types of auditory region such as that of *Taxidea taxus* could be easily derived from a simple procyonid type. The family, however, is probably polyphyletic, with some addition of genera developed from later Canidae, which also show mustelid features in the dentition. A more exhaustive study of the fossil mustelids and their relation to the modern genera is needed before these affinities can be properly evaluated.

SELECTED REFERENCES

- Cope, Edward D., 1884, The vertebrata of the Tertiary formations of west: U. S. Geol. Surv. Territories. Hayden, vol. 3, pp. 1-1009.
Davis, Dwight, and Story, H. E., 1943, the carotid circulation in

- the domestic cat: Zool. Ser. Field Mus. Nat. History, vol. 28, no. 1, pp. 5-46.
Dobzansky, Theodore, 1941, Genetics and the origin of the species, 2d edition: Columbia University Press.
Flower, W. H., 1869, On the value of the characters of the base of the cranium in the classification of the order Carnivora and the systematic position of *Bassaris* and other disputed forms: Proc. Zool. Soc. London, pp. 4-37.
Gregory, W. K., 1939, On the evolution and major classification of the Civets (Viverridae) and other fossil and recent Carnivora: a phylogenetic study of skull and dentition: Proc. Am. Phil. Soc., vol. 81, no. 3, pp. 309-342.
Haas, O. A., and Simpson, G. G., 1946, Analysis of some phylogenetic terms with an attempt at redefinition: Proc. Am. Phil. Soc., vol. 90, no. 5, pp. 319-349.
Hough, M. J., 1948, The auditory region in some members of the Procyonidae, Canidae and Ursidae: its significance in the phylogeny of the Carnivora: Bull. Am. Mus. Nat. History, vol. 92, art. 2, pp. 73-118.
Jepsen, Glen L., 1926, the oldest known cat, *Hoplophoneus oharrai*: Black Hills Engineer, vol. 14, no. 2, pp. 1-6.
——— 1933, American Eusmiloid saber tooth cats of the Oligocene epoch: Proc. Am. Phil. Soc., vol. 62, no. 5, pp. 355-399.
Matthew, W. B., 1910, Phylogeny of the Felidae: Bull. Am. Mus. Nat. History, vol. 28, art. 26, pp. 319-349.
——— 1930, The phylogeny of dogs: Jour. Mammalogy, vol. 11, pp. 117-138.
Merriam, John C. and Stock, Chester, 1932, Carnegie Inst. Washington: Publ. no. 422, pp. 3-231.
Piviteau, Jean, 1931, Les chats des Phosphorites du Quercy: Annales de Paleontologie, vol. 20, no. 14, pp. 107-184.
——— 1948, Un Felide du Pliocene du Roussillon: Annales de Paleontologie, vol. 34, no. 13, pp. 3-124.
Pocock, R. I., 1916, The tympanic bulla in Hyaenas: Proc. Zool. Soc. London, pp. 303-307.
Scott, W. B. and Jepsen, G. L., 1936, The mammalian faunas of the White River Oligocene, Part I, Insectivora and Carnivora: Trans. Am. Phil. Soc., new ser., vol. 25, pp. 1-153.
Stock, Chester, 1934, Skull and dentition of the American Miocene cat, *Pseudaelurus*: Bull. Geol. Soc. America, vol. 45, pp. 1031-1038.
Teilhard de Chardin, Pierre, 1914-1915, Les carnassiers de Pl osphorites du Quercy: vol. 9, pp. 103-182.
——— 1945, Les Felides de Chine: Institute de Geobiologie, Peking, Feb. 1945, no. 11, pp. 1-58.
Turner, 1848, On the evidence of affinity afforded by the skull of carnivorous mammals: Proc. Zool. Soc. London, pp. 63-88.
Van der Klaauw, C. J., 1931, The auditory region of some fossil mammals with a general introduction to this region of the skull: Bull. Am. Mus. Nat. History, vol. 67, pp. 1-352.
Van Kampen, P. N., 1905, De tympanalgegend des Saugtier-schadels: Morphol. Jahrbuch, vol. 34, pp. 321-722.
Winge, Herluf, 1895, Jordfundne og nulevende Rovdyr (Carnivora) fra Lagoa Santa, Minas Geraes, Brasilien. Med. Udrgt over Hovdyrenes indbyrdes Slaegstab. Carnivores fossiles et vivants de Lagoa Santa, Minas Geraes, Brsil. Avec un apercu des affinites mutuelles des Carnassiers. E. Musee Lundii, Andet. Bind, Andet Halvbind, Kjobenhavn, pp. 1-130.
Wortman, J. L. and Matthew, W. B., 1899, The ancestry of certain members of the Canidae, Viverridae and Procyonidae: Bull. Am. Mus., Nat. History, vol. 12, no. 6, pp. 109-138.
Zangerl, Rainer, 1948, The methods of comparative anatomy and its contribution to the study of evolution: Evolution, vol. 2, no. 4, pp. 331-374.

