THE AUDITORY REGION IN SOME MEMBERS OF THE PROCYONIDAE, CANIDAE, AND URSIDAE

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JEAN RINGIER HOUGH

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INTRODUCTION

MANY DIFFERENT STRUCTURES and systems of structures have been used as a basis of classification in the Mammalia. Gervais, in his "Histoire naturelle" (1854), comments on the multiplicity of schemes in use in his time and the absence of any agreed basis for subdivision. The obviousness of the features of the limbs and dentition led naturally to their being the first to receive attention, and we find them used by all the early systematists. Ray, Linnaeus, and Georges Cuvier placed especial importance on the limbs, Frederic Cuvier on the dentition. For the Mammalia as a whole, however, De Blainville's classification based on the reproductive system proved most fruitful in determining relationships and was generally adopted.

In the Carnivora, however, the limbs and teeth continued to be used as a basis for family divisions until Turner (1848) pointed out the parallelism characteristic of these features and the possibility of the use of the basicranium. His death from a dissection wound prevented any further development of the idea on his part, but it was revived by Flower (1869) who made the further contribution of dividing the order into three major divisions based on a character of the auditory region, namely, the presence or absence of a septum bullae.

In the arctoid division, the bulla is entirely undivided and consists of a single chamber; in the aeluroid division, on the other hand, the interior of the bulla is completely divided by a septum and consists of two chambers arranged anteriorly and posteriorly of each other. In the third division, the Cynoidea, the condition is somewhat intermediate between the two, a partial septum being present but too low to seal off the chambers.

A number of other features of the auditory region and other parts of the anatomy were found by Flower to correspond with these divisions.

In the Arctoidea, the inferior lip of the meatus is always prolonged; the paroccipital process is triangular and directed backward, outward, and downward; the mastoid process is separated from the paroccipital and generally very prominent; the carotid foramen is always large and usually placed near the middle (although sometimes more posteriorly) of the medial wall of the bulla; the condyloid foramen is distinct and exposed, never sunk into a common opening with the foramen lacerum posterius; a glenoid foramen is always present and generally conspicuous; the intestinal canal is without a caecum; there is a large penis with a well-developed bone; and there are no Cowper's glands.

The Aeluroidea have usually no prolongation of the meatus into a tube; the paroccipital process is closely applied to the posterior margin of the bulla; the carotid foramen is a minute groove in the fossa for the foramen lacerum posterius; the mastoid process is not widely separated from the paroccipital; there is no alisphenoid canal; the penis is usually small with no bone; a short caecum is present in the intestine; and Cowper's glands are prominent.

The Cynoidea present a series of characters of which some agree with one division and some with another. There is no tubular meatus, but an alisphenoid canal is present; the carotid foramen is enclosed in a fossa with the foramen lacerum posterius, but the glenoid foramen is prominent. The mastoid process is not prominent, but the paroccipital process is a distinct, rod-like projection similar to that of the Arctoidea. There is a large caecum, but there are no Cowper's glands. The os penis is large and of characteristic shape.

Mivart summarized these characters and added to them in detailed studies of the Aeluroidea (1882) and the Arctoidea (1885). A monograph on the Canidae followed (1890). The concepts and terminology introduced by Flower were thus firmly established in zoological literature and have remained so, with only minor changes as to the grouping of the families comprising the respective divisions and the status of the Canidae as a separate section. These changes are summarized by Scott and Jepsen (1936) and Simpson (1945). In general the tendency has been to unite the Canidae with the Arctoidea and separate the Felidae more and more widely from any of the other families. Recently Simpson (1945) proposed the name Canoidea for the combined

Cynoidea and Arctoidea of Flower, and this terminology is followed in this paper.

The auditory region has also been used in the determination of genera and species (e.g., Pocock, 1921, 1922), and several studies have been written for the Mammalia as a whole. Van Kampfen (1905) summarized the literature on the basicranial region in general, and Van der Klaauw (1931) brought together every conceivable fact connected with the auditory region in fossil as well as living forms, with a few original descriptions. The work is arranged comparatively, however, structure by structure, so that a complete describtion of the region as a whole in any one family is never given. The Chicago Museum studies on the giant panda necessitated such a description, and Segall, to fill the need, made dissections and described (1943) typical members of the arctoid Carnivora.

These studies have brought about a wide acceptance of the taxonomic value of the basicranial region in recent mammals. They have had little practical effect on paleontology. In part, of course, this is because many specimens consist of only lower jaws, partial upper dentitions, or incomplete skulls, and because the basicranium is unknown. In many instances, however, even where the auditory region has been described in detail from many specimens, there is a tendency to disregard features of this region if they show disharmony with the dentition.

Daphoenus, for example, has long been known to have a demi-bulla, the posterior part of which remains unossified. If the criteria in use among taxonomists of living forms were applied, this character would place *Daphoenus* in the Viverridae and specifically link it with *Nandinia*. No one, however, has suggested such a classification. *Daphoenus* has always been considered a canid because of the dental characters and canid proportions of the skull. The condition of the auditory region is then interpreted as a primitive character retained in the Viverridae and modified in later members of the arctoid families. Similarly, the basicranium of the saber-tooth cats is not at all feline, and many features of the skeleton agree with those of *Daphoenus*, but *Drepanodon* and *Nimravus* are included in the Felidae on the basis of the undoubted cat-like character of the dentition, while the characters shared with *Daphoenus* are regarded as primitive.

The inadequacy of the dentition as a sole criterion of relationships, was, however, brought forcibly to the attention of the writer in the course of the study of some Miocene carnivores from the Daimonelix beds of western Nebraska. All of these had been referred to *Oligobunis* on the basis of the dentition, which was musteline in character except for the presence of a small M². The limbs, however, were of such different proportions as to indicate different genera. Two of the specimens consisted only of skulls, making necessary an attempt to find features of the skull which could be used as a basis for differentiation. Since the dentition was too much alike to be of value, a dissection was made of the auditory region. The result was the discovery that the two specimens belonged not only to different genera, but if the criteria applied to living forms were used, to different families (Hough, 1944).

The results of this study, which was started under the direction of Mr. E. S. Riggs, then Curator of Paleontology at the Chicago Natural History Museum, and continued under Dr. E. C. Olson of the University of Chicago, were presented as a Master's thesis in the Department of Zoology of the latter institution. A further dissection of the auditory region of *Aletocyon multicuspis*, a small carnivore from the Harrison beds of western Nebraska which has been thought to be ancestral to the pandas, brought out unmistakably canid features. In view of these surprising results it seemed desirable to examine the auditory region of as many fossil carnivores as possible. The study, which is presented in this paper, proved very significant, leading not only to certain taxonomic rearrangements but to theoretical conclusions as to the stability of the characters of the basicranium, their relationship to the more adaptive characters of the dentition and limbs, and their value in classification.

The study was presented as a part of the requirements of the Ph.D. degree in the Department of Zoology, the University of Chicago. It was much enlarged in scope by the assistance of Mr. Bryan Patterson, Curator of Paleontology, Chicago Natural His-

tory Museum, and Dr. G. G. Simpson, Chairman of the Department of Geology and Paleontology, the American Museum of Natural History, New York City, who arranged for the employment of the writer during the study of the specimens there and whose criticisms and suggestions were important in working up the material. Thanks are due to all of the American Museum departmental staff, but especially, in addition to Dr. Simpson, to Mrs. R. H. Nichols whose wide knowledge of the collections and literature in the Osborn Library were of great assistance.

Mr. J. C. Hansen, artist in the Department of Geology of the Chicago Natural History Museum, made the drawings for the text figures.

The names of institutions whose specimens are referred to in the text are abbreviated as follows:

A.M.N.H., The American Museum of Natural History
C.M., Carnegie Museum, Pittsburgh
C.N.H.M., Chicago Natural History Museum
M.C.Z., Museum of Comparative Zoölogy, Harvard College
P.M., Princeton University Museum
U.C., The University of Chicago
Y.P.M., Peabody Museum, Yale University

RECENT CARNIVORA
CANIDAE

Adaptive Characters and Classification

The Canidae comprise the wolves, dogs, jackals, coyotes, foxes, South American canids, and the problematical dingo of Australia, as well as several more aberrant and less well-known forms, the Indian dhole, the Brazilian bush dog, and the large-eared South African Cape dog. In adaptive characters they are an exceptionally uniform group. Typically predatory and securing their prey by running it down, all of the body structure is modified for this type of existence. The chest is barrel shaped; the limbs are long and slender with an elongate metacarpus and metatarsus; the feet are digitigrade; there is little rotation of the forearm, and no clavicle. The senses are exceptionally keen, especially the sense of smell, and the large brain is visible evidence of the mental development which has made the dog from earliest times the close companion of men.

In common with all Carnivora, the Canidae have the teeth differentiated into incisors, canines, premolars, and molars. The canines are long and pointed; P^4 and M_1 are specialized into shearing or carnassial teeth, and the molars are triangular in general shape with a well-developed postero-internal cingulum. The dental formula is the largest of all the Carnivora, with a maximum of three incisors, one canine, four premolars, and three molars in each jaw. M^3 is absent in all living forms except *Otocyon*, which also has an additional lower molar. A reduction from the standard formula takes place in *Cuon* (the dhole) and *Speothos* (the bush dog), M_3 being always absent and M^2 reduced or lost.

The first digit in both hind and fore feet is rudimentary and does not reach the ground. In one genus, *Lycaon*, it is not visible externally and consists of only a minute rudiment under the skin. The metapodials have squared edges and are arranged in symmetrical fashion, three and four being of the same length, one and two matching. The entire carpus and tarsus are very compact. The modification, in fact, is very like that of the artiodactyls and includes a reduction of the ulna and fibula, enlargement of the radius and tibia and an interlocking of the latter with the humerus so that all power of rotation is lost.

The dentition within the family is very uniform, all canids agreeing with one another even in very minute details of cusp formation. The principal variation consists of the size of the teeth proportionally to the skull, and the length of the carnassial in relation to the molar dentition. This is expressed as a ratio

$$\frac{M^1 + M^2}{P^4} \times 100$$

also called the molar index. The carnassial is largest proportionally in *Cuon* and *Speothos* and smallest in *Dusicyon* (*Lycalopex*) *vetulus*.

Otocyon is the most aberrant of all canids dentally, not only in the number of teeth, which exceeds that of most placental mammals, but in their size and shape, which is more insectivore-like than canid.

Other structural differences, however, are not correlated with the dentition. *Otocyon* does not differ greatly in appearance from many of the other large-eared African foxes. *Cuon* and *Speothos*, with similar dental modifications, are quite different adaptive types. *Cuon* is slender and agile, resembling a large jackal. *Icticyon* is the smallest of the Canidae, except *Fenecus zerda;* a short-legged, thick-necked, large-headed creature, it does not look much like any dog.

Lycaon is a typical canid in appearance except for the spots, an unusual feature in a wild member of the family, but common enough in domestic breeds.

Features of the soft anatomy are also very uniform, and such differences as exist are distributed at random. It would be hard to find two members of the Canidae more contrasted in adaptive characters than the maned wolf *Chrysocyon brachyurus*, with its long, stilt-like legs and slender muzzle, and the bush dog, *Speothos venanticus*, short and

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thick set as a poodle. Yet the caecum, which is coiled and contorted in the majority of canids, is straight in these species as well as in *Nyctereutes procyonoides* and *Dusicyon (Lycalopex) vetulus*.

The lack of conspicuous differentiation in morphology is matched by apparent ease in hybridization. "Such evidence as exists with respect of *Canis cancrivoris*, the jackal, the dog, and the wolf tends to the conclusion that species of the same size are capable of fertile unions" (Huxley, 1880). Recently (Iljin, 1941) a genetic study has been made of the wolf-dog cross. All hybrids were found to be fully fertile, and such characters as size of bullae, presence or absence of the septum, orbital size and angle, as well as other skull characters and hair color, eye color, eye form, ear form, and size, were found to segregate in typical Mendelian fashion. Iljin concludes that the high degree of similarity in genetic constitution and the complete interfertility make plausible the origin of the various races of dog from a single wild species.

Matings in captivity have also been reported between wild species such as the jackal and the wolf, the coyote and the wolf, all of which interbreed also with the domestic dog (Lydekker, 1896; Beddard, 1902). The South American canids are also said to mate with domestic dogs, and certain races of *Dusicyon gymnocercus* and *Dusicyon patagonicus* are said to be intermediate between the two species and are probably hybrids (Kraglievich, 1930). No authentic instance is known of the successful mating of any of the species of foxes with species of *Canis*, which sufficiently accounts for their separation in nature, although the morphological differences are slight. *Canis aureus* and *Canis latrans*, whose range overlaps that of the wolf, remain distinct from the wolf. This is probably due to ecological isolation rather than genetic incompatibility. Large individuals of *Canis latrans* are almost indistinguishable morphologically in essential structure from small wolves. Biometric studies have shown that all wolves of North America, Europe, and Asia are one species, including such diverse types as *Canis lupus simensis* (Abyssinian wolf) and the stocky, dark, Iberian race of *Canis lupus lupus*, and that there is more intergradation between the jackal and

the wolf and the coyote and the wolf than is generally recognized.

Because of the interbreeding and uniformity of the family as a whole, until recently only five genera were recognized, as follows: *Cuon, Speothos, Otocyon,* and *Lycaon;* with the wolf, the jackal, the coyote, the foxes, and the South American canids all included in *Canis.*

There has been an increasing tendency, however, to separate *Canis* into many genera, some of which, such as *Vulpes, Urocyon,* and *Alopex,* are admitted by all systematists, while others are still in dispute. This is particularly the case with the South American canids, which are included in *Canis* by some mammalogists and split up into five or six genera by others.

Osgood (1934) attempted to resolve these differences and at the same time recognize what he considered the collective distinction between South American canids and *Canis.* In the latter, according to Osgood, the carnassial is typically large, its length equal to or greater than the combined length of the two upper molars (molar index, 70–100); the occiput is triangular in shape; the sagittal crest drawn up into a ridge; the upper incisors are heavy, the inner pair distinctly trifid. In all the South American genera, on the other hand, the carnassial is proportionally small, its length always less than the combined length of the two upper molars (molar index, 100–150); the occiput is rectangular in shape; the sagittal area is flattened and lyriform; and the upper incisors are weak and not trifid.

The South American genera, according to this scheme, differ among themselves largely in the degree to which these tendencies are realized. Some approach *Canis* more in one feature, such as the structure of the sagittal area, others in another, such as the size of the carnassial. *Chrysocyon*, for example, with a pronounced sagittal crest has a small carnassial, while *Dusicyon australis* with a lyrate sagittal area approaches *Canis* in the size of the carnassial, the molar index being 97–100. Popularly the Canidae have always been divided into foxes and wolves. Huxley (1880) attempted to give these popular subdivisions a scientific basis and erected his thooid and alopecoid sections of the Canidae, based on

the presence or absence of the frontal sinuses. The thooids, which comprise the wolves, jackals, coyotes, South American canids, and some of the African species, have frontal sinuses; the alopecoids, which include the various genera of foxes, are without these sinuses.

Within each group the species may be arranged in a scale corresponding to a gradual increase in the relative and absolute size of the sectorial teeth. The lowest alopecoids and lowest thooids agree in being microdont, that is, small toothed. They also tend to have a lyrate sagittal area and strongly lobate mandible. Ascending the scale the sectorials become progressively larger, *Urocyon cinereoargenteus* and *Vulpes* paralleling the wolf and jackal in the size of the sectorial. According to this theory *Otocyon* is the most primitive canid.

Matthew (1924) expressed his disagreement with these subdivisions and pointed out the relationship between the size of the animal and the development of frontal sinuses. Large animals tend to develop strong sagittal crests and other built-out features of the skull, and in consequence certain areas are left vacant. These become sinuses. Small animals lack this additional space and also lack sinuses. In primitive canids, such as the Miocene species, the braincase is proportionally smaller so that a sagittal crest is developed even though the animal is of small size. This would apply also to primitive living members of the family.

Although exception may be taken to too rigid an interpretation of the size and sinus development relationship, since moderately sized South American species have frontal sinuses and no sagittal or occipital crests, nevertheless the character is too dependent on structural conditions, as Matthew pointed out, to be a valid basis for the erection of higher categories.

In place of Huxley's subdivisions, Matthew proposed a division of the family into Caninae and Cuoninae, based on the presence or absence of a basined heel to the lower carnassial. In the majority of canids the heel is basined, and these Matthew termed Caninae. In a few living genera and many fossil forms, *Cuon, Speothos, Temnocyon, Enhydrocyon* and others, the heel is trenchant; these Matthew

termed Cuoninae. In addition to the trenchant heel to the carnassial the Cuoninae tend towards a reduction of the molar teeth, a shorter, broader skull, and shorter limbs. Criticism has been made of these subdivisions because they seem to imply a separate descent of the two lines from the Miocene, and the actual affinity of *Cuon* with the jackal, and *Speothos* with the other South American canids, is such that such a long independent development seems unlikely. This problem will be discussed more at length in connection with the fossil genera included in the Cuoninae.

AUDITORY REGION

Text figure 1

The features of the auditory region are also very uniform throughout the family and sharply differentiated from those features in the other arctoid families. The bullae are always inflated and generally quite large, extending from the foramen lacerum medium, which they entirely cover, to the paroccipital process to which they are united by suture. Although ossified from a tympanic and an entotympanic center with the line of demarcation sometimes visible externally in young animals, there is no division of the bulla into distinct chambers.

The external auditory meatus consists of a circular opening formed entirely of the tympanic except in very young animals. The facial nerve leaves the skull through the foramen stylomastoideum primitivum, formed of the tympanic and mastoid, which together make a bony canal extending from opposite the fenestra cochleae to the tip of the mastoid process. A depression for the tympano-hyal is just anterior to, and confluent with, the stylomastoid foramen. The mastoid process is poorly developed and almost covered by the tympanic.

The carotid canal does not traverse the bulla but runs forward to the foramen lacerum medium in a groove in the roof of the bulla formed by the periotic and the basisphenoid-basioccipital dorsally and medially, the tympanic laterally. About midway along the bulla the groove is converted into a canal by the inbent margin of the bulla which here forms the floor of the canal. The

groove and canal are variable in size. In the domestic dog they seem to be large. In *Vulpes* they are smaller, with the canal more anterior.

The tympanic is ankylosed to the mastoid process and to the postglenoid process, forming the posterior boundary of the large postglenoid foramen.

The crista tympani extends into the bulla at an angle of about 45 degrees. It reaches approximately the middle of the roof of the bulla. A septum taking its origin immediately

and slightly posteriorly. A process from the promontorium slopes forward to meet the alisphenoid in close contact, forming the posterior margin of the foramen lacerum medium. A lateral process meets a process of the basioccipital-basisphenoid to form the roof and sides of the carotid canal. Posteriorly, a similar process forms the anterior margin of the foramen lacerum posterius which in the Canidae is situated in a large, obliquely placed depression which also includes the opening of the carotid canal.
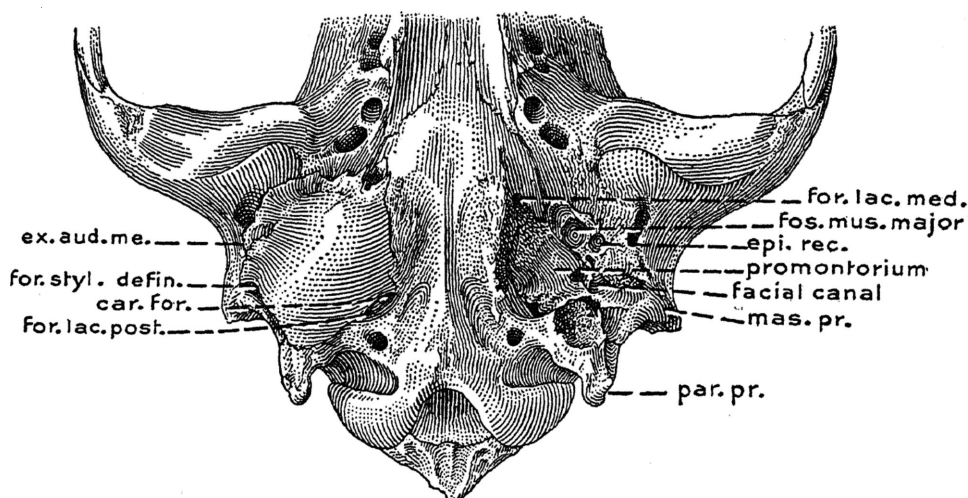

FIG. 1. *Canis lupus*, auditory region, part of tympanic removed. ×1/1. *Abbreviations:* car. for., carotid foramen; epi. rec., epitympanic recessus; ex. aud. me., external auditory meatus; for. lac. med., foramen lacerum medium; for. lac. post., foramen lacerum posterium; for. styl. defin., foramen stylomastoideum definitivum; fos. mus. major, fossa muscularis major; mas. pr., mastoid process; par. pr., paroccipital process.

above this point extends across the roof of the bulla, perpendicular to the crista tympani, terminating along the inbent margin of the tympanic just below the foramen lacerum medium. Although this septum is in somewhat the same position as that of the Felidae, it is not considered by most anatomists to be homologous. There is some question about this, however, which will be discussed later in connection with a septum in the bulla of *Nasua*.

The fossa for the muscularis major, and the epitympanic recess are both large, circular depressions of characteristic type. The promontorium is pear shaped and smooth with the fenestra cochleae facing laterally

There is no extension of the tympanic cavity into any of the surrounding elements, and, with the exception of the septum described above, no rafters or radiating ridges.

These features are very constant within the recent Canidae, and, as will be shown, in the fossil Canidae as well. There is little variation except in degree of inflation of the bulla, or development of the septum. *Fennecus zerda* has unusually large bullae, *Speothos* very small ones; all degrees between the two are common. The bulla is never flat except in one or two reported cases where there was an abnormality of some sort. There is never a pronounced tubular meatus, although the lip is more developed in *Urocyon* than in

Canis. In *Vulpes* there is only a very low septum.

These differences are not correlated with differences in limbs and dentition. The most aberrant of all dogs in dental characters,

Otocyon, has the usual type of auditory region differing in no important respect from any other canid. *Cuon* has a very large bulla similar to that in *Lycalopex*, while *Speothos* has a very small one.

PROCYONIDAE

Adaptive Characters and Classification

In contrast to the Canidae, the Procyonidae are arboreal or semi-arboreal and plantigrade, with a semi-opposable first digit to the fore paw. All are vegetable feeders with a lack of development of the carnassial and a tendency towards broadening of the molars. The muzzle and head tend to be proportionally short and broad, the limbs long.

In *Procyon*, the dentition is markedly non-sectorial. P^4 consists of three external cusps continuous with a small internal cingulum and two internal cusps placed opposite the interspaces of the external cusps. M^1 is as broad as long, with four large cusps. M^2 is also quadrate in form with four cusps. Like P^4, M_1 is not a shearing tooth at all but consists of five cusps, the posterior ones of which correspond to the talonid of a canid M_1, but are as high as the rest of the tooth, much as in *Paradoxurus*.

The raccoons comprise two species, *Procyon lotor* with a range from Alaska to Costa Rica, and the South American species *Procyon cancrivorus*. They are not strictly arboreal but often make their homes in the trees. Fish form an important part of the diet, although they also gather nuts and are capable of husking corn with their dexterous hand-like paws. The digits are unusually long and mobile, with the first digit semi-opposable. There is no median cleft to the nostril.

Nasua closely resembles *Procyon* in habits and anatomy. The important differences are less motility in the fore paws, the digits of which are enclosed in skin to the last phalanx, a short proboscis, and more strictly arboreal habits. The dentition is very similar to that of *Procyon* with only slight differences in cusp development.

Bassariscus, of which there are two species, *B. astutus* from Texas to California, northward into Oregon and southward into Mexico as far as Vera Cruz, and *B. sumichrasti* from

southern Mexico to Parana, Brazil, is smaller than *Procyon*, but like that form is semi-arboreal and nocturnal. The auditory region is a miniature of that of *Procyon*. The teeth, however, are sectorial, with a triangular carnassial differing from that of the small-toothed dogs only by the cingulum which forms a broad shelf in one species and is produced into a cusp in the other. The molars are rather musteline than procyonid in type.

Potos is the most aberrant of all the family. The dentition is like that of *Procyon*. The food is ordinarily fruit which it finds in abundance in its native habitat, the forests of Central America to the Rio Negro in Brazil. The body is long, with short limbs and a long prehensile tail. The head is broad and round, with a short muzzle. The palate is not prolonged beyond the tooth row as in other Procyonidae. There is no median nasal groove.

Bassaricyon is externally almost identical with *Potos* except for the lack of a prehensile tail. The skull is more like that of *Procyon*, but the orbits are very large.

Both *Potos* and *Bassaricyon* have lemuroid characters. The globular head and large orbits are superficial likenesses, and the concavity of the inferior margin of the mandible and the expansion of the postero-inferior part are as in *Microrhynchus* (*Lemur laniger*). Mivart, who cites these resemblances (1885), notes also that a strong similarity exists between *Potos* and *Bassaricyon*, the most arboreal of arctoid carnivores, and *Arctictis*, the most arboreal of the aeluroid group, particularly in the proportions of the limbs and the presence of chevron bones beneath the tail.

Auditory Region
Text figures 2–6

The auditory region is more variable than in the Canidae, although there are a number

of common characters throughout the family. The bulla is always globular, inflated, and without division into chambers. There is no continuation of the tympanic cavity into any of the surrounding elements, and there are no radiating rafters or septa in the interior of the bulla.

The walls of the carotid canal, which

forms the lateral margin of the small posterior lacerate foramen which does not include the carotid foramen. It has a broad contact with the paroccipital and laterally forms the margin of the foramen stylomastoideum primitivum. It forms only the posterior margin of the mastoid process, which in all members of the family is prominent.
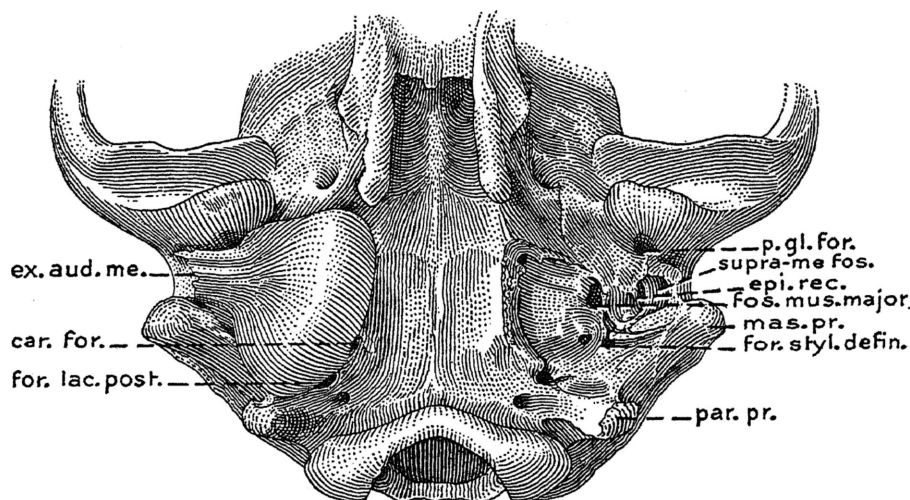

FIG. 2. *Procyon lotor*, auditory region, part of tympanic removed. ×1/1. *Abbreviations:* car. for., carotid foramen; epi. rec., epitympanic recessus; ex. aud. me., external auditory meatus; for. lac. post., foramen lacerum posterium; for. styl. defin., foramen stylomastoideum definitivum; fos. mus. major, fossa muscularis major; mas. pr., mastoid process; p. gl. for., postglenoid process; par. pr., paroccipital process; supra-me. fos., suprameatal fossa.

always runs in the medial wall of the bulla, are formed entirely of the tympanic. In *Procyon*, the bulla is not ankylosed to any of the surrounding cranial elements. There is a foramen stylomastoideum primitivum, which is only partially covered by the bulla. It is confluent with the foramen stylomastoideum definitivum formed by the lateral margin of the tympanic ventrally and the mastoid dorsally. There is no bony canal and no pronounced grooving of the mastoid process.

In all living Procyonidae there is a long tubular meatus, in *Procyon* composed of the tympanic ventrally and laterally, the squamosal dorsally. A suprameatal fossa is always present in all genera. The foramen lacerum medium is always small. The periotic extends laterally at a smooth level to the basisphenoid which it meets in close contact. Posteriorly it

The Procyonidae are by no means a uniform group. Segall (1943) has called attention to the fact that *Potos* combines features of the Mustelidae and Procyonidae. *Nasua* also has differences from *Procyon*. These are variable and perhaps dependent on age.

Two specimens of *Nasua* examined in the Chicago Natural History Museum and several examined in the American Museum of Natural History showed the following features.

The bulla externally resembles that of *Procyon*, being of the usual flask shape, globular medially, depressed laterally with a long tubular meatus. However, the meatus is formed entirely of the tympanic and not of the tympanic and squamosal. The squamosal appears only as a narrow strip left by the incomplete closure of the tympanic dorsally.

The anterior portion of the bulla is exceptionally depressed and marked off from the posterior part by a ridge on the surface of the bulla, which corresponds internally with a septum running from the crista tympani to a point at the anteromedial margin of the bulla just posterior to the foramen lacerum medium. The septum is open above, allowing a connection between the two chambers. It extends at right angles to the crista tympani and is, therefore, not a septum bullae, i.e., not a septum formed by the fused margins

The margins of the bulla are strongly reflected over the promontorium, leaving but little of it exposed. Low ridges radiating from the internal margin of the bulla extend across the inner surface.

The carotid foramen is placed more anteriorly than in *Procyon*. The canal is very short and almost diagonal.

One of the specimens of *Nasua* in the American Museum has an unusual extension of the squamosal on the under side of the skull and a consequently long meatus. The
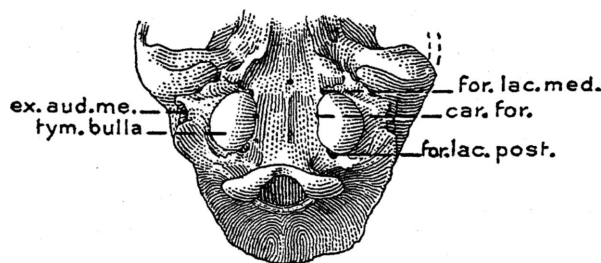

Fig. 3. *Nasua*, auditory region, part of tympanic removed. × ⅔. *Abbreviations:* car. for, carotid foramen; ex. aud. me., external auditory meatus; for. lac. med., foramen lacerum medium; for. lac. post., foramen lacerum posterium; tym. bulla, tympanic bulla.

of the ectotympanic and entotympanic. At the same time, the position is precisely that of the septum in the Felidae, and it is a question whether greater inflation of the anterior chamber might not raise it to a position parallel to the crista. The septum in the Canidae has the same position but also is not formed from the ectotympanic and entotympanic, and so is presumably not homologous.

bullae in this individual are very small and situated far from the lateral margin of the region. The anterior portion of the bulla is much flattened, and the ridges dividing the parts are so pronounced that the posterior portion extends forward and overhangs the depressed portion. In consequence the internal septum almost shuts off the anterior chamber from the posterior.

URSIDAE

ADAPTIVE CHARACTERS

The general appearance of the Ursidae is well known. They are all big animals with powerful limbs and claws. The lower part of the leg characteristically is short and heavy, the upper part long so that the knee joint swings free of the body, giving the bear its ability to stand erect and its peculiarly human gait. The feet are completely digitigrade with

five well-developed digits in each foot. These are armed with high, compressed claws which are non-retractile. There is no entepicondylar foramen to the humerus, except in *Tremarctos*, and only a short olecranon. The centrale is very large, and the magnum sharply keeled.

The skull and dentition are also very characteristic. The braincase is large, the
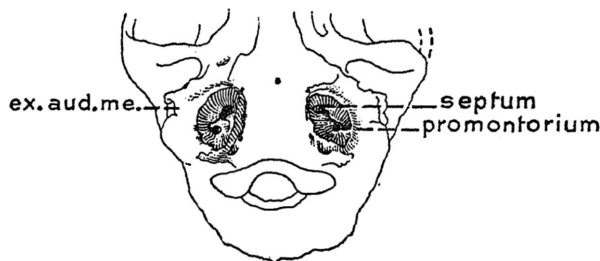
FIG. 4. *Nasua*, auditory region. ×⅔. *Abbreviations:* ex. aud. me.,
external auditory meatus.

forehead concave, the facial region short and broad. The premolars are reduced, the sectorial is non-trenchant, with a median internal cusp, and the molars are longer anteroposteriorly than transversely, a reversal of the canine pattern.

The uniformity of the family is even greater than that of the Canidae, and all living bears are included in three genera: *Ursus*, the true

floor of the meatus is very thick and formed of cancellous bone in older bears, and the mastoid, which is also cancellous in some individuals, is fused with the meatus. The tympanic cavity is deeper than that of the raccoons or canids, in spite of the flattened bulla. The promontorium is surrounded with a space communicating with the cranial cavity. The foramen lacerum medium is large,
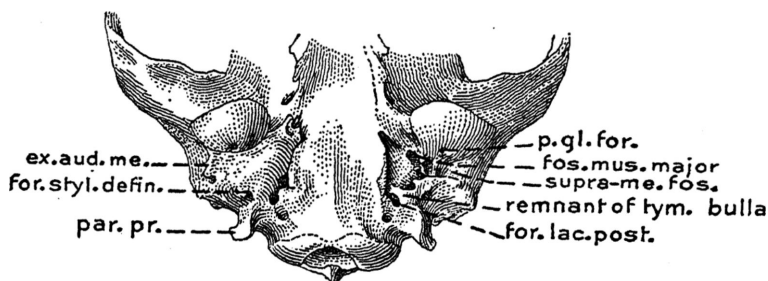

FIG. 5. *Ailurus*, auditory region, part of tympanic removed.
×⅔. *Abbreviations:* ex. aud. me., external auditory meatus; for. lac. post., foramen lacerum posterium; for. styl. defin., foramen stylo-mastoideum definitivum; fos. mus. major, fossa muscularis major; p. gl. for., postglenoid process; par. pr., paroccipital process; supra-me. fos., suprameatal fossa; tym. bulla, tympanic bulla.

bear of Europe and North America, *Thalas-sarctos*, the polar bear, and *Tremarctos*, the spectacled bear of South America.

AUDITORY REGION

The auditory region of the Ursidae resembles that of the Procyonidae in many features such as the position of the carotid canal and the long, tubular, external auditory meatus. Yet there are notable differences. The bulla is flattened, the hypotympanic sinus extends along both sides of the meatus, which itself extends far into the tympanic cavity. The

and in some species the alisphenoid and periotic are not in contact. The anterior margin of the meatus may be fused with the postglenoid process.

In older bears the posterior entrance to the carotid canal comes to be concealed by the prominent lip of the basioccipital which overlaps the inner edge of the bulla. This forms a fossa, bounded posteriorly by the base of the paroccipital process, which includes both the posterior carotid foramen and foramen lacerum posterius.

NANDINIA

TAXONOMIC POSITION

It is not within the scope of this paper to discuss the auditory region of the Viverridae. The African palm civet, *Nandinia*, however, is unique among living carnivores in having an unossified entotympanic. Since this is also characteristic of a number of fossil genera, notably *Paleoprionodon* and *Daphoenus*, a description of *Nandinia* is included for purposes of comparison.

In addition to the peculiarity of the auditory region *Nandinia* presents a puzzling assortment of characters which has prevented any agreement as to its exact systematic position. The feet and scent glands ally it with the Paradoxurini, but the dentition, which is almost of a pure trenchant type according to Gregory, lacks the procyonid-like frugivorous specializations of this group. The basicranial region is rather "arctoid" than "aeluroid," i.e., there is a prominent mastoid process and a triangular paroccipital process resembling those of the Canidae. The auditory region, as will be seen from the following description, aside from the lack of ossification is quite typically viverrine.

AUDITORY REGION

The bulla is small and ring shaped, composed only of the tympanic and enclosing only the anterior portion of the auditory region. The entotympanic remains cartilaginous throughout life. This is a continuation into adult life of a condition which is present at birth in all Carnivora. Usually, however, a slight ossification at the entotympanic center spreads rapidly and forms, as the animal develops, a complete posterior chamber.

The space occupied by the middle ear structures in *Nandinia* is narrow owing to the great breadth of the basioccipital and basisphenoid.

The promontorium is a rounded oval with the fenestra cochleae situated near the center and facing more posteriorly than laterally. The promontorium extends medially almost at a level to the basioccipital, making a slight contact with that bone. Posteriorly it forms the anterior margin of the foramen lacerum posterius, from which it extends laterally in a broad contact with the paroccipital. Since there is no entotympanic, the stylomastoid foramen is that termed by Van der Klaauw the primitive one, which is bounded anteriorly by the tympanic process of the squamosal and the tympano-hyal(?) and medially by the promontorium and laterally by the mastoid. It is situated just opposite the fenestra cochleae.

The epitympanic recess is very shallow compared to that of *Canis* and extends farther medially. The fossa for the muscularis major is also shallow and broadly oval, with the alisphenoid forming the entire anterior margin and the periotic the posterior margin and the greater part of the roof.

The porus acusticus externus consists of a large circular opening. There is no tubular meatus of any sort, external or internal. A narrow rim of the squamosal forms the roof of the porus, and the sides and floor are formed of the tympanic. The crista tympani is narrow and projects very little into the tympanic cavity.

The mastoid process is unusually large for a viverrid and projects as a stout knob. The paroccipital process is also projecting and of the same size and shape as that of *Canis*.

The postglenoid foramen is small. There is no posterior carotid foramen. The course of the artery may be marked by a deep groove which commences at the posteromedial margin of the promontorium and continues laterally for a short distance and then divides, one branch running forward to the tympanic cavity. When an entotympanic is present, of course, the posterior carotid foramen pierces the posterior chamber of the bulla about midway along the medial margin. The course of the artery is, however, the same.

FOSSIL CARNIVORA
PALEOCENE AND EOCENE CARNIVORA

ADAPTIVE CHARACTERS

THE EARLIEST FOSSIL CARNIVORES are an archaic group known as the creodonts. In the structure of the limbs and dentition they parallel living carnivores to such an extent that when they were first described almost all of the genera were considered ancestral to one or another fissipede family. This view has been rejected, however, in favor of the derivation of all the modern families from the Miacidae, which are included in the Fissipeda because of their ancestral relationship. (See Simpson, 1945, for a discussion of this problem.)

The Miacidae, unlike the other creodont families, have P^4 and M_1 specialized as shearing teeth. These same teeth are specialized for that function in the modern Carnivora. All of the other creodonts have a different arrangement. Either there are no specialized carnassials at all, or M^1 and M_2 are so developed, or in some instances there may be two sets—P^4, M_1 and M^1, M_2.

AUDITORY REGION

The bulla is not preserved in its entirety in any of the creodonts or miacids. In most instances this is probably because it was unossified. In others it may have been partially ossified and so loosely attached to the skull as to be easily lost in fossilization. A horizontally placed annulus tympanicus is found in one specimen of *Oxyaenodon* (C.M. No. 3051); and a fragment of the annulus, in *Thinocyon* (A.M.N.H. No. 12351). In the absence of the distinctive features that result from the various ways in which ossification of the tympanic and entotympanic take place, the auditory region of these early forms seems to present little of diagnostic value in determining relationships, although perhaps a more thorough study would disclose features of the periotic which could be used for the purpose.

Matthew (1909) has described the Bridger Carnivora in detail. With the exception of the lack of an ossified bulla the essential structures of the middle ear are like those of later families. Matthew suggests that a certain groove on the promontorium in *Viverravus minutus* may mean that the external branch of the carotid artery had the size and importance in these forms that it has in the living Insectivora and also calls attention to an open space around the promontorium which communicates with the braincase and, if not due to the displacement of the petrosal, may be significant. A similar condition is found in the Ursidae.

Dennison (1938) in describing the Pseudocreodi suggests that an ossified bulla may have been present in *Patriofelis ferox*, basing this idea on the presence in that form of a groove starting at the position of the primitive stylomastoid foramen and continuing across the mastoid process. He argues that this groove may have been a stylomastoid canal, or external part to the Fallopian aqueduct, and that if this is true, an ossified bulla was present. The groove in question was probably the stylomastoid canal. It does not follow, however, that an ossified bulla was necessarily present. It could well have been cartilaginous in whole or in part.

In any event, there seem to have been two types of auditory region in the Pseudocreodi, one with the typically primitive stylomastoid foramen bounded by the tympano-hyal(?) anteriorly, the periotic medially, the mastoid laterally and posteriorly, and the other with this foramen covered over by the periotic and its place taken by a deep groove for the facial nerve running laterally and posteriorly across the mastoid process. These same types, modified, of course, by the presence of the bulla, are found in recent carnivores.

In the creodonts the two types occur in families quite different adaptively. Of the two the more "advanced" type adaptively, *Thinocyon*, a slender, digitigrade, semicursorial animal, has the primitive stylomastoid foramen.

OLIGOCENE CARNIVORA

QUERCY CARNIVORES

The Phosphorite Beds of Quercy, France, contain a rich carnivore fauna probably including late Eocene to early Oligocene forms. They have been described in considerable detail by Teilhard de Chardin (1915). In addition to the primitive types held over from the Eocene, more advanced forms are found, some with the bulla still unossified, as in *Miacis*, others with a demi-bulla, and still others with fully ossified, large, well-inflated bullae. Presumably the three types lived contemporaneously.

Adaptive features of the dentition are correlated with the types of auditory region. The group with the unossified bulla, the Cynodictoides of Teilhard, have a microdont canid type of dentition which tends on the one hand towards a "viverroid" type and on the other to a heavier dentition which might be called "procyonid." The central species of the group is *Cynodictis intermedius* which is so like our American *Pseudocynodictis*, except for the unossified bulla, as to have been thought to be the same species (Scott, 1898). Some of the specimens described by Teilhard have an M³ and some do not. All are variable, M² being more or less long, M¹ more or less trenchant, with both of these variations appearing independently of each other. Some of the forms of *Cynodictis*, such as *C. longirostris*, grade into *Amphicyon*. Others approach the viverrine type of dentition. *C. compressidens* and especially *C. palmidens* being the most extreme. Teilhard de Chardin distinguishes four different types, three of which differ among themselves by minor details of the cusp formation but have a basined talonid to the lower sectorial, while a fourth has the beginning of a trenchant heel on this tooth. Some of this type have an M₃ and some do not. Those that do not, merge into the *Plesictis* forms of the following group.

This group which Teilhard calls the Cynodontoides have a well-ossified and inflated bulla. They also vary in dentition from a central type, *Cynodon typicus*, in which the molar structure is almost a replica of that of *Cynodictis intermedius*, to *Cephalogale* with rounded tubercular molars, of the procyonid

type, at the one extreme, and *Plesictis robustus* with a very viverrid-like dentition at the other. *P. robustus* resembles *Bassariscus* in many respects as will be discussed later. Other of the Plesictoides approach the Stenoplesictoides in dentition.

The Stenoplesictoides have a demi-bulla. They include many small forms typically viverrine or musteline in dentition but with a tendency towards felid specializations. P⁴ tends to develop into a rectilinear, highly shearing type of tooth with little development of the antero-internal cusp, while M¹ is small or absent. The upper canine is long, sharp, and recurved with channeled enamel. In the lower dentition the sectorial becomes high and trenchant, with both the metaconid and talonid much reduced and M₂ small or absent. *Stenoplesictis cayluxi* is the central type of this group with *Palaeoprionodon*, *Proailurus*, and *Palaeogale* representing specializations. *Proailurus* is more specialized in the direction of the cats, i.e., metaconid reduced, talonid very short, M₂ with a metaconid but no talonid. *Palaeogale* is definitely musteline, having no M² and M¹ being elongate transversely with the inner portion broadened into a tongue-shaped flange. *Palaeoprionodon* is in some respects more primitive, that is, nearer *Miacis*, than *Stenoplesictis*. This is seen especially in the form of M₂ which, independently of absolute size, has four cusps.

The European collections were not available for study. Two specimens of the Phosphorite Carnivora, however, are in American museums, one of them a small skull originally described by Riggs (1898) and referred to *Amphictis* in the Princeton collection, and another, *Plesictis genettoides*, in the American Museum of Natural History. A study of the auditory region of both specimens was made by the writer, and since this proved significant, the postcranial skeleton of *P. genettoides*, described by Helbing (1930), was re-examined. The result of both studies was to establish *P. genettoides* as a procyonid and to make certain the generic identity of the Princeton specimen with *P. genettoides*. The latter is described first because of the greater completeness of the specimen. It is, however,

from the Lower Miocene (Aquitanian) and so not contemporaneous with the Quercy carnivores just described.

Plesictis genettoides

Plate 9, figure 2

SPECIMENS EXAMINED: A.M.N.H. No. 11001; Aquitanian, France.

AUDITORY REGION

The auditory bullae are moderately large and evenly rounded, with the longitudinal axis parallel to the midline of the skull. The highest portion is just laterad of the median edge, from which point there is a gentle slope in either direction, without marked depression or flattening.

The external auditory meatus is a triangular opening directed laterally, with the anterior margin rolled into a lip making a short tubular meatus, incomplete ventrally. The cavity of the bulla is simple, with no rafters or septa. The internal meatus is short and does not project into the tympanic cavity. There is no extension of the hypotympanic sinus along the sides of the meatus and no thickening of the floor. The entire roof is formed of the squamosal in which there is a suprameatal fossa like that described for *Zodiolestes* (Hough, 1944) but shallower, resembling the same feature in *Potos*. In *Bassariscus* this fossa is exceptionally deep.

The carotid foramen is situated about a third of the way along the median margin of the bulla and leads into a stout tube running forward and somewhat downward to the foramen lacerum medium.

The opening for the Eustachian tube is marked by a short styliform process and leads into a distinct groove in the tympanic, which passes laterally and posteriorly to the tympanic cavity proper. The fossa for the muscularis major is a deep, oval depression almost identical in form and position with that of *Zodiolestes*. There is no epitympanic sinus.

The sulcus facialis is a narrow groove leading around the fenestra vestibuli, through a minute opening to the foramen stylomastoideum primitivum, which is bounded anteriorly by a process from the posttympanic process of the squamosal (tympanohyal) exactly as in *Zodiolestes*.

The promontorium is low and broadly oval, extending to the edge of the hypotympanic sinus posteriorly and medially. The bulla follows closely around the margin of the promontorium. The fenestra cochleae is directed somewhat more posteriorly than in *Zodiolestes*.

The foramen lacerum posterius is moderate in size and widely separated from the posterior carotid foramen. The paroccipital process is a stout bar extending downwards and backwards. The mastoid process is little developed, a marked difference from *Zodiolestes*. The development is as great as in *Bassariscus*, however, which is nearer the size of *Plesictis*.

The characteristics of the auditory region are definitely procyonid, especially the presence of the suprameatal fossa, the position and structure of the carotid canal, the shape of the promontorium and the fossa for the muscularis major, and the course of the facial nerve. A mustelid type of ear is very different (Segall, 1943).

OTHER ASPECTS OF THE SKULL AND POSTCRANIAL SKELETON

The characters of the skull other than those of the auditory region are also closely similar to those of *Bassariscus*. The proportions of the skull, for example, are the same in the two genera. *Mustela putorius*, on the contrary, has a shorter muzzle and basicranium. The configuration of the sagittal area in *Plesictis* is very similar to that of *Bassariscus*, although since the braincase is less inflated in the former the lyrate area is lower and more rounded. It is pronouncedly different in this respect from *Mustela*, in which, as in all modern mustelines, there are a distinct sagittal crest and crescent-shaped occipital region.

The dentition of *Plesictis*, although similar to that of *Bassariscus*, differs in several respects, and these differences are in a musteline direction. There is no postero-internal cusp or shelf on the carnassial in *Plesictis*, M^1 has more of an internal cingulum, and M^2 is absent. The dentition of *Mustela*, however, differs from that of *Plesictis* in many more features.

The postcranial skeleton of *Plesictis* agrees in all diagnostic characters with that of *Bassariscus*. Helbing's description although en-

tirely accurate is, in the writer's opinion, misleading in this respect. He compared *Plesictis* primarily with *Mustela putorius* and to a limited extent with *Helictis*, noting as he did so the many points of divergence. He considered these differences to be due to individual variation and without phylogenetic significance. A comparison with *Bassariscus*, such as has been made in this paper, would have shown that those characters in which *Plesictis* differs from *Mustela* agree with *Bassariscus* and that the resemblances between *Plesictis* and *Mustela* are generalized carnivore characters shared by all three genera.

The atlas, for example, is similar to the point of identity with that of *Bassariscus*, *Potos*, and *Procyon* but agrees in essential features also with members of the Felidae, Mustelidae, and Viverridae. The canal for the vertebral artery in these forms pierces the posterior border of the transverse process, running horizontally through the process. In the Canidae, the opening is ventral and the canal almost vertical. It is interesting to note that *Pseudocynodictis* and *Phlaocyon*, soon to be described, show an intermediate condition approaching that of *Canis*.

The axis is also similar to that of *Bassariscus* and *Procyon*, differing from *Putorius* in the greater size and thickness of the neural spine. The posterior portion of the spine being broken, it is impossible to tell whether this was prolonged backward over the succeeding vertebrae as in *Bassariscus*, *Procyon*, and the Felidae and Viverridae generally, or ended in a blunt, upwardly directed process as in *Mustela putorius*. That there was some prolongation of the spine and not a gradual curve into the postzygapophyses as in the Canidae is shown by the curve of the margin of the portion remaining. The shape of the odontoid process and the shape and size of the articular facets are entirely like those of *Bassariscus*. In *M. putorius* the articular facets are smaller, face more anteriorly, and do not project below the centrum.

The scapula is represented by only a fragment. This shows no feature not found in *Bassariscus*, but this does not mean very much since the diagnostic features are not available. The articular surface for the head of the humerus has not the obliquity found in *Putorius*.

The humerus is similar to that of *Bassariscus*, the shaft being less curved and proportionally longer than that of *Mustela putorius*. The supinator ridge is pronounced, but not so much so as in *Mustela*. It has the same configuration as in *Bassariscus*, extending almost to the center of the shaft but without the lateral flare characteristic of the Mustelidae. The shape of the trochlea and the position of the entepicondylar foramen are almost identical with the same features in *Bassariscus*. The deltoid ridge is prominent as in *Bassariscus*, which is significant because this feature is not pronounced in *Mustela* and *Felis*. The head is shaped like that of *Bassariscus*, but there is little difference between *Bassariscus* and *Mustela* in this feature.

The radius is identical with that of *Bassariscus*, differing from that of *Mustela* in its greater length and less curvature to the shaft. The ulna is also like that of *Bassariscus* and differs from that of *Mustela* in that the olecranon is longer and the facet for the radius is larger and more extended medially so that the radius and ulna are less crossed.

The carpal bones are not sufficiently well preserved for a comparison to be made.

Only fragments of the pelvis are preserved. Taken together, however, these give a fairly accurate picture of the girdle. Feature for feature it is quite similar to that of *Bassariscus*. The ilium is broader than in *Mustela putorius*, with a more expanded anterior portion. The gluteal surface is a simple concavity but shallower than is usual in recent Carnivora. The acetabulum is larger than in *Mustela* and placed more ventrally, bringing the limbs into a more lateral position with respect to the body. The cotyloid notch is broad and shallow, which indicates, according to Dennison (1938), an ambulatory type of locomotion with probably arboreal habits. *Bassariscus*, which has that type of locomotion, has a similar type of pelvic girdle. In *Mustela* the cotyloid notch is narrower and deeper but not so narrow or so deep as in a truly cursorial form such as *Canis*. Only the inferior portion of the ischium is preserved, and this is broken anteriorly. However, the shape of the obturator foramen seems, from the part preserved, to have agreed well with that of *Bassariscus*. The ischium has about the same proportions.

The femur lacks the proximal end but in all available features compares well with *Bassariscus*. Helbing points out that the tibia is slightly longer than the femur in *Plesictis*, a point of difference from *Helictis* to which Schlosser compared it. However, the relationships of these two bones are identical with those found in *Bassariscus*. The tibia differs from that of *Putorius* in being very much stouter, with a longer articulation for the fibula, and without any twist to the shaft.

The astragalus is very like that of *Bassariscus*. The axis of the trochlea is directed obliquely to the axis of the foot. There is no very deep grooving. The neck extends medially from the trochlea and almost in the same plane. In *Helictis* and still more in *Mustela*, the trochlea is less oblique, the grooving deeper, and the neck extends less medially but more ventrally. In *Canis* the trochlea is perpendicular to the axis of the foot, and the neck extends but little beyond the median margin of the trochlea and is placed entirely distal to it. The articular surface of the head of *Plesictis* is larger and resembles *Bassariscus* in having almost the shape of a sphere. It differs markedly from that of *Putorius* in which this surface has the shape of a saucer. These various conditions cause a difference in the inclination of the ankle joint and point to a plantigrade gait in *Plesictis* and considerable climbing ability.

The calcaneum agrees almost exactly with that of *Bassariscus* and differs from that of *Canis* in that the facets for the articulation of the astragalus are more oblique. *Mustela* is halfway between the two. The tuber is the same length proportionally as in dogs and *Bassariscus*, being longer than in *Mustela* and more enlarged proximally.

Plesictis robustus

Amphictis sp.? RIGGS, 1898, Amer. Jour. Sci., ser. 4, vol. 5, p. 257.

Pseudobassariscus riggsi POHLE, 1917, Aitzber. Gesellsch, Naturf. Fr. Berlin, no. 6, p. 408.

SPECIMENS EXAMINED: P.M. No. 11455.

PREVIOUS WORK

This specimen was originally described by Riggs (1898) and referred to *Amphictis*. On the basis of Riggs' figures, Pohle showed the resemblance of this fossil to *Bassariscus* in dentition and skull proportions and the probable error of the reference to *Amphictis*. He could not, of course, examine the basicranium because he had only the figures published by Riggs. A careful comparison of the specimen in question with *Plesictis genettoides*, just described, which the writer was able to make through the courtesy of Dr. Glenn L. Jepsen, made certain the generic identity of the two. *Pseudobassaris* is therefore referred to *Plesictis robustus*, since it agrees well with the published figures of this species from the same horizon.

AUDITORY REGION

The bullae are similar in shape to those of *Plesictis genettoides* but with an exceptionally large triangular opening for the external auditory meatus. The anterior margin of this meatus is rolled into a slight lip; the ventral portion is incomplete. The tympanic forms the sides of the meatus, the squamosal the roof; a cartilaginous floor must have been present. There is a deep suprameatal fossa.

The internal meatus extends well into the tympanic cavity. The bulla is lightly attached and not coössified with any of the surrounding elements. The carotid foramen is situated in the posterior third of the median margin of the bulla and leads into a stout tube in the median wall of the bulla, exactly as in *Zodiolestes* and *Plesictis genettoides*.

OTHER CRANIAL CHARACTERS

The proportions of the skull agree well with those of *Bassariscus*, as pointed out by Pohle, and the dentition is also closely similar, differing only in the lack of a cingulum to the carnassial. That of *Plesictis genettoides* is much more musteline, M^1 being more elongate transversely with the pronounced internal flange found in many recent Mustelidae. *Zodiolestes* and certain of the Miocene canids to be described later, however, had a similar type of dentition, so it cannot be taken as a decisive indication of affinities.

AMERICAN OLIGOCENE CARNIVORA

The American Oligocene carnivores, known principally from the White River deposits of Colorado and Utah, are sufficiently differenti-

ated to be readily placeable in modern families and will be described as such, although the combinations of characters exhibited by them are by no means the same as those characteristic of the living genera belonging to the same family.

PROCYONIDAE

Mustelavus priscus

SPECIMENS EXAMINED: P.M. No. 13776; White River formation, Colorado.

The earliest American procyonid that can be definitely identified as such is *Mustelavus priscus* Clark. In his original description Clark pointed out the likeness of *Mustelavus* to *Plesictis*, from which, however, he considered it separated by the presence of M². However, the Oligocene specimens of *Plesictis*, *P. robustus*, have an M² (Teilhard de Chardin, 1915, pl. 7). Simpson (1946) expressed his opinion that *Mustelavus* is congeneric with *Plesictis robustus* and suggested the possible separation of the Oligocene forms of *Plesictis* from *P. genettoides*, which is the type of the genus.

Through the courtesy of Dr. Jepsen, the writer had the opportunity of examining the type specimen of *Mustelavus* in the Princeton Museum. It proved too badly crushed for a detailed description of the auditory region. A suprameatal fossa is present, however, and the external auditory meatus has a shape similar to that of *Plesictis*. The carotid canal seems to be the same. In fact, everything that could be determined about the auditory region confirmed the earlier conclusions as to the relationship between *Mustelavus* and *Plesictis*. If *Plesictis* is a procyonid, as seems to be the case, then *Mustelavus* is also. The presence of an American form so similar to a European one is also significant in a consideration of the relationship of the faunas of the two continents.

In many ways the Quercy fauna, previously described, is transitional between the Bridger Eocene (Teilhard de Chardin, 1915) and the White River Oligocene. It seems probable, therefore, that the European fauna spread over the two continents by way of the arctic land bridge. Such a deployment of animals naturally would give rise to the type of geographical speciation termed by Rensch "Rassenkreise," that is, a chain of species, the extremes of which may be sufficiently un-

like to be morphologically distinct species or even genera, but are nevertheless connected by intergrades. The European species *Cynodictis intermedius* and the American *Pseudocynodictis gregarius* may be taken to represent two such extremes in the canid stock, *Mustelavus priscus* and *Plesictis* in the Procyonidae, *Paleogale* and *Bunaelurus* in the Mustelidae.

Zodiolestes daimonelixiensis

SPECIMENS EXAMINED: C. N. H. M. No. P12032; Harrison beds, western Nebraska.

A preliminary report of the occurrence of this fossil in the daimonelix beds of the Harrison formation was given by Riggs to the Paleontological Society in 1908; the auditory region was described by the writer (1944), and the postcranial skeleton by Riggs (1942). These descriptions, somewhat abridged, are repeated here for the sake of completeness.

AUDITORY REGION

The bulla is an oval, evenly rounded capsule, formed by the tympanic only, and consisting of a single undivided chamber. The hypotympanic sinus is small and entirely devoid of rafters or septa. It has no extension into the exoccipital. The divisions of the bulla cannot be distinguished externally. There is no bony meatus; the porus acusticus externus is a circular opening interrupted ventrally by a narrow slit. The external meatus is a curved gutter closed dorsally by the superficies meatus of the squamosal. In this roof immediately external to the porus margin there is a large fossa, the suprameatal fossa described by Segall as characteristic of *Procyon*.

The epitympanic recess is quite small and lies almost directly under the porus. The true tympanic cavity is also small and well separated from the epitympanic recess by a thin shelf of bone. From the tympanic cavity a groove for the Eustachian tube runs forward in the alisphenoid. This fissure leads into an

opening at the anteromedial angle of the bulla, which is just laterad to the opening for the foramen lacerum medium and separated from it by a short styliform process.

The reflected margins of the bulla extend but little over the periotic, and the rounded promontorium is extensively exposed. From the anterior margin of the eminence a thin lamella of bone extends forward between the alisphenoid laterally and the tympanic medially.

foramen stylomastoideum primitivum rather than through a bony canal connecting this foramen with the foramen stylomastoideum definitivum.

The carotid canal is a rather large tube, formed by the tympanic. It runs along the medial wall of the bulla from a point slightly anterior to the foramen lacerum posterior to a point just ventral to the foramen lacerum medium. The latter foramen is small and penetrates the alisphenoid at the posterior
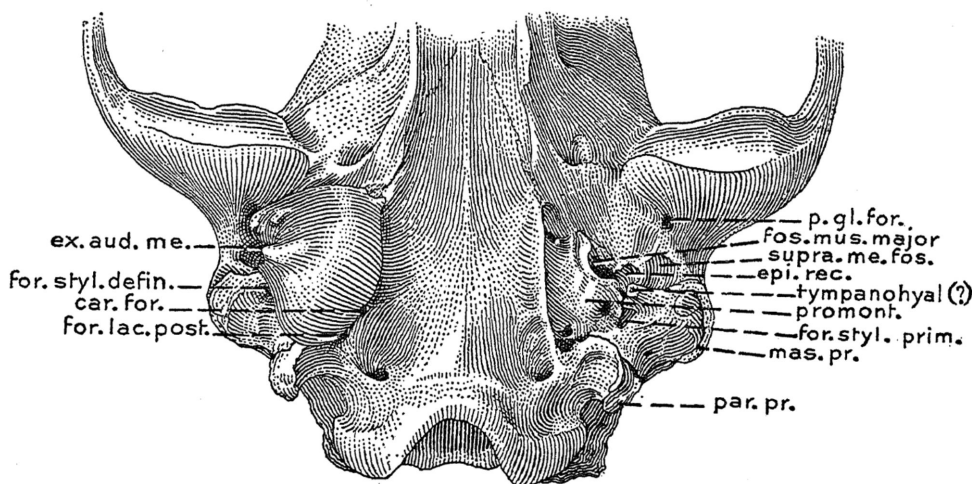

FIG. 6. *Zodiolestes daimonelixiensis*, auditory region, part of tympanic removed. ×4/3. *Abbreviations:* car. for., carotid foramen; epi. rec., epitympanic recessus; ex. aud. me., external auditory meatus; for. lac. post., foramen lacerum posterium; for. styl. defin., foramen stylomastoideum definitivum; for. styl. prim., foramen stylomastoideum primitivum; fos. mus. major, fossa muscularis major; mas. pr., mastoid process; p. gl. for., postglenoid process; par. pr., paroccipital process; promont., promontorium; supra-me. fos., suprameatal fossa.

The fenestra cochleae is a small opening facing more posteriorly than laterally. The fenestra vestibuli is slightly larger and faces laterally. The fossa for the muscularis major is broad and deep and lies just medial and anterior to the epitympanic recess.

The apertura tympanica facialis opens just above the fenestra vestibuli. Above and slightly laterad to the fenestra is a small foramen leading into a short canal which continues around the lateral margin of the promontorium to the foramen stylomastoideum primitivum and from there to a wedge-shaped groove on the mastoid. The canal and the groove mark the course of the facial nerve which thus leaves the skull through the

margin of an oval fossa, lying immediately medial and slightly posterior to the opening for the Eustachian tube. The foramen and foramen and fossa are entirely covered by the bulla.

Medially, the bulla is in contact with the basisphenoid and the basioccipital, these two bones curving downward slightly to embrace part of the medial wall. The contact with the basioccipital is slight because of the large size of the foramen lacerum posterius. Posteriorly, the bulla falls just short of contact with the base of the slender, backwardly directed paroccipital process. The suture between the paroccipital and the mastoid process runs obliquely from the lateral edge of the pro-

montorium. The mastoid process, which ex-
tends forward and laterally as a broad rough
process, thus forms the entire lateral margin
of the foramen stylomastoideum definitivum.

pattern, with the exception of the retention of
M². It is very similar to that of *Plesictis*
(compare figs. 6 and 7). The skeleton of
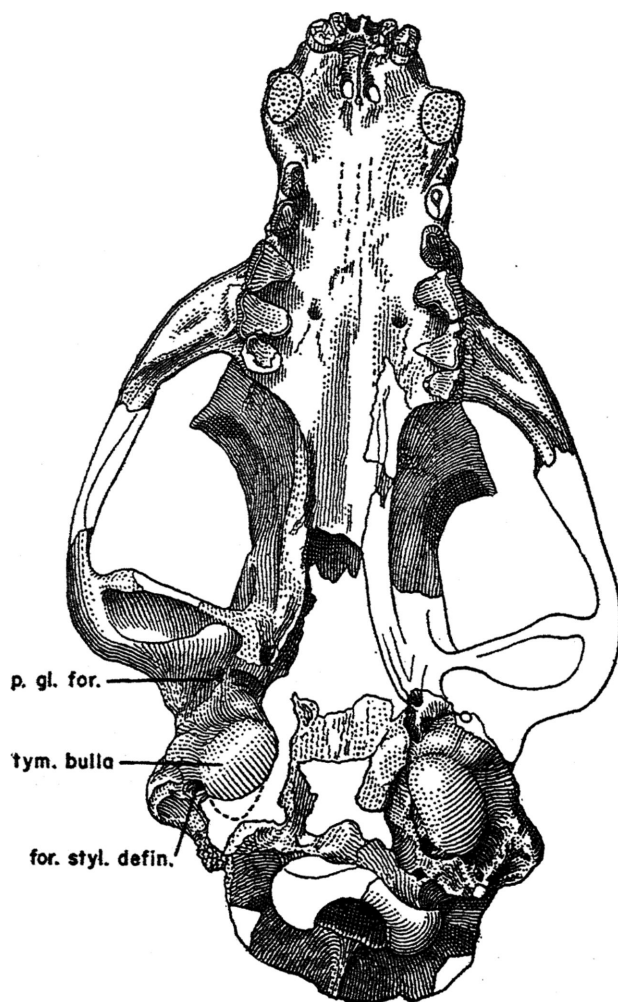*Zodiolestes* has not been described in detail.

FIG. 7. *Cyonasua brevirostris*, auditory region. ×⅗. *Ab-
breviations*: for. styl. defin., foramen stylomastoideum
definitivum; p. gl. for., postglenoid process; tym. bulla,
tympanic bulla.

Anteriorly the bulla presses closely to the
base of the postglenoid process, almost cover-
ing the small postglenoid foramen. The at-
tachment of the bulla to all of the surround-
ing elements is slight and the bulla easily
broken away.

OTHER FEATURES

The dentition of *Zodiolestes* is musteline in

The general aspect, however, is not that of an
arboreal animal. The feet are subdigitigrade,
the limbs slender and brought under the body
with nothing approaching the specializations
of *Procyon*. The specimen described here was
found curled up in one of the *Daimonelix*
spirals. Two rodents and a small musteline
were recovered from the same spiral. The
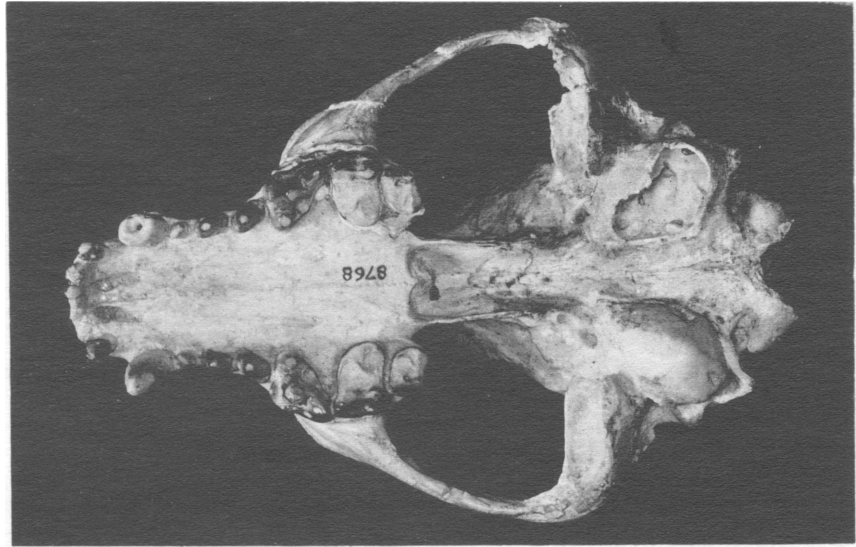ecological implications of this association are

PLATES 9–15
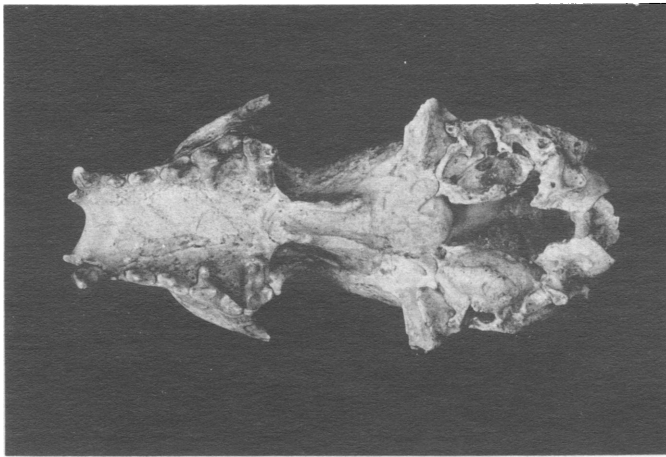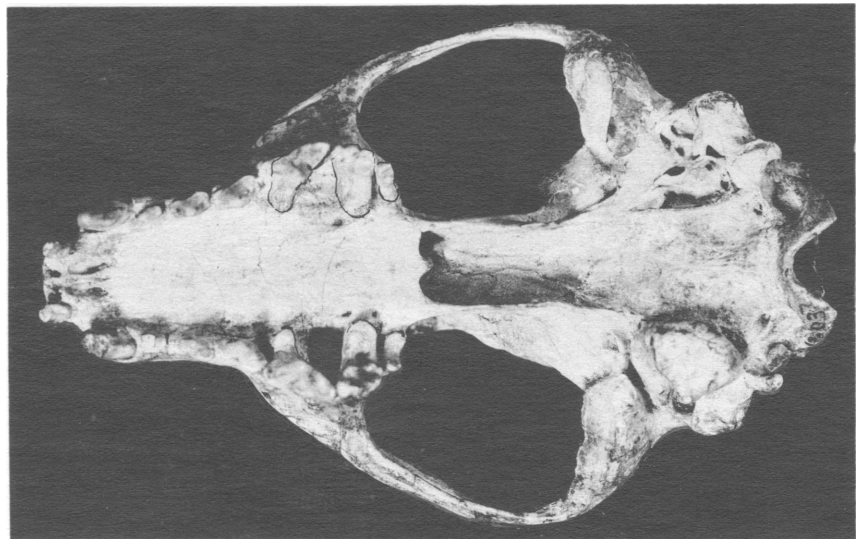
Skulls of (1) *Zodiolestes*, (2) *Plesictis*, and (3) *Phlaocyon*. Ventral views with left bulla removed. × 1/1
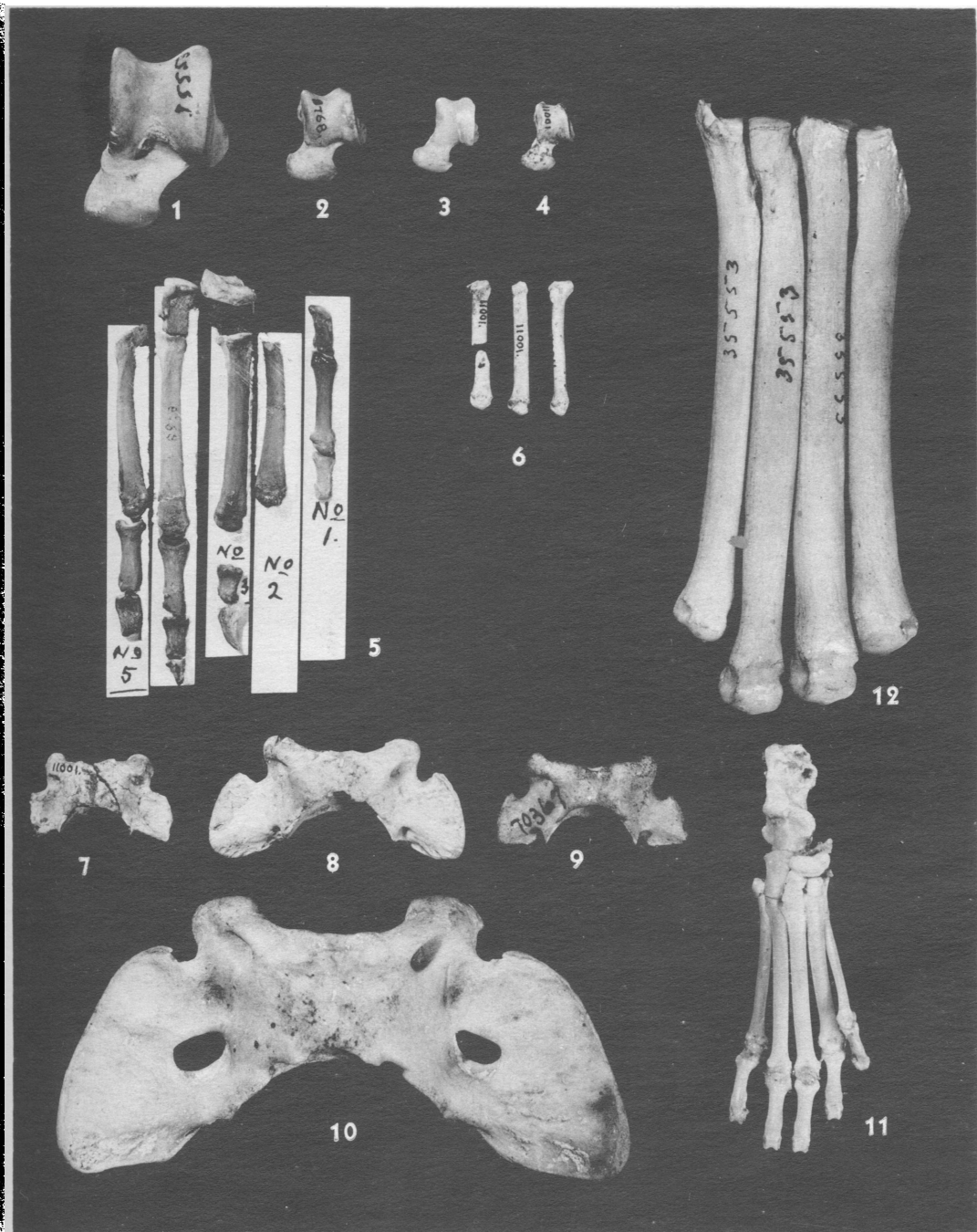
Limb bones of *Canis*, *Phlaocyon*, *Bassariscus*, and *Plesictis*. × 1/1. 1. *Canis*, astragalus. 2. *Phlaocyon*, astragalus. 3. *Bassariscus*, astragalus. 4. *Plesictis*, astragalus. 5. *Phlaocyon*, metatarsals. 6. *Plesictis*, metatarsals. 7. *Plesictis*, atlas. 8. *Phlaocyon*, atlas. 9. *Bassariscus*, atlas. 10. *Canis*, atlas. 11. *Bassariscus*, hind foot. 12. *Canis*, metatarsals
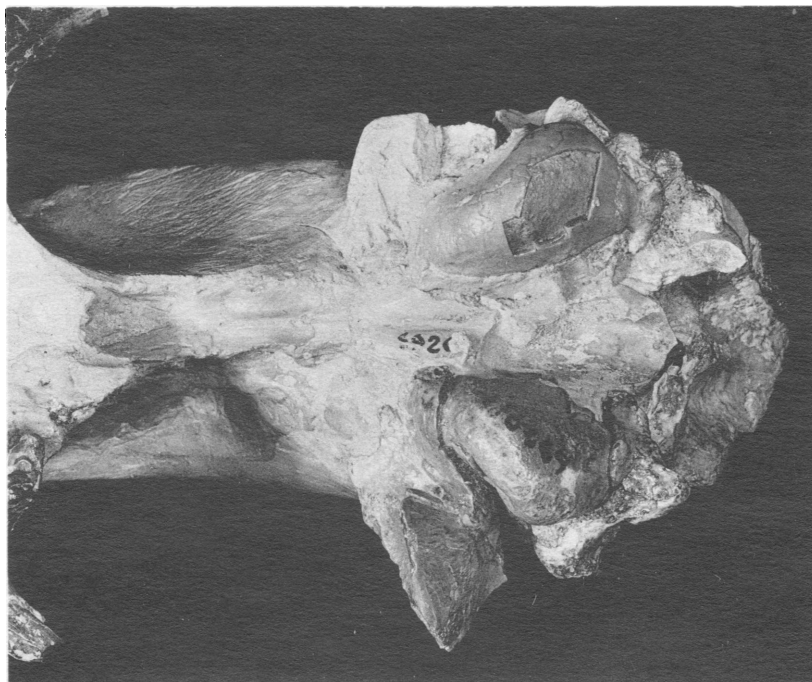
Mesocyon, ventral view of skull.   × 1/1
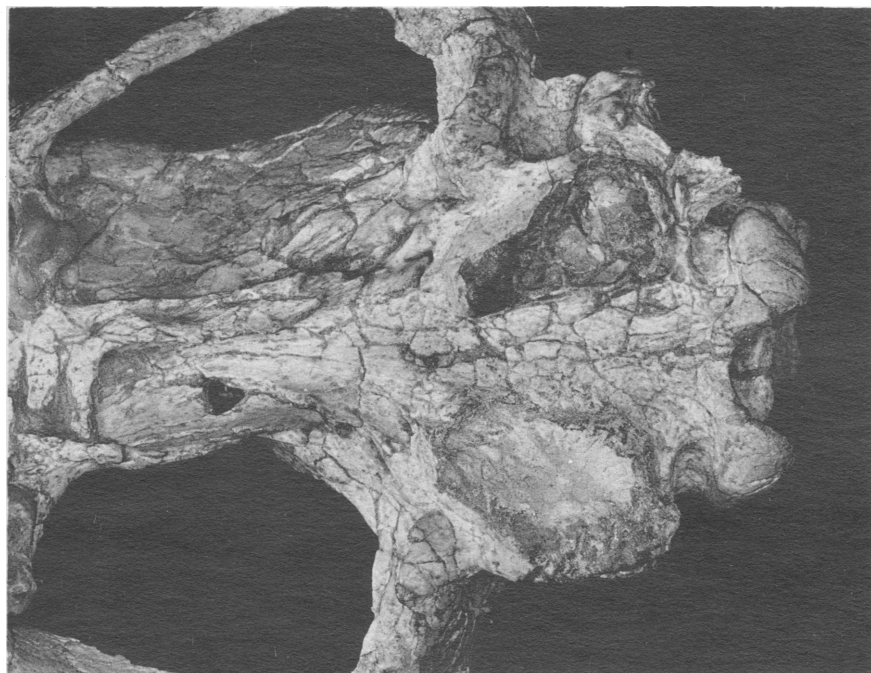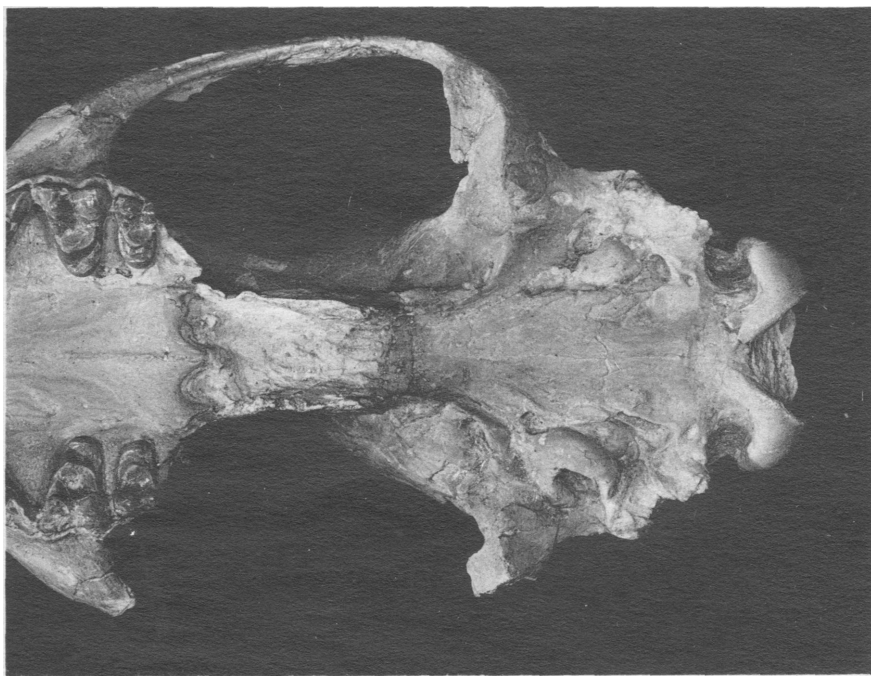
Skulls of (1) *Daphoenus hartshornianus* and (2) *Enkydrocyon*, ventral views.   × 1/1

Skulls of (1) *Paradaphoenus cuspigerus*, (2) *Aletocyon*, and (3) *Enhydrocyon*. × 1/1

Skulls of (1) *Hemicyon barstowensis* and (2) *Arctotherium.* × 1/2

indisputable. *Zodiolestes* must have pursued the small animals inhabiting the *Daimonelix* burrows, and itself used the burrows as a refuge. This points to a semi-cursorial, predatory existence unlike that of *Procyon*, or, in fact, of any of the living representatives of the family.

Cyonasua

SPECIMENS EXAMINED: C.N.H.M. No. P14537.

AUDITORY REGION

Text figures 7, 8

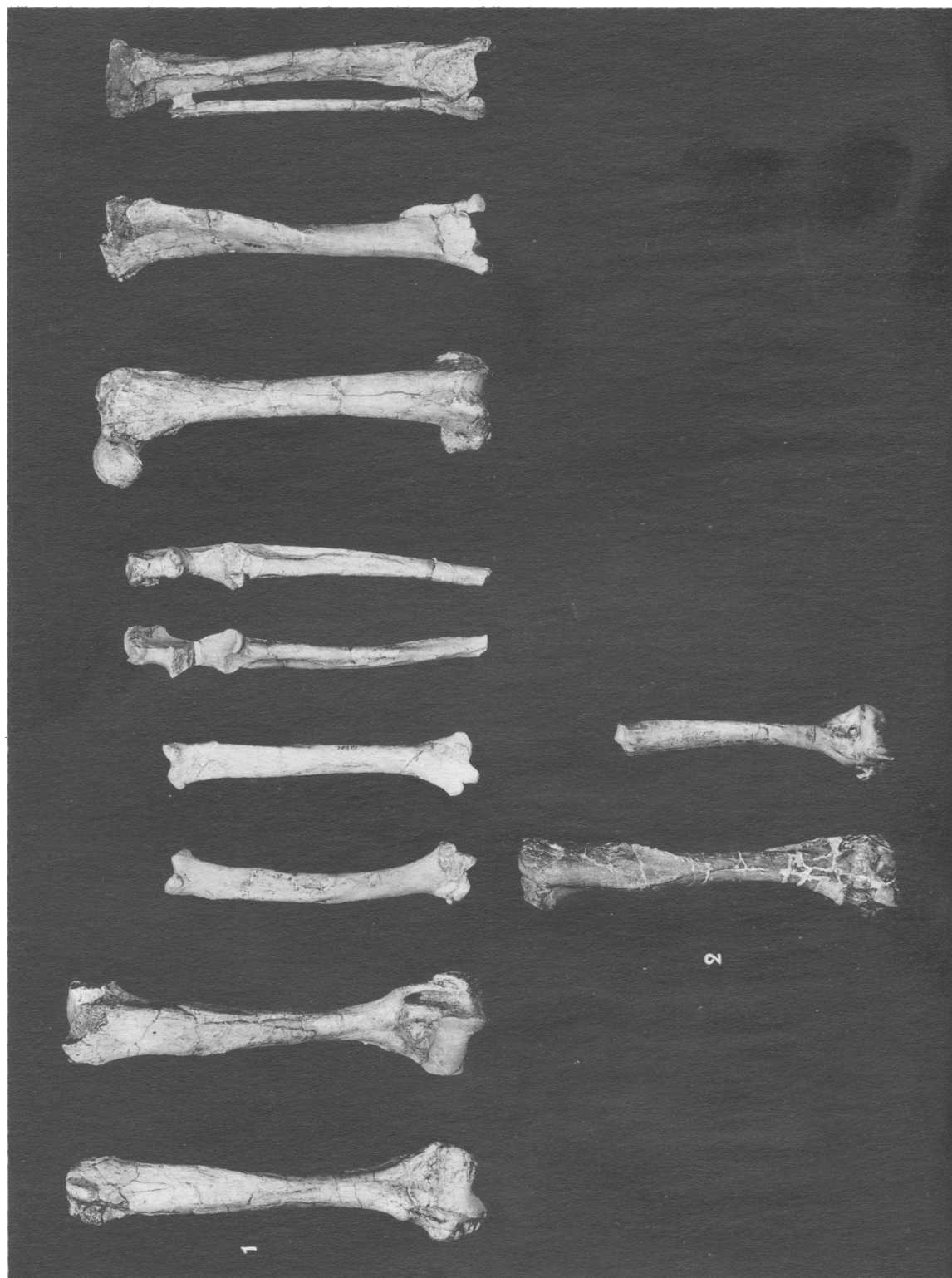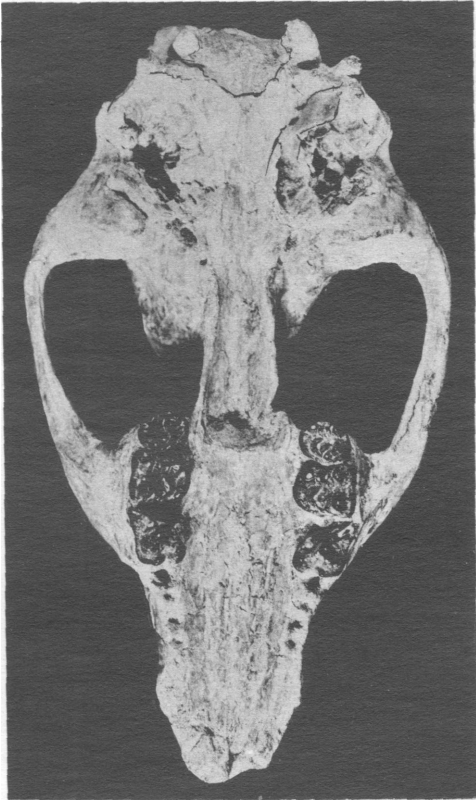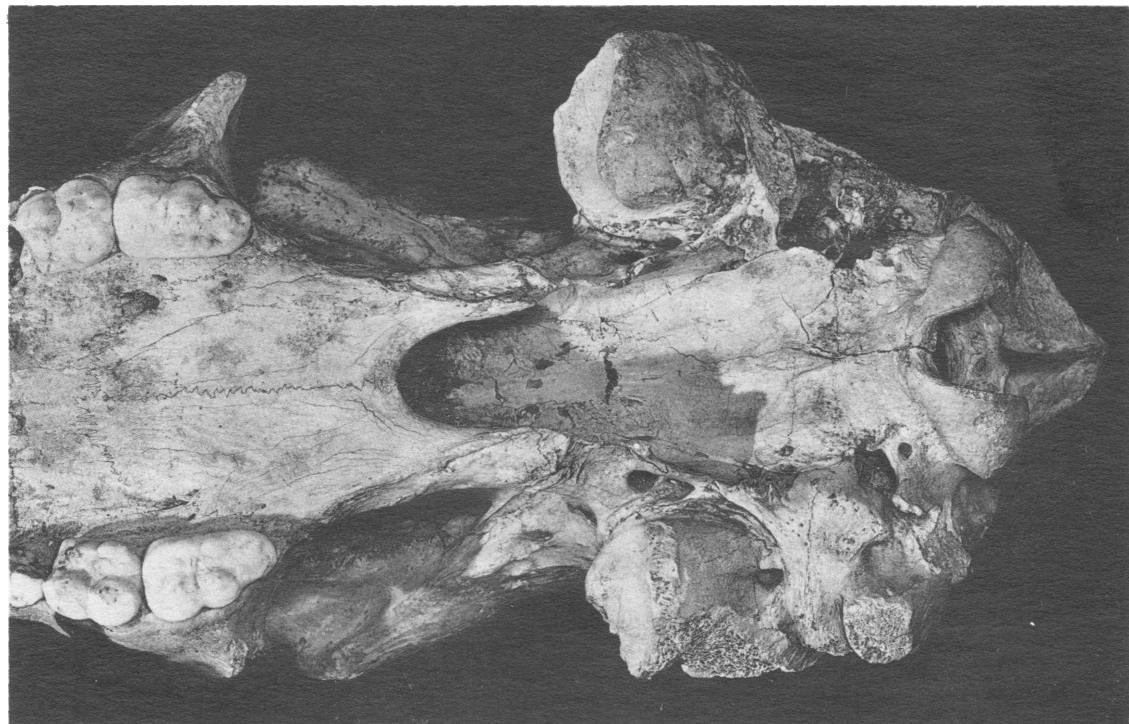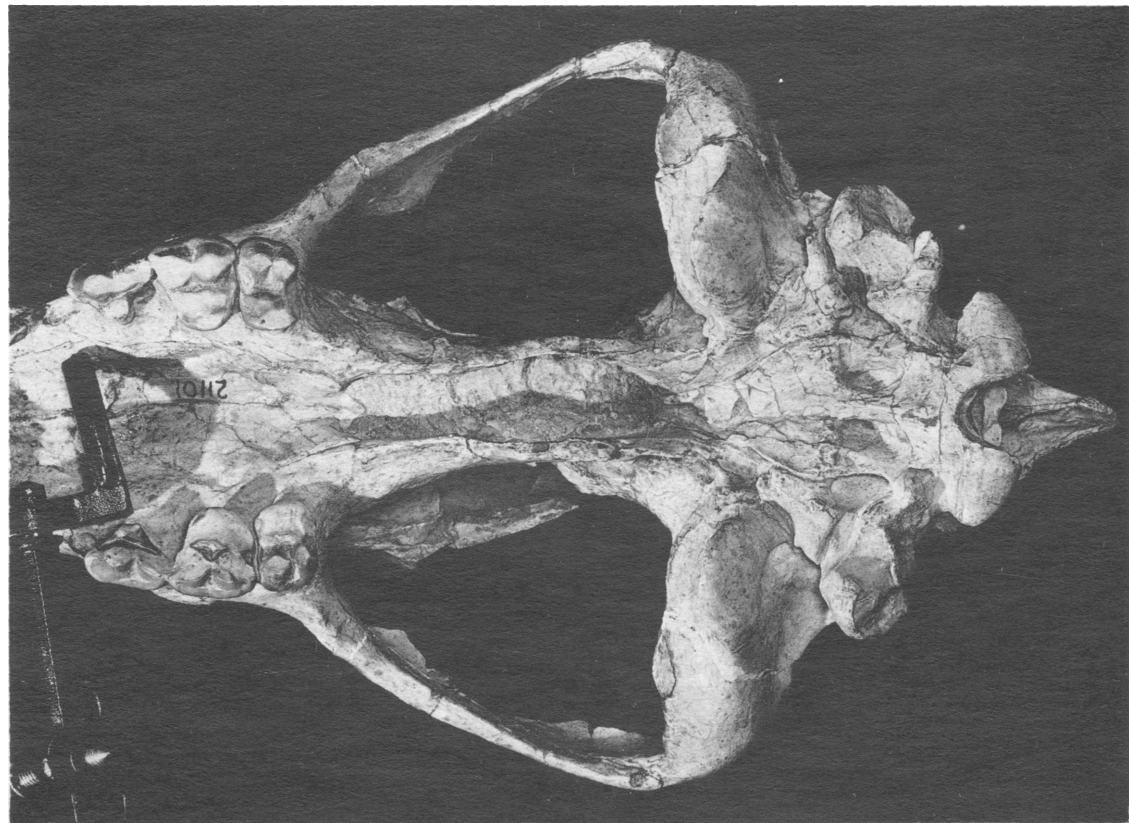The bulla has the typical procyonid flask shape, globular medially and depressed laterally with a long, broad, bony meatus formed of the squamosal dorsally and to a large extent laterally, by the tympanic ventrally. The bulla is very much flattened anteriorly, rises to its greatest height medially, and slopes gently into the paroccipital.

The anterior flattened portion is set off from the posterior globular part by a line which runs from a point just posterior to the foramen lacerum medium laterally and posteriorly to the junction of the posterior margin of the meatus with the mastoid. A similar demarcation is found in *Nasua*, in one specimen raised to a ridge. It marks the position of the internal septum running from the sulcus tympanicus to the medial wall of the bulla. In the left bulla of the specimen of *Cyonasua* studied, a break having occurred in this position, a portion of the septum is exposed (fig. 8).

The mastoid process is prominent, and the paroccipital process is exposed to a large extent because of the relative smallness of the bulla. This region resembles that of the bears more than of *Nasua*, but this similarity is probably the result of larger size.

The external auditory meatus is unusually broad with much the same structure as that of a young bear skull examined. This suggests strongly that a part of the hypotympanic sinus ran along the sides of the meatus. There is a suprameatal fossa, a character almost diagnostic of the Procyonidae.

The stylomastoid foramen appears much

FIG. 8. *Cyonasua brevirostris*, auditory region, part of tympanic removed. ×⅓. *Abbreviations:* car. for., carotid foramen; epi. rec., epitympani recessus; for. lac. med., foramen lacerum medium; for. lac. post, foramen lacerum posterium; for. styl. prim., foramen stylomastoideum primitivum; fos. mus. major, fossa muscularis major; o. t. t., orifice for tuba tympani; p. gl. for., postglenoid process; prom., promontorium; supra-me. fos., suprameatal fossa.

as in the bears and raccoons. There is a foramen stylomastoideum primitivum connected by an open groove with the foramen stylomastoideum definitivum formed of the mastoid and tympanic. The broken condition of the specimen prevents any more detailed description.

CANIDAE

WHITE RIVER

Pseudocynodictis gregarius

Text figure 9

SPECIMENS EXAMINED: C.N.H.M. No. P15427; White River formation, Colorado.

The earliest specimens referable to the Canidae are found in the White River Oligocene of North America. They are among the most numerous fossils in the formation and have been described in detail by Cope (1884) and Scott and Jepsen (1936). A description of

the auditory region was given by the author in an earlier paper. This description is repeated here, with some additions, for the purpose of comparison.

AUDITORY REGION

The bullae are very like those of the modern Canidae, larger proportionally and more inflated than those of the Procyonidae just described. The walls are very thick and the medial wall is steep, much more so than in *Canis*. A cylindrical bony meatus is lacking,

laris major lies entirely forward of the tympanic cavity. It is large and shallow. The tympanic process of the alisphenoid extends almost to the anterior margin of the promontorium. There is only a slight grooving to indicate the position of the tuba auditiva. It is evidently enclosed in cartilage, not bone. There seems to be no division of the large opening at the anteromedial corner of the bulla, and if the Eustachian tube and the entrance to the foramen lacerum medium were separated by a partition, this must also
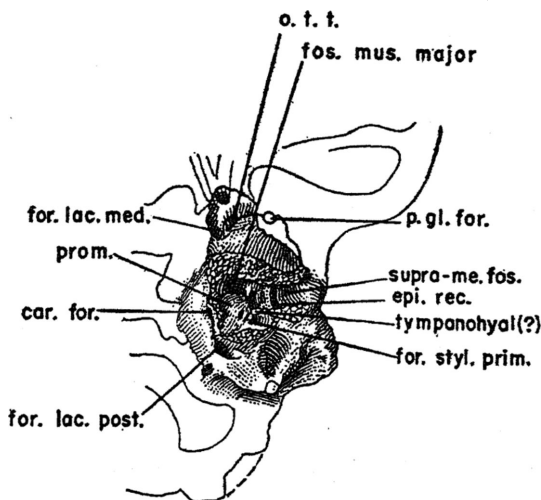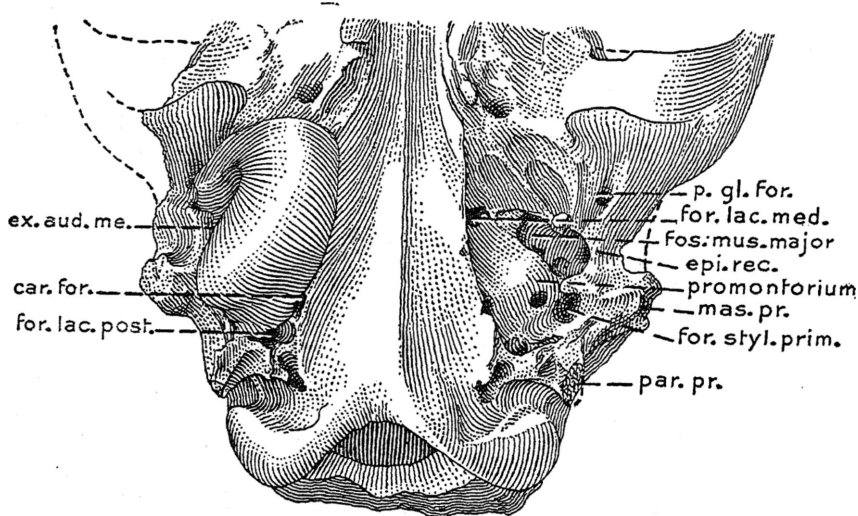

FIG. 9. *Pseudocynodictis*, auditory region, part of tympanic removed. ×2/1. *Abbreviations:* car. for., carotid foramen; epi. rec., epitympanic recessus; ex. aud. me., external auditory meatus; for. lac. med., foramen lacerum medium; for. lac. post., foramen lacerum posterium; for. styl. prim., foramen stylomastoideum primitivum; fos. mus. major, fossa muscularis major; mas. pr., mastoid process; p. gl. for., postglenoid process; par. pr., paroccipital process.

the membranous external auditory meatus having evidently rested directly on the squamosal. The porus acusticus externus is an oval opening inclined forward, with the largest diameter dorsoventral.

The crista tympani is thin and sharp, lying close to the lateral wall of the bulla. It has much the same extent and relations as that of *Canis*. The large, shallow, epitympanic recess is almost entirely medial of the porus. It is separated from the tympanic cavity by the outer wall of the sulcus facialis. The tympanic cavity is deep and lies medial and forward of the recess. The fossa for the muscu-

have been of cartilage. The foramen lacerum medium is bounded by the basisphenoid medially, the periotic posteriorly, and the alisphenoid anteriorly.

The promontorium is prominent and pear shaped, with a small fenestra cochleae looking posterolaterally and a large fenestra vestibuli facing outward and forward.

The apertura tympanica canalis facialis is minute and opens into a definite sulcus facialis somewhat anteriorly to the fenstra vestibuli.

The bulla appears to be ankylosed to all of the elements of the skull surrounding it, the

basisphenoid medially, the mastoid and post-glenoid process laterally, and the base of the paroccipital process posteriorly. There is little overlap, however, of the inbent dorsal margin of the bulla on the promontorium, that portion being largely anteromedial where its dorsal surface forms the roof of the canal between it and the periotic through which the carotid artery reaches the foramen lacerum medium.

The mastoid process is moderately developed, and its medial point is ankylosed to the posterior leg of the tympanic. The posterolateral corner of the bulla is firmly attached to the base of the paroccipital process, which is blunt and straight, pointing directly backwards with only a slight downward inclination.

The foramen stylomastoideum is large. There does not seem to be any process representing the tympanohyal, or any groove or depression in the bulla to mark its place. Removal of the bulla reveals a large foramen stylomastoideum primitivum.

The auditory region of *Pseudocynodictis* is definitely canid, with all the characteristic features of the family well developed. It is a remarkable fact, and certainly indicative of the relative conservatism of the auditory region, that as early as the Oligocene a typically procyonid type existed side by side with a canid type.

Other Features of *Pseudocynodictis*

The adaptive features of *Pseudocynodictis*, although more civet- than dog-like, as Scott and Jepsen point out in their description (1936), nevertheless show some approach to *Canis*. The transverse processes of the atlas are large and wing-like and the foramen for the vertebral artery, although still facing posteriorly, has shifted somewhat ventrally. The astragalus shows some canid characters, most significant of which is the fact that the cuboidal facet is very small and in some individuals wanting. The first metacarpal is reduced, although not nearly so much so as in *Canis*, and the metacarpals are arranged in symmetrical pairs.

The dentition closely resembles that of the microdont living Canidae, especially *Dusicyon* (*Lycalopex*) *vetulus*. The skull proportions are also very similar, but no frontal

sinuses are present. *Pseudocynodictis* thus belongs to Huxley's alopecoid division, while *Dusicyon* (*Lycalopex*) is a thooid.

Daphoenus

Plate 12, figure 1

Specimens Examined: Of *Daphoenus hartshornianus*, A.M.N.H. No. 9797; of *D. vetus*, A.M.N.H. Nos. 9759, 12450, 39098, 39099, and C.N.H.M. No. P12021; White River formation, Colorado.

Taxonomic Position

The genus *Daphoenus*, although very canid in dentition and features of the skull, has, as is well known, skeletal features that are more feline than canine and that link it closely with the contemporary *Dinictis*. These features are usually interpreted not as indications of a close affinity with the Felidae, but rather as representing primitive characters retained by the felids and lost in the other carnivore families. It is well, however, to emphasize that while *Pseudocynodictis* shows viverrid characters which can be interpreted in the same way, nevertheless there are tendencies towards the development of the adaptive features of the Canidae, as well as an auditory region characteristic of the family. This is not the case with *Daphoenus*. The auditory region is not at all canid but resembles, in fact, that of *Nandinia* described earlier in this paper.

Auditory Region

Text figure 10

The most striking similarity is the bulla, the shape and size of which are almost identical in the two forms. It is very loosely attached in *Daphoenus* and *Nandinia* and not ankylosed to the surrounding parts as in *Pseudocynodictis*. The external auditory meatus is a large circular opening with no trace of a bony meatus. The bulla in shape and the meatus are similar to those of *Pseudocynodictis* except for the larger size of the latter.

The tympanic cavity is narrow as in *Nandinia* and deeper than that of *Canis*. There is no expansion of the cavity into any of the elements.

The cartilaginous external auditory meatus must have been long, owing to the large size

of the mastoid process and the exposure of the squamosal on the under side of the skull. The latter bone forms the roof and sides of the meatus, and in those specimens where a bulla is present it is evident that a cartilaginous extension formed the floor.

The epitympanic sinus in *Daphoenus* lies just above and medial to the porus acusticus externus. It is shallow and separated from the large and shallow fossa for the muscularis major by a narrow rim of bone.

The anterior portion of the auditory cavity

question did not seem to be present in the American Museum specimens. If the artery followed the course of the groove, the condition is similar to that of *Canis*, or would readily become so with the expansion of the tympanic to cover the posterior part of the auditory region. If, on the other hand, the promontorium continued on a level to the basioccipital and the artery crossed the promontorium the condition is as in *Nandinia*, and unfortunately the evidence is conflicting.

The foramen lacerum medium is large and
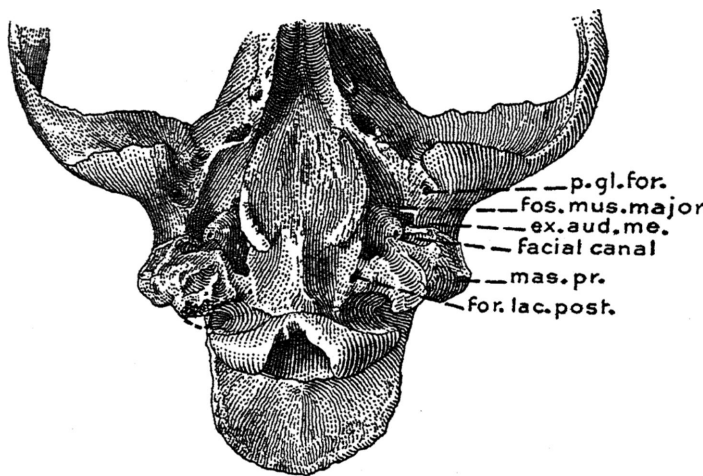
FIG. 10. *Daphoenus vetus*, auditory region, part of tympanic removed. X⅓. *Abbreviations:* ex. aud. me., external auditory meatus; for. lac. post., foramen lacerum posterium; fos. mus. major, fossa muscularis major; mas. pr., mastoid process; p. gl. for., postglenoid process.

is roofed by the alisphenoid which anteriorly slopes gently towards the foramen ovale and posteriorly meets the periotic along an irregular line, but without suture. The surface of the alisphenoid is smooth with only a faint grooving for the Eustachian tube.

The promontorium is large and pear shaped, very similar to that of *Canis*, the fenestra cochleae facing posteriorly and laterally, the fenestra vestibuli laterally and anteriorly. In the Chicago Museum specimen the basisphenoid and basioccipital send a process upward and laterally to meet a similar process from the promontorium. Together they make a deep groove, running forward to the foramen lacerum medium. It is possible that this was the carotid canal. The groove in

situated above the promontorium. The apertura tympanica canalis facialis opens just above the fenestra vestibuli and leads into the sulcus facialis in the usual way. The sulcus, however, is not completely bridged over by the posttympanic process of the squamosal, nor is there any trace of the spur found in *Pseudocynodictis*, *Plesictis*, *Zodiolestes*, the recent *Nandinia*, and others. This may not be so important as it appears since the process is easily broken.

The paroccipital process is blunt and extends backward and downward. This is an arctoid character, but one shared by *Nandinia*. The foramen lacerum posterius is about the size of that of *Canis*. There is, of course, only the primitive stylomastoid foramen and

this is large and bounded in the usual manner.

There is no doubt that the features of the basicranium of *Daphoenus* are more like those of *Nandinia* than any other carnivore, which would seem to argue for the primitiveness of *Nandinia* and suggest that *Daphoenus* is not far from being a stem form near the ancestry of both canids and viverrids.

OTHER CHARACTERS

The dentition of *Daphoenus* differs from that of *Pseudocynodictis* in several important respects. In addition to the absence of M^3 in the latter, the carnassial is much less triangular in shape and is larger proportionally, the carnassial molar index being 100, which is within the range of *Canis*. The carnassial molar index of *Daphoenus*, on the other hand, is 120–122, more nearly that of *Dusicyon*.

Daphoenus has frontal sinuses and thus is in Huxley's thooid division. It is ordinarily considered as representing the larger of the Oligocene dogs. The size range, however, is very great. If A.M.N.H. No. 39099 is properly referred, there are specimens of *Daphoenus* as small as the smaller but not the smallest *Pseudocynodictis*, for this little skull is only 88 mm. in length, while another skull, A.M.N.H. No. 1382, referred to *Pseudocynodictis*, is 124 mm. in length. Fragments of the bulla of this specimen clearly indicate that it was of large size as is that of *Pseudocynodictis*, and since the dentition also agrees there seems no doubt of the correctness of the reference.

Phlaocyon leucosteus

SPECIMENS EXAMINED: A.M.N.H. No. 8768; White River formation, Cedar Creek, Logan County, Colorado.

Phlaocyon is ordinarily included in the Procyonidae, its ancestral relationship with that family not having been questioned, except by von Ihering (1910), since the original description by Wortman and Matthew (1899). A reëxamination of the type material, however, and a thorough study of the auditory region clearly indicate that *Phlaocyon* is a canid.

AUDITORY REGION

Plate 9, figure 3

The bullae are moderately rounded and inflated, very similar in size and structure to those of *Urocyon cineargentus*. The external auditory porus is a circular opening with no trace of a lip or tubular prolongation. It is composed almost entirely of the tympanic with the squamosal forming a very small part of the roof, as in young canids.

The mastoid processes are small, and the paroccipital processes are broad, blunt projections standing well away from the skull and extending downwards and backwards as in *Canis*.

The median basicranial bones are narrow, and the auditory region is relatively broad as in *Canis*. In *Bassariscus*, *Procyon*, and the Viverridae the proportions are exactly the opposite. The relative distance from the posterior margin of the bullae to the condyles is also about as in *Canis*. In the Procyonidae and the Viverridae this distance is always greater.

The interior of the bulla is a single chamber, with, however, a low septum extending from the ventral portion of the sulcus tympanicus obliquely around the interior of the bulla to a point just laterad to the foramen lacerum medium. This septum is in the same position as that of *Canis*, but is less strongly developed than in most species.

The epitympanic recess and the fossa for the muscularis major are round and deep as in *Canis*. There is no epitympanic sinus and no extension of the hypotympanic sinus around the meatus. There is no suprameatal fossa as in *Zodiolestes*, *Plesictis*, *Cyonasua*, and recent Procyonidae.

The inbent margin of the tympanic covers the alisphenoid anteriorly and surrounds the promontorium, leaving only a small median strip and the fenestra cochleae exposed. Medially the tympanic fossa forms the roof of the carotid canal which apparently followed the same course as in *Vulpes*. In this species the carotid foramen, situated at the anterior end of the fossa for the foramen lacerum posterius, leads into a sulcus, the roof of which is the periotic, the sides the tympanic. At the anterior end of the bulla this sulcus becomes a canal formed by the tympanic ventrally, the periotic dorsally, and the basisphenoid medially. These same relations are found in *Phlaocyon* except for the fact that the carotid foramen is not included in the foramen lacerum posterius, although situated very near it. The carotid canal also seems covered

by the tympanic throughout its length.

Segall in his study of the auditory region of the arctoid Carnivora (1943) points out that the Canidae are an exceptionally compact group in the structure of the auditory region, with no aberrant forms among living members. They are sharply set off from the Procyonidae by the following characters:

Pseudocynodictis the atlas is modified in the direction of *Canis*, and in *Phlaocyon* this modification is carried still further, the transverse processes being wing-like with a wedge-shaped posterior surface. The arterial opening is posterior but very ventral, and the canal is oblique. The axis is too fragmentary for comparison. The other vertebrae are not

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PROCYONIDAE

External auditory meatus formed mainly of the squamosal

Reflected margin of the bulla covers only the base of the promontorium

No septae or ridges in the bulla

Foramen stylomastoideum primitivum present, with no bony third part to the facial canal

Carotid canal a tube in the medial wall of the bulla, foramen separate from the posterior lacerate foramen.

CANIDAE

Formed entirely of the tympanic except in young individuals

Overlap of the tympanic on the promontorium extensive

Partial septum extending obliquely across the bulla perpendicular to the crista tympani

No foramen stylomastoideum primitivum, facial canal enclosed by the tympanic and mastoid

Carotid canal formed in the roof of the bulla, foramen included in the foramen lacerum posterius

Phlaocyon agrees with *Canis* in four of these diagnostic characters of the auditory region, the only point of disagreement being the separation of the posterior carotid foramen and the foramen lacerum posterius. This character is shared with *Pseudocynodictis*, which is certainly a canid. It would seem, therefore, that at least in the auditory region there is no approach towards *Procyon*.

THE SKELETON

Plate 10, figures 2, 5, 8

The skeleton of *Phlaocyon* has been described by Wortman and Matthew (1899) who found it intermediate between *Canis* and *Procyon*. The writer on reëxamining the material was unable to find a single feature which could be said to approach *Procyon*.

The atlas is almost a miniature of that of *Canis* and especially interesting because of the position of the foramen for the vertebral artery. In *Daphoenus*, *Plesictis*, *Pseudocynodictis*, and almost all living procyonids and viverrids the transverse processes of the atlas are relatively short and truncated with a triangular face. The foramen for the vertebral artery pierces this face, and the canal runs forward horizontally, opening about midway on the dorsal surface of the processes. In

particularly like those of either *Procyon* or *Canis*. This is probably due to size, the resemblance to *Bassariscus* being much closer.

The scapula is fragmentary and has been restored so that it is impossible to tell the nature of the dorsal margin. The spine has the same configuration as that of *Canis*.

The humerus does not resemble that of *Procyon* at all, lacking the stoutness, the rugosity, the pronounced deltoid and supinator crests. It does resemble that of *Bassariscus* very markedly, with an approach to *Canis* in the deeper grooving of the trochlea and the more feeble development of the supinator crest, which in *Canis* hardly exists. The ulna and radius are approximately the same length as the humerus, a proportion quite different from that of *Canis* where the forearm is longer. In the gray fox the disparity is even greater. A few breeds of domestic dogs have about equal proportions of the two elements and *Fennecus*, *Cuon*, and *Speothos* among wild canids have the same proportions as *Phlaocyon*. The raccoon has a much longer ulna and radius and shorter humerus relatively than *Canis*. The cross sections of these bones in *Phlaocyon* are, as Matthew points out, trihedral or irregular rather than roundly oval as in *Procyon*.

The metacarpals are definitely canid, show-

ing an advance over *Pseudocynodictis*. Mc I is only half the length of Mc III, Mc V is three-fourths as long as Mc III but stouter. Mc II is paired with Mc V and Mc III with Mc IV, the symmetry of the foot being paraxonic as in the artiodactyls. The cross section of the metacarpals is square with sharp edges, showing that the bones were closely pressed together as in the typical Canidae. This is one of the most striking adaptive features of the family and, of course, quite unlike the condition in *Procyon* where the adaptation is entirely in the other direction, i.e., a grasping fore foot with a semi-opposable first digit.

The femur presents no differences of significance from that of *Canis*. The lesser trochanter is somewhat more prominent. The whole aspect of the bone is different from that of *Procyon*. In the latter the head is joined to the heavy shaft with virtually no neck. The greater trochanter is a low rugosity with little separation from the head, rather than the sharp, upwardly directed process characteristic of *Canis* and found also in *Phlaocyon*. These differences determine the difference in position of the limbs, which in the raccoon extend laterally from the body and are capable of a high degree of rotation, but in the Canidae are brought closely under the chest, with only a fore-and-aft movement. The canid limb is much the more highly specialized of the two. *Phlaocyon* has clearly gone a long way towards this specialization.

The tibia and fibula also agree well with those of *Canis*. They are approximately the same length as the femur, a proportion found also in *Canis*.

The astragalus and calcaneum are canid in form and position, differing from those of *Procyon* especially as noted in the description of *Plesictis*. The pulley of the astragalus in *Canis* and *Phlaocyon* makes a right angle to the axis of the calcaneum and, in fact, the entire foot, while in the raccoon, as in all arboreal animals, this angle is oblique. This has the effect of throwing the foot over on its border on the outer side. *Phlaocyon* differs from *Canis* as do all of the Miocene Canidae in that the trochlea of the astragalus is less deeply grooved, and the neck less directly ventral.

The tarsal bones do not present any marked differences from those of *Canis*. The

metatarsals have the characteristic quadrangular cross section and symmetrical pairing described for the fore limb. This is still more pronounced in the hind limb and, as mentioned before, is diagnostic of the Canidae.

RELATIONSHIPS

Wortman and Matthew based their theory of procyonid ancestry for *Phlaocyon* on 11 cranial characters which they considered progressive features pointing towards the raccoons (Wortman and Matthew, 1899, p. 134). These features, however, are found more or less developed within the Canidae themselves, or families other than the Procyonidae. The postero-internal cusp to the upper sectorial, for example, is found not only in *Bassariscus astutus* but in numerous mustelids. The low, rounded cusps of the molars and the arrangement of the incisors in a transverse row are characteristic of the South American canid *Lycalopex*. In fact, the arrangement of the incisors, which differs from that of *Canis*, is a diagnostic feature of the South American canids (Osgood, 1934). Five of the other characteristics deal with skull proportions or related features, and it is true that *Phlaocyon* closely matches *Procyon* in these, except for the relatively greater length of the basicranium in the raccoon. Skull proportions in the Canidae, however, are so variable in the wild species, to say nothing of the extremes found in domestic breeds, that little phylogenetic importance can be attached to them. The diagnostic features of the skull are all canid.

The skeleton of *Phlaocyon* is intermediate between *Pseudocynodictis* and *Canis*, in some features closer to the latter. The dentition is aberrant for a canid. An internal cingulum to the carnassial and any stylar cusps developed from it, however, are not exclusively procyonid features. They are found in many mustelines and especially *Lutra* and *Taxidea*. Lydekker has described a specimen from the Siwalik beds (Lydekker, 1884) which he refers to *Lutra*, although the proportions of the skull are somewhat different than those of the living otter. From the illustration this specimen has a carnassial extremely like that of *Phlaocyon*. (Apparently the matrix was not removed from the basi-

cranium so the shape and size of the bulla could not be seen.)

No living canid has stylar cusps, it is true, but this does not preclude the possibility that this feature was a canid variation at an earlier date. The dentition of the Carnivora is extremely plastic and subject to a great deal of parallelism and convergence. A minor radiation in the matter of dentition occurred among Miocene canids to be described, several of which show a type of carnassial similar to that of *Phlaocyon.*

JOHN DAY

Nothocyon

SPECIMENS EXAMINED: Of *Nothocyon lemur,* A.M.N.H. No. 6888; of *N. urosticus,* A.M.N.H. (Dept. Mammals) No. 391; of *N. geismarianus,* A.M.N.H. No. 6886.

TAXONOMIC POSITION

In addition to *Pseudocynodictis gregarius* which continues on into the John Day almost unchanged, there are several species of small canids which were included by Matthew in the genus *Nothocyon* which was established by Wortman and Matthew on a specimen of the South American *Canis urosticus* (A.M.N.H. Dept. Mammals No. 391). *Canis urosticus* is synonymous with *Canis (Lycalopex) vetulus* Lund. Osgood has recently separated all of the South American canids from *Canis* and made *Lycalopex* a subgenus of *Dusicyon,* which also includes the Argentine dogs and the Falkland wolf. If the original type is used, therefore, the name of the Miocene species would have to be *Dusicyon (Lycalopex) vetulus.* There is much in the skeleton of *Nothocyon geismarianus,* the only species besides *Pseudocynodictis gregarius* in which the skeleton is known, to warrant such a grouping. The limb bones are extremely modernized. However, to include a Miocene species with a living species seems a rather extreme application of the principle of vertical classification, and one not followed by Matthew for other Miocene forms such as *Mesocyon* or *Cynodesmus* which also approach *Canis* in many features.

AUDITORY REGION

The auditory region of *Nothocyon* does not differ from that of *Pseudocynodictis* except for the generally larger size of the bulla. In *N. lemur* and *N. latidens* this reaches very large proportions, only equaled in living canids by that of the fennec.

OTHER FEATURES

The skeleton of *N. lemur* and *N. latidens* is unknown. That of the John Day *Pseudocynodictis* does not differ in any essential feature from the White River species. *Nothocyon geismarianus,* however, is definitely nearer *Canis.* The body is elongate with short legs, but less so than in *Pseudocynodictis.* The cervical vertebrae are very like those of *Canis.* The astragalus and calcaneum are almost identical with those bones in the modern genus. The metatarsals have squared edges and are symmetrically arranged. This is in contrast to *Pseudocynodictis* where the ankle bones are intermediate in character, the digits wide apart with rounded edges. The humerus has an epicondylar foramen. The ilium has the same general shape as that of *Canis* but more expanded. The acetabulum is almost as deep as that of *Canis,* and the limbs were evidently held directly under and close to the body. The groove of the trochlea is somewhat shallower than in *Canis.*

Temnocyon

SPECIMENS EXAMINED: Of *Temnocyon altigenis,* A.M.N.H. Nos. 6855, 6856, Y.P.M. No. 59001; of *T. wallovianus,* A.M.N.H. No. 6858; of *T. ferox,* P.M. No. 6857.

Cope in his original description of the John Day Carnivora (1878) established the genus *Temnocyon* on *T. altigenis,* the type of which is a lower jaw, and gave as the diagnostic characters: lower sectorial with a trenchant heel, M^2 with trenchant cusps, and M^3 absent. He also referred to the genus *T. josephi* and *T. coryphaeus,* of which both skulls and skeletons were known. In 1890 Scott proposed the name *Mesocyon* for *T. coryphaeus* and *T. josephi* because these species lack the trenchant heel to the sectorial which is one of the diagnostic characters of the type. Eyerman (1894) referred *T. coryphaeus* to *Hypotemnodon,* a new genus created by him and added *T. ferox* to that genus. *Hypotemnodon* actually is a synonym of *Temnocyon* while *T.*

coryphaeus properly belongs in *Mesocyon* for the reason stated.

AUDITORY REGION

The basicranial region is missing in the type of *T. altigenis*, but a specimen in the Peabody Museum, Yale University, has the region fairly well preserved. Eyerman did not describe the basicranium of *T. ferox*, probably because of the imperfection of the specimen.

The bulla has been weathered away on the right side of the Yale specimen, and the underlying structures are somewhat worn away and flattened. The left side, however, is almost intact except for the loss of a small part of the posterior wall of the bulla. The bulla is of the demibulla type and closely resembles that of *Daphoenus*, i.e., it consists of only a ring of bone covering the anterior part of the auditory region.

The porus acusticus externus is an oval opening as in *Daphoenus*, the margin of which is incomplete ventrally. There is no bony tubular meatus. The cartilaginous meatus, roofed by the squamosal, must have been long as there is a large exposure of the squamosal on the under part of the skull. The mastoid process is prominent and continuous with the paroccipital which projects from the posterior margin of the skull as a blunt process.

The median basicranial bones are broad, and the auditory region is correspondingly narrow. The tympanic cavity is deeper than in *Canis*. The epitympanic recess is large and shallow as in *Daphoenus*, and the fossa for the muscularis major is also shallow. The stylomastoid foramen is situated just opposite the fenestra cochleae. A deep groove formed anteriorly by the rolled edge of the tympanic and posteriorly by the mastoid leads from the foramen to the exterior of the skull. At the posteromedial corner of the auditory region there is a large fossa extending posteriorly and laterally to the middle of the paroccipital process. The foramen lacerum posterius is situated in the fossa, but the course of the carotid artery could not be ascertained.

RELATIONSHIPS

The auditory region of *Temnocyon altigenis* is definitely like that of *Daphoenus*

vetus. The two species differ markedly in the dentition, although there is some question as to whether the absence of M^3 is a diagnostic character of *Temnocyon* as Cope thought. In the type specimen, as Dr. Simpson pointed out to the writer while going over the material, there is a minute alveolus for M^3. The referred specimens are broken in such a way that the presence or absence of the tooth in question could not be ascertained. It was smaller, however, in *Temnocyon* than in *Daphoenus* and probably had a tendency to be lost. The carnassial of *Temnocyon* also differs from that of *Daphoenus*. The shear is more transverse, and the antero-internal cusp more prominent and more internally placed. M^1 has two high external cusps separated by a sharp depression. The trenchant heel of the lower sectorial fits into this depression. There is also a broad cingulum equally developed anteriorly and posteriorly. M^1 of *Daphoenus* follows much more the typical canid pattern.

The general shape of the skull is similar in the two forms, but the skeleton differs in a number of features. *T. ferox* agrees with *Daphoenus* in the length of Mc I, but the metapodials in general are longer and have the typically canid squared edges. *Temnocyon* could easily be derived from *Daphoenus* and possibly bears the same relation to that genus that the dholes do to the modern *Canis*.

Mesocyon

Plate 11

SPECIMENS EXAMINED: From the Lower Miocene, John Day, Oregon: *Mesocyon coryphaeus* (A.M.N.H. Nos. 6859, 6860, 6862, 6922); *M. josephi* (A.M.N.H. Nos. 6878, 6863, 6908, 6921). From the Lower Harrison of Nebraska: *Mesocyon hortulirosae* (M.C.Z. No. 2102).

The auditory region in all of the specimens referred to *Mesocyon* is very similar and characterized by exceptionally large bullae, very inflated medially. Since *Mesocyon* included the majority of Miocene canids and since there were other genera with greatly inflated bullae, the character apparently was one typical of Miocene Canidae, although not occurring in all. What environmental conditions or processes of selection influence this

development is not known. High altitude and desert forms today tend to have large bullae. A group of quite unrelated animals, the oreodonts, living at the same time and in the same locality with *Mesocyon*, had similar bullae. There is no evidence, however, according to Dr. Simpson, of high altitude or desert conditions in the deposits where the fossils are found.

The internal structure of the auditory region is like that of all other canids, except for the unusual size of the septum. This septum is in the same position as that of *Canis* or *Vulpes*, but it is very much deeper and more extended posteriorly than found in these genera or any other canid examined by the writer.

Although the auditory region is so similar in all of the *Mesocyon* specimens, the other characters vary widely. A.M.N.H. No. 6959, the type of *M. coryphaeus*, has approximately the same proportions of the skull as *Daphoenus* and teeth of the same general type. The carnassial is larger in *Mesocyon*, however, the molar index being 90, within the range of *Canis*, while that of *Daphoenus* is 120. M² is also smaller in *Mesocyon*. Other specimens have quite different proportions. The muzzle is shortened and broadened, giving a very musteline aspect to the skull; the teeth are smaller proportionally to the skull; and the carnassial is small in relation to the molars. In a series of specimens there is an almost complete gradation in this shortening of the muzzle between the type and *Oligobunis crassivultus*, in which the proportions are virtually identical with those of the living *Gulo*.

The limb bones are also very variable. In A.M.N.H. No. 6920 the humerus is a stout bone with prominent deltoid and supinator crests (which have virtually disappeared in *Canis*) giving it a very wolverine aspect. Another specimen, A.M.N.H. No. 6910, on the other hand, is much smaller, very slender, and canid-like throughout. There is no epicondylar foramen and the wall of the anconeal fossa is so thin as to be broken through into a minute foramen, a characteristic of modern canids not found in any other Miocene form. The Museum of Comparative Zoölogy specimen of *Mesocyon hortulirosae* has the same proportions.

Paradaphoenus cuspigerus

Plate 14, figure 1

SPECIMENS EXAMINED: A.M.N.H. Nos. 6852 and 6853; John Day Valley, John Day formation, Oregon.

DESCRIPTION

The *Daphoenus* group of canids are continued into the John Day by *Daphoenus felina*, which the writer was not able to examine but which is described as closely similar to *Daphoenus vetus*, and a smaller species, *Paradaphoenus cuspigerus*, which is also very similar. The carnassial of the latter is less obliquely placed than that of *Daphoenus vetus* but still small in comparison to the molar dentition. The teeth closely resemble those of *Urocyon* in shape. The tympanic is like that of *Daphoenus*, small, ring-like, anteriorly placed, but larger, leaving only a small portion of the periotic exposed. The periotic itself is very like that of *Daphoenus*, the promontorium being pear shaped with the fenestra cochleae facing laterally and posteriorly. The epitympanic recess and the fossa for the muscularis major are large and shallow as in *Daphoenus*. A groove just lateral to the promontorium running between the basioccipital and the periotic probably represents the course of the carotid artery. There is no trace of a groove for the passage of the artery over the promontorium as in *Nandinia*, nor is the auditory prominence in direct contact with the basioccipital.

The braincase is much more expanded than in *Daphoenus*, less so than in *Urocyon*, agreeing in this respect with *Nandinia*. There is a lyriform sagittal area, but it is not so broad as in *Urocyon*, and again it closely resembles *Nandinia*.

RELATIONSHIPS

Paradaphoenus is clearly not approaching *Amphicyon*. In fact, there would be nothing to preclude its being ancestral to *Urocyon*. Another specimen (A.M.N.H. No. 6851) referred to *P. transversus*, which consists of only the anterior part of the skull, has a much more *Amphicyon*-like configuration of the muzzle and dentition. *Amphicyon* has, however, a very distinctive type of auditory region (to be described in the next section)

which makes it difficult to link it up with any of the Canidae.

LOWER ROSEBUD

Cynodesmus

SPECIMENS EXAMINED: *Cynodesmus thompsoni*, A.M.N.H. No. 12874; Lower Rosebud, South Dakota.

DESCRIPTION

The auditory region is very like that of *Pseudocynodictis gregarius*. Certain tendencies in the John Day species are exaggerated, however: the steepness of the medial wall of the bulla, its height and inflation posteriorly. The porus acusticus externus is prolonged in a short lip ventrally and posteriorly. Anteriorly the lip is much prolonged and, as noted by Matthew, is in such close contact with the postglenoid process as to obscure the postglenoid foramen. The mastoid process is small, and the paroccipital process is a narrow rod extending backward and downward as in the typical Canidae.

The dentition is very modernized, closely resembling that of the *Dusicyon* group of South American canids, as Matthew pointed out. The carnassial is much larger than in *Pseudocynodictis gregarius*, smaller than in *Canis*. The shear, however, is almost directly anteroposterior. The antero-internal cusp is inconspicuous and anteriorly placed, much more like that of *Canis* than some species of *Dusicyon*. (South American canids are very variable in this regard.) M^1 is typically canid. M^2 is a small oval tooth of the same proportions as in the wolf.

RELATIONSHIPS

Cynodesmus was suggested by Matthew (1924) as ancestral to *Tomarctus* and the later typical Canidae. This view would certainly be confirmed by the dentition which, as McGrew pointed out (1935), is hardly distinguishable from that of *Canis*. The characters of the limbs, which are little more advanced in the direction of *Canis* than are those of *Pseudocynodictis*, seem to indicate a somewhat less direct relationship. Many earlier canids, notably *Nothocyon gesimanianus* of the John Day and even the White River *Phlaocyon*, attained a much higher cursorial adaptation.

In fact, the Miocene Canidae present a very interesting example of variation in the rate of evolution of different systems of structures. In one genus the limbs are more specialized in the canid direction, in another the dentition, until trial and error guided by natural selection produced the particular combination of characters which make up the genus *Canis* as we know it.

Enhydrocyon crassidens

Plate 12, figure 2

SPECIMENS EXAMINED: A.M.N.H. No. 12886; Lower Rosebud, South Dakota.

DESCRIPTION

The bullae are large but not so inflated as those of *Mesocyon* and are of somewhat different shape, slightly depressed anteriorly and laterally. The auditory meatus consists of a circular rim of bone formed entirely of the tympanic. The cavity of the bulla is simple without even the suggestion of a septum, resembling in this and general appearance the bulla of *Hyaena*. The latter has a peculiar specialization in that the excavation of the paroccipital process forms an additional cavity behind the true tympanic cavity and is separated from it by a septum running parallel to and immediately above the inbent posterior margin of the tympanic.

In *Enhydrocyon* the roof of the tympani covered the periotic to a large extent, but without excavation into the paroccipital.

The dentition of *Enhydrocyon* differs from the more typical canid dentition in the large size of the carnassial, the elongation of the first molar, and its peculiar shape due in part to the pitting of the tooth for the trenchant heel of the lower sectorial. $M^2_{\underline{2}}$ are very small, and M_3 is a nubbin placed almost on the edge of the palate on one side and absent on the other. The reduction in molars and the large size of the carnassial parallel the condition in the recent dhole. The tendency is carried further, however, than in the modern form, and the shape of the teeth is very different. M^1 of *Cuon* is not elongate transversely and does not have the extensive development of the internal cingulum. The carnassial is not so large or broad, and it has a distinctly separated internal cusp and no trace of a

parastyle. The parastyle is very pronounced in *Enhydrocyon*.

The characters of the limbs are, as Matthew described them, unlike those of any living canid, the fore limbs being longer and larger than the hind limbs as in *Hyaena*.

RELATIONSHIPS

Temnocyon and *Enhydrocyon* are usually linked with the recent *Cuon*, *Speothos*, and *Lycaon* to form a cyonine section of the Canidae. There is no doubt of the parallel specializations in all of these forms. In fact, the likeness is very striking. The inclusion of *Cuon*, *Speothos*, and *Lycaon* in one group, if this is intended to imply a genetic connection, involves difficulties, and the fossil forms complicate the problem. *Cuon*, as Huxley pointed out, has all the features of a modified jackal. The dentition is that of *Canis* reduced. The incisors are tripartite, and the occipital crest is triangular. There is virtually no precarnassial constriction of the muzzle, a feature found in some breeds of domestic dogs. The teeth are very crowded, P³ being turned sidewise, and M¹ is reduced but has the triangular form of *Canis*. There is no third lower molar, and M² is much reduced.

Speothos is very much smaller than *Cuon*, agreeing with *Lycalopex* and the smaller *Dusicyon pseudalopex*. The constriction of the muzzle is about as in *Urocyon*. There is no second upper molar. The entire dentition is much smaller than that of *Cuon* and of a different cast. The bullae are small, and the braincase is much less expanded than in *Cuon*. A lyriform area is present.

The general appearance of *Cuon* and *Speothos* is altogether different, as described in the beginning of the paper. *Cuon* resembles the canids of the region in which it dwells, that is to say the jackals, while *Speothos* resembles the canids of Brazil and Argentina. The two species (*Cuon* and *Speothos*) agree in the reduction of teeth, and an accompanying change in the shape of the heel of the carnassial, a change which may be effected by a simple suppression of the outer cusp, and which may have occurred repeatedly in the history of the Canidae.

The only characteristic which *Lycaon* has with the dhole and the bush dog is the trenchant heel to the lower carnassial. The head is short and broad, but there is no reduction of the dentition. Taking all of the features into consideration, *Lycaon* has more in common with *Canis*, from which it differs only by the complete suppression of the pollex, than with *Cuon* or *Speothos*.

Enhydrocyon represents still a different type. The pattern of the dentition is different, and the structure of the limb bones entirely out of line with the evolutionary development which has culminated in the living Canidae, including *Cuon* and *Speothos*.

In discussing the features of the molars in his first description of the Lower Rosebud fauna Matthew wrote (1907, p. 182), "Whatever the value of these characters of the molars may prove to be they do not give an adequate basis for subfamily division of the Canidae, nor does it appear to the writer that there are any such well marked distinctions among them at any epoch of their evolution as to warrant subfamily division. On the contrary they appear a rather homogenous group, and the diversity among them is by no means comparable to that which exists among the Mustelidae. It is possible to disentangle and trace out several phyla more or less accurately, but to give these phyla subfamily distinction would be misleading." In later papers Matthew seemed to alter this opinion and attach more importance to the characters in question. In view of the fact that a trenchant heel to the lower sectorial can be shown to have occurred repeatedly from the earliest carnivores on (*Vulpavus* and some species of *Viverravus* have such a development), it would seem more probable that it is a mutation fairly common in the canid stock and no particular indication of relationships.

LOWER HARRISON

Aletocyon multicuspis

SPECIMENS EXAMINED: U.C. No. 1482; Lower Harrison, western Nebraska.

Aletocyon, like *Phlaocyon*, is ordinarily classified with the Procyonidae. A study of the auditory region seems to show convincingly, however, that *Aletocyon*, like *Phlaocyon*, is a canid.

AUDITORY REGION

Plate 14, figure 2

The left bulla is weathered away and the

right bulla is partially destroyed, but a cast in case-hardened matrix has preserved the form of the one part, and the damage to the other is not sufficient to obscure the size and shape. The bullae are large and oval and obliquely set in the basicranium. The medial wall rises abruptly from the basisphenoid to a height proportionally greater than in *Canis lupus*, but corresponding closely with such forms with large bullae as *Fennecus zerda* and the Miocene *Nothocyon lemur*.

There is no division of the bulla into cham-

the squamosal to form the roof of the meatus. The tympanic aperture is oval and was apparently directed in the same way as in *Canis*. (The floor of the aperture is broken so that there is some doubt of the shape.)

The epitympanic recess and the fossa for the tensor tympani muscle are both deep, but there is no epitympanic sinus and no extension of the hypotympanic sinus around the meatus. There is no fossa in the squamosal as in *Zodiolestes*, *Procyon*, and *Ailurus*.

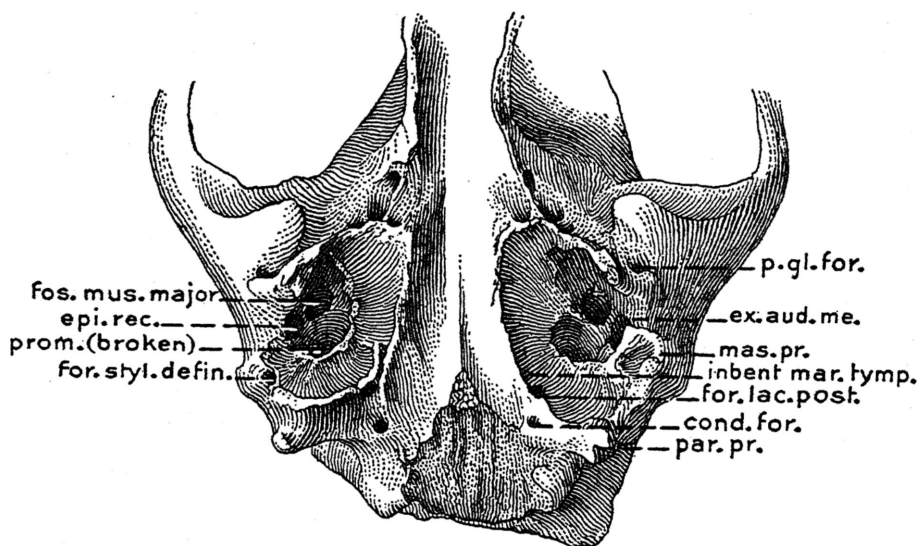The promontory is too weathered for the

FIG. 11. *Aletocyon*, auditory region, part of tympanic removed. ✕2/1. *Abbreviations:* cond. for., condylar foramen; epi. rec., epitympanic recessus; ex. aud. me., external auditory meatus; for. lac. post., foramen lacerum posterium; for. styl. defin., foramen stylomastoideum definitivum; fos. mus. major, fossa muscularis major; mar. tymp., margin of the tympanic; mas. pr., mastoid process; p. gl. for., postglenoid process; par. pr., paroccipital process; prom., promontorium.

bers or evidence of an entotympanic. However, a low ridge extending from a point just lateral to the entrance of the Eustachian tube to a point on the medial wall of the bulla seems to give rise to other low septa which radiate to the edge of the reflected margin of the part of the bulla which covers the periotic. Similar structures exist in the Mustelidae and to some extent in *Canis*. They are never found in *Procyon*.

There is no tubular meatus and the internal meatus is short. It is composed of the tympanic which sends a thin slip of bone across

apertura tympanica facialis to be identified, but the sulcus facialis is evidently represented by a groove in the periotic just posterior and medial to the epitympanic recess. It leads into a short canal formed by the mastoid and tympanic and opens to the exterior across the posterolateral angle of the mastoid process. This, of course, is the same position as that occupied by the facial canal in *Canis*, and the roughened condition of the mastoid process seems to indicate that the hyoid, attached just laterally to the stylomastoid foramen, partially closes the latter.

In the fox, the carotid foramen situated at the anterior end of the fossa for the foramen lacerum posterius leads into an open sulcus the roof of which is the periotic, the sides the tympanic. At the anterior end of the bulla, this sulcus becomes a canal formed by the tympanic ventrally and the periotic dorsally and the basisphenoid medially. Apparently the carotid followed much the same course in *Aletocyon*, except that the foramen is not in a common fossa with the foramen lacerum posterius and the sulcus seems to have been covered by the tympanic and formed into a canal throughout its length.

The basicranial foramina are exactly as in *Canis*, except for the separation of the carotid and foramen lacerum posterius mentioned above. There are the same absence of a prominent mastoid process, which is typical of the Canidae, and a similar configuration of the paroccipital processes. Romer and Sutton (1927) point out that this attached over a large area, but this is true also of the fox and all young canids and is owing to the relatively large size of the bulla. There is an alisphenoid canal, which is present also in bears but not in *Procyon*.

OTHER CHARACTERS

The shape and proportions of the skull are very similar to those of *Vulpes*. The difference between the two consists primarily in the smaller cranium of *Aletocyon* and the consequent greater development of the occipital and sagittal crests. The skeleton is not known.

The dentition is extraordinary. The carnassial, which is very like that of *Phlaocyon*, has a well-developed parastyle and postero-internal cusp. The molars are not only quadrate but have several extra cusps formed from the cingulum which with the wrinkled appearance of the surface of the teeth gives a strikingly panda-like dentition.

RELATIONSHIPS

When Romer and Sutton (1927) described *Aletocyon* they pointed out the many points of resemblance to the contemporary canids *Nothocyon* and *Cynodesmus* in size, general characters of the skull and basicranial region, canid build of the carnassial, and the presence of distinct conules on, and a strong internal

cingulum to, the molars. Even the large size of the molar teeth and their subquadrate form are approached in *Nothocyon latidens* and *N. lemur*. The dentition of *Aletocyon*, however, strongly resembles that of *Phlaocyon leucosteus* which was considered ancestral to the Procyonidae (Wortman and Matthew, 1899). Romer and Sutton, therefore, placed *Aletocyon* in the Procyonidae and suggested, while noting the difficulties, that it had ancestral relationships with the pandas.

The auditory region is, however, clearly canid and since *Phlaocyon* is canid in limb structure also, it seems certain that the two genera represent early canid dental types resembling the procyonid-like, frugivorous specializations of certain living civets and mustelids (*Bdeogale* and *Meles*).

Nothocyon annectens Peterson

Peterson (1906) described a small carnivore from the Lower Harrison Beds of Sioux County, Nebraska, which he considered a canid and referred to *Nothocyon*. This specimen, which consists of a lower jaw and partial upper dentition, including a portion of the orbit, has subquadrate molars and an internal cingulum to the carnassial very like that of *Phlaocyon*. The skull is smaller, however, and has larger orbits which are more forwardly placed than those of either *Phlaocyon* or *Aletocyon*.

Cynarctus and Cynarctoides

A number of small carnivores known only from lower jaws and maxillary fragments have been assigned to the Procyonidae on the basis of their resemblance to *Phlaocyon* (McGrew, 1938). This resemblance consists primarily in the presence of cingula, often developed into stylar cusps, on the molars and carnassials, giving these teeth a quadrate bunodont appearance superficially, at least, very similar to the Procyonidae. There are all gradations of this development. For example, *Cynarctoides* has an internal cingulum to the carnassial but no cusp. M^1 of C.N.H.M. No. P25548 has a parastyle, a postero-internal stylar cusp an antero-internal cingular cusp and postero-internal as well as median cusps. M^1 of U.C. No. 1564 is similar but without median cusps. *Cynarctus* has no internal cingulum to the carnassial but

shows a small distinct cusp between the deuterocone (antero-internal cusp of the carnassial) and the antero-external cusp. M^1 is quadrate in shape with weak external and internal cingula. M^2 is greatly expanded anteroposteriorly. *Aletocyon* has a postero-internal cusp to the carnassial and in other respects closely resembles *Cynarctus* but has two small cuspules on M^1 posterior to the antero-internal cusp evidently formed from the posterior cingulum. *Phlaocyon* shows other minor variations.

In all cases these modifications consist of cusps or cingula added to the typical canid carnassial and molar pattern. As pointed out in the discussion of *Aletocyon*, there is no real approach to the Procyonidae.

PLIOCENE

The Canidae of the Snake Creek, Loup Fork, Republican River, and other Pliocene formations are so closely similar to *Canis* as to have been included in that genus by Cope. The limbs are very modernized, the dentition and general appearance of the skull very like the same regions of the living dogs and the auditory region is entirely so. There are a number of minor differences, however: the small braincase, the greater development of the occipital and sagittal crests, and the presence of a parastyle on the carnassial.

Only *Tomarctus* is described, since other genera are either not known from the basicranial region or present nothing of significance.

Tomarctus brevirostris

SPECIMENS EXAMINED: A.M.N.H. No. 18234; Snake Creek formation, Nebraska.

The auditory region of *Tomarctus* is like that of *Mesocyon* except for the smaller size of the bullae, which are nevertheless much more inflated than those of *Canis*. The paroccipital process is sutured to the bulla as in the recent Canidae.

The general proportions of the muzzle are very similar to those of the domestic dog of the more generalized type. This similarity is due to the absence of a precarnassial constriction to the muzzle, which tapers gradually. The dentition resembles that of a domestic dog also, especially the shape of the carnassial and the position of the antero-

internal cusp which is placed internal to the protocone but not markedly separated from it. The forward position of the orbits also agrees well with that of the domestic dog.

The bullae, as mentioned before, are much more inflated than in any specimen of *Canis familiaris* examined, the tendency in that species being towards flattening.

The profile is very similar to that of the dog due to the abrupt rise of the frontal bones, a feature even more pronounced in another Pliocene canid, *Aelurodon saevus*.

The braincase is much smaller, the sagittal crest high, and the occipital crest more pronounced, giving the occiput a quadrangular shape very different, as Matthew pointed out, from that of *Canis* but agreeing with the South American canids.

Tomarctus confertus

SPECIMENS EXAMINED: A.M.N.H. No. 18253; Snake Creek formation, Nebraska.

The braincase in this specimen, which is very much smaller than *T. brevirostris*, is much more expanded, almost as much so as in the living *Urocyon*. There is no sagittal crest. The muzzle is very short and deep.

RELATIONSHIPS OF *Tomarctus*

Tomarctus was considered by Matthew ancestral to all of the modern canid genera with the possible exception of the Cyoninae. This view has been challenged by Kraglievich (1930) who points out that *Dusicyon (Lycalopex) vetelus* has a smaller carnassial than *Tomarctus*. Matthew himself seems to imply by the inclusion of the living species in his genus *Nothocyon* a direct relationship between the two incompatible with the idea of *Tomarctus* ancestry. If Osgood's separation of the South American canids into a separate category is really a natural distinction, then a separate origin of *Canis* and the South American genera would be necessary.

There seems to be no reason, however, genetically speaking, why a simple character, such as relative size of the teeth, should be irreversible. Numerous genera of living canids have microdont and macrodont species. Merriam (1914), for example, has described these for races of *Canis latrans*. Mutations leading to small teeth are probably of common occurrence. In regions where selection is very

severe, such forms are quickly eliminated. Among other groups where competition is not so strong all gradations of size may have an opportunity for survival.

URSIDAE

Amphicyon sinapius

Plate 14, figure 3[1]

SPECIMENS EXAMINED: A.M.N.H. Nos. 18257 and 3797; Lower Miocene.

Amphicyon is ordinarily classed with the Canidae and considered as a link between the canids and sub-ursids (Matthew, 1924; Scott and Jepsen, 1936). Frick (1926) has challenged this viewpoint and attempted to show that the characters in which *Amphicyon* resembles the Ursidae are due to convergence. A dissection of the auditory region shows this region to be ursid.

DESCRIPTION

The bullae of *Amphicyon* are flask shaped with a long tubular meatus curved abruptly upward. They are small and but little inflated, covering only the anterior portion of the auditory region. The shape and position, however, are altogether different from *Daphoenus*. The bullae of the latter are simple rings lying loosely over the middle ear structure with no tubular prolongation of any sort. In *Amphicyon* the inflated part of what appears to be the bulla is only a knob attached to the much more prominent meatus. The left bulla is broken in such a way in one specimen (A.M.N.H. No. 18257) as to make it clear that the structures are not true bullae, i.e., did not enclose the tympanic cavity, but are parts of the meatus. The tympanic cavity proper lies above the cavity of these false bullae. This situation is brought about by the tubular meatus' being hollow, with an upper and lower surface similar to that of the bears, but not filled, as in the Ursidae, with cancellous bone. Since the meatus extends far into the cavity of the ear and the crista tympani almost touches the medial wall of the cavity of the meatus, very little space is left for the communication with the real tympanic cavity.

The promontorium has the same relative

position as in the Ursidae, that is, above the level of the basioccipital, from which a process extends dorsally and laterally to meet a similar process from the promontorium. The prominence itself is similar in shape and rugosity to that of *Ursus*.

The mastoid processes have very much the same form and position as in *Ursus*, with the same groove for the passage of the facial nerve. The foramen lacerum posterius is large, the paroccipital process a blunt projection extending backward and downward, very similar to *Ursus*.

The postglenoid processes are like those of *Ursus* and were formed of cancellous bone. The basioccipital is very broad, again an ursine feature. The carotid circulation was evidently like that of the bears also.

RELATIONSHIPS

The auditory region of *Amphicyon* is very much more ursine than canine. The peculiar configuration of the auditory meatus is, of course, not exactly like any structure of either bears or dogs, but it could be derived from an ursid type of meatus with very much less change than from a canid type. There is no basis in the auditory region for the association of *Amphicyon* and *Daphoenus*. They both have small bullae, but, as shown from this description, they are altogether different in structure in the two forms and, in fact, not homologous.

Species of *Amphicyon* are known from the Middle Miocene of Europe (Sansan) and the Sheep Creek locality, also Middle Miocene, of America. The genus is connected with *Daphoenus* by *Daphoenodon*, a type very like the White River species but with a small anteriorly placed bulla resembling that of *Amphicyon* in superficial appearance. The writer did not have the opportunity of visiting the Carnegie Museum so a detailed study of *Daphoenodon* could not be made. It seems probable, however, that when it is made, it will show a type of bulla more like that of

[1] The caption on plate 14 (fig. 3) is erroneous; it should read *Amphicyon* instead of *Enhydrocyon*.

Hemicyon than *Amphicyon*. As described above, the auditory bullae of *Amphicyon* are so peculiar and so bear-like that a close relationship with *Daphoenus* seems improbable.

Hemicyon ursinus

SPECIMENS EXAMINED: A.M.N.H. Nos. 21101 and 20820; Pliocene, Nebraska.

DESCRIPTION

The bullae are small and flask shaped with a twisted, spout-like meatus incomplete ventrally and anteriorly. The floor is very thick. The sides as well as the roof are formed of the squamosal. The tympanic is not coössified with the mastoid or postglenoid process. The mastoid processes are very large as in the Ursidae and of almost identical shape as those of a grizzly bear of equal size. The basisphenoid and basioccipital are very broad with the lateral edges slightly curved downward.

The small size and anterior position of the bullae leave the posterior part of the auditory region exposed, although the tympanic cavity itself is completely covered. There is a foramen stylomastoideum primitivum which opens into a broad groove across the anterior margin of the mastoid process. The foramen and the groove are identical with those of *Ursus* except that in the latter the tympanic surrounds and covers the groove, turning it into a canal.

The posterior margin of the bulla does not meet the paroccipital as in *Ursus*, nor does the promontorium extend posteriorly beyond the foramen stylomastoideum primitivum, and as a consequence this opening is confluent with the fossa which contains the foramen lacerum posterius.

The foramen for the carotid artery lies just anterior to the foramen lacerum posterius, separated from it by only a rim of bone as in *Ursus*. The canal itself runs forward to the foramen lacerum medium entirely enclosed in the tympanic as in *Ursus*.

The bulla bears the same relationship to the base of the postglenoid process as in *Ursus* except that the overlap of the tympanic on the base of the process is not so great.

Hemicyon barstowensis

SPECIMENS EXAMINED: A.M.N.H. No. 20822.

The bullae are flattened anteriorly, somewhat smaller posteriorly than in *H. ursinus*. The squamosal forms the roof and lateral walls of the meatus, the tympanic the floor. This portion of the meatus is very much thickened as in *H. ursinus.* It may have been filled with cancellous bone or have been hollow as in *Amphicyon*.

RELATIONSHIPS OF *Hemicyon*

Hemicyon is usually classed with the Ursidae. Nevertheless in the absence of certain distinctive specializations of the auditory meatus, it is further from the bears than *Amphicyon*, which is usally classed with the Canidae. The skeleton of *Hemicyon* in some respects resembles *Procyon* rather than *Ursus*. The skeleton of *Amphicyon* has not been fully described from an authentic specimen. White of Harvard states, however, that foot bones of *Amphicyon* which he is in the process of studying are a composite of felid and ursid characters.

Arctotherium

SPECIMENS EXAMINED: A.M.N.H. No. 8222; Pleistocene, South America.

DESCRIPTION

The auditory region is essentially like that of *Ursus*. The bulla is flattened and the meatus longer than in *Euarctos*. The meatus has a very thick and upwardly directed floor as in *Ursus*. *Euarctos* has a shorter, more tubular meatus as in the Procyonidae.

Arctotherium differs from *Ursus* in having the bulla more inflated posteriorly and not in contact with the paroccipital. This causes the stylomastoid foramen to be a fossa confluent with that which encloses the foramen lacerum posterius and the posterior arotid foramen.

The floor of the meatus is extremely thick and formed of cancellous bone which extends into the auditory cavity. The left bulla is broken in such a way as to show a perfect section of the meatus. It can be seen from this that if the bony filling of the meatus were removed in such a way as to make a cavity continuous with the interior of the meatus, the condition would be as in *Amphicyon*.

SIGNIFICANCE OF MENDELIAN HEREDITY IN THE
PHYLOGENY OF THE CARNIVORA

DARWINIAN EVOLUTION postulates that all of the higher categories traced back to their origin will be found to disappear in the large undivided species from which they were differentiated. From a very variable species, which may be designated species X, certain types more adaptive than others will be selected and distinguished from the parent species, first as varieties, then as subspecies, and finally, when enough differences have accumulated, as species. These in turn give rise by the same process to varieties, subspecies, and finally species. A series of such species evolved from a common ancestor constitutes a genus; a series of such genera, a family. Evolution is thus an explanation of the ordered hierarchy of forms in nature, and this hierarchy as expressed in the Linnaean system of classification was, to Darwin (1909), a proof of evolution.

Darwin and the early evolutionists generally were unable to work out a satisfactory mechanism by which this process of selection and differentiation could be brought about. Darwin himself, at least later in life, came to place considerable importance on the inheritance of acquired characters and sexual selection, factors which are now believed to have a relatively insignificant role in the evolutionary process. No more satisfactory ones were known at the time, however, and even after the rediscovery of Mendel's laws there was little application of the principles of Mendelian heredity to the problem. Thanks to the work of Haldane (1932), Fisher (1922), Wright (1931, 1932), Dobzhansky (1938, 1940), Mayr (1940), and others the role of genetics in the evolution of natural populations has been thoroughly established. Wright, in particular, in his concept of adaptive peaks (Wright, 1932) has provided a mechanism by which subspecies and eventually species may be differentiated from a large, variable, undivided population such as Darwin postulated.

Of the millions of potentially possible gene combinations (with 10 allelomorphs of each of 1000 loci, the number of possible combinations is 10^{1000}) certain ones are more favorable than others. These favorable gene combinations constitute adaptive peaks. The majority of the members of any living species may be said to be clustered around a certain adaptive peak, that is, they possess certain gene combinations in common which are favorable for a particular mode of life. The members of each local population in turn are clustered about other minor peaks, that is, they have favorable gene combinations which, added to the common genotype of the species, fit them for particular ecological niches. If the frequency of one combination within a local race is very great the population is said to be closely grouped. If, on the other hand, a scattering of variability occurs, the field occupied by the population may be said to spread along the slopes of the peak. Mutation is constantly operating to increase the spread; selection, considered in the broad sense, is constantly forcing the population to higher adaptive levels.

These two pressures interact in such a way that, given the mechanism of Mendelian inheritance, a certain equilibrium in gene frequency is reached. Evolution is essentially a change in gene frequency. This may take place by an increase in mutation pressure, which will cause a scattering of genotypes, or an increase in selection pressure, which will cause a closer grouping around the adaptive peak.

There are two evolutionary possibilities. A change in environment may occur which will cause the formerly more adaptive combination to be less favorable and the formerly less adaptive more favorable. In this case, the population must remake its genotype or, if conditions are very unfavorable and selection is severe, it will become extinct. Another possibility is that the population may find its way to a new adaptive peak without any change in environment having taken place. If the mutation rate is greatly increased for any reason, the effect will be the spreading of the field occupied by the species. There will be an average lowering of the adaptive level of the species, but the resultant spreading of the field may include another adaptive peak,

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in which case the entire species may shift by interbreeding to this peak (Wright, 1932, p. 6). A species, for example, which has become fairly well adapted for a cursorial type of existence might, if the mutation rate became sufficiently high, develop other less adaptive types of limb structure. Some of these might be combined with characters of the dentition especially adapted to carrion feeding. This combination constitutes a new adaptive peak and it is possible that the entire species might shift to it if the selection were very strong.

We find in the higher categories with which this paper has been largely concerned that one of the striking things about the modern Carnivora is that in general each family conforms to a certain adaptive type. Mention has been made of the extraordinary uniformity within the Canidae and the ease of interbreeding within the family. This can only mean that within the group the genotypes are for the most part similar and are obviously such as will fit the individuals most efficiently for the cursorial and predatory life which is characteristic of the family. In a similar way, the Procyonidae occupy another adaptive peak, that of semi-arboreal fish and vegetable feeders; the Ursidae, still another, that of large forest dwellers. The Mustelidae, which have not been discussed in this paper, are a large group of such diversity that they might be said to be climbing and descending a half a dozen peaks.

Fossil carnivores, however, are very far from having the same combination of characters as those possessed by their modern descendants. On the contrary, one of the reasons for the confusion in tracing phylogenies in the order is that clear-cut lineages may be traced by means of one character alone, but when all of the characters are considered, the complexity becomes almost inextricable. This phenomenon, which in human evolution Weidenreich (1943) has termed the "disharmony of seemingly fixed characters," was clearly brought out in the previous descriptions.

The Oligocene *Plesictis*, for example, *P. robustus*, in characters of the auditory region is closely similar to *Bassariscus*. The dentition is of a pattern which could be morphologically ancestral to the recent genus. However, the

Miocene *Plesictis*, *P. genettoides*, although retaining the *Bassariscus*-like basicranium and structure of the limbs, has a clearly musteline dentition with the loss of M^2 characteristic of the Mustelidae.

On the other hand the dentition of *Procyon* and *Nasua* is approached by numerous Oligocene carnivores of the same horizon as *Plesictis robustus*, especially *Cephalogale* and *Pachycynodon*. Teilhard de Chardin proposes a double origin of the Procyonidae on this basis, the one from *Plesictis* to *Bassariscus*, the other from *Pachycynodon* through *Phlaocyon* to *Procyon*.

Paleoprionodon, of the same epoch, has a demi-bulla similar to that in *Nandinia* and a viverrine dentition. In the American White River, *Daphoenus* combines a type of bulla virtually identical with that of *Paleoprionodon*, with a canid dentition and a rather feline type of skeleton.

In the Miocene, side by side with genera showing combinations of characters closely approaching *Canis*, there are forms with a similar auditory region but an altogether different type of limb structure, some approaching *Gulo*, others *Hyaena*, and a dentition paralleling that of the Mustelidae with a tendency towards the loss of the second molar and the development of an internal flange to M^1.

Another species, *Phlaocyon leucosteus*, with the most typically canid features of the basicranium and limbs, parallels the raccoon in its dentition, so much so as to have been considered ancestral to the Procyonidae by as eminent a paleontologist as Matthew. *Aletocyon multicuspis* carries this extra cuspidation of the molars still further so that it strongly resembles the pandas in dental characters and has been thought ancestral to that family.

This widespread parallelism and convergence, which is so much a feature of the fossil record of any group, has caused one paleoanthropologist to wish to abandon any consideration of stratigraphy in tracing phylogeny in hominids (Weidenreich, 1943) and another to despair of a natural solution altogether (Broom, 1946).

Actually the apparent confusion of the fossil record means only that the living families of the Carnivora, at least, have reached

their respective peaks by a method of trial and error on a grand scale. Every possible combination of characters has been tried in almost every family, and selection has eliminated the least adaptive and forced the most favorable to the highest level of adaptation.

The Quercy Carnivora, for example, present at one period, according to Teilhard de Chardin (1915), every type of dentition possible for the order, all intergrading to such an extent that "de genres de carnassiers faissent un bouquet si serré . . . il était possible de passer (que de l'une à l'autre) presque sans secousse." The French paleontologist thinks that nevertheless each possessed what he calls an "orientation intimé," that is, an interior direction or entelechy, which separates them as widely as a dog or a cat. This is not a necessary explanation, however, and in view of the intergradation improbable. In fact, it seems possible to the writer that the species determined from this horizon may not be true species at all. Differences in dentition, which in modern groups would mean more than specific distinction, in these ancient types may be only variants within a subspecies. Simpson (1937) found through a biometric study of a large sample of notoungulate dentitions, on which Ameghino had based three families, seven genera, and 17 species, that they all belonged to one species, *Henricosbornia lophodonta*. That, of course, is an extreme example, but there are many other known instances of a change in the taxonomic value of a character. The union of the scaphoid and lunar bones, for example, is a character used to distinguish the Miacidae from the earliest Canidae. This character existed in *Claenodon* (Matthew, 1937) as an individual variation. It is perfectly possible, therefore, that the sections into which Teilhard de Chardin divides the Oligocene Carnivora may correspond to variations within a species rather than to any higher category.

Such a population (a large species divided into a number of partially isolated local races) has been described by Wright as the most favorable for evolution. Without marked secular change of conditions or any notable increase in mutation and selection such a species will tend to change in space and time because of accidents of sampling. Not all of the genotypes of one generation contribute

equally to the next; certain types predominate over others merely by chance. Under certain conditions this can have important evolutionary results.

The frequency of genes involved in the multiple factor characters, such as those used to define species, fluctuates widely within a species, although, especially if many factors are involved, even extreme differences in the frequencies of one or two genes might not affect the phenotypic expression. Let us suppose, for example, we have a series of genes each affecting the ossification of the tympanic bulla in such a way that any two positive factors produce complete ossification, while complete homozygosity for the negative factors results in no ossification at all, with all degrees in between depending on the balance of positive and negative factors. If only as many as four factors are involved and the alleles a and A are present in equal numbers the genotype, $aa\ a_1a_1\ a_2a_2\ a_3a_3$, resulting in complete lack of ossification, will occur in only 1/256th of the population. If the alleles are not present in equal numbers but the frequency of A to a is in the proportion 9 to 1 the genotype, $aa\ a_1a_1\ a_2a_2\ a_3a_3$, will occur in only 1/640th of the population. If A_1 and a_1 are also present in a 9 to 1 ratio the completely homozygous combination will occur in only 1/1600th of the population. In fact, in a small population such a combination may not appear at all.

A portion of such a population taken at random, however, will not be a true sample of the group as a whole but may have a much higher frequency of one or other of the alleles. If such a population becomes isolated, or partly so, with only a small interchange of genes with the parent population, as almost invariably happens if the species spreads over a large area, a genotype, the expression of which would be an unossified or partially ossified bulla, might appear suddenly. As explained above this would not be owing to the appearance of a new mutation (the character in question is too complex for that) but to the expression phenotypically of accumulated variations in the parent population.

Moreover, random sampling could be expected to produce a reassortment of characters. Each character is determined by its own set of alleles, which are inherited ulti-

mately independently of every other set. A hypothetical genotype for a carnivore might be written, for example, $A_1A_2A_3$, $B_1B_2B_3$, $C_1C_2C_3$, where each of the letters represents a factor which affects ossification of the bulla, lengthening of the digits, development of molar cusps, etc., and the number of factors determines the grade of the character, $a_1a_2a_3$, for example, resulting in very short digits, $A_1A_2A_3$ in long, slender digits. Any combination of genes producing any grade of character may be inherited with a combination producing an entirely different grade of another character. Thus $a_1a_2a_3$ (very short digits) may be combined with $B_1B_2B_3$ (complete ossification of the bulla) or with $b_1b_2b_3$ (no ossification of the bulla) and either of these with combinations of the C factors, producing a variety of dental differences. This produces the disharmony of seemingly fixed characters mentioned before. A harmonious combination of characters may be broken up by this process of reassortment and an entirely new one formed. Random sampling causes a reassortment of genes, bringing out different grades in different combinations. Thus complete ossification of the bulla may be combined with broad, quadrate molars in one local race, and with triangular molars with the cusps arranged in sharp cutting V's in another. A demi-bulla may be combined with high-crested teeth in one race, and with strongly developed crushing molars in another. The fossil record abounds with this kind of assortment of characters.

Selection, however, is operating at every level, from that of the physiology of the individual to the complex of characters which fits the group as a whole for a particular part in the economy of nature. This tends to give direction to an otherwise random process. Throughout the history of the Canidae, for example, there is an increasing development of longer, more compact digits, more slender limbs, reduction of the fibula and radius,

changes in the hip and ankle joints to provide more efficient fore-and-aft movement of the limbs, as well as progressive evolution towards a more effective type of carnivorous dentition. Thus the most modernized member of the family in the Miocene has not the development of these characters that is found in the living genera.

At the same time a very wide range of canid types occurred, some approaching the wolverine type in adaptive features, others with a dentition paralleling that of the raccoons. Today we have *Otocyon* with its almost insectivorous dentition, and the cyonine group of dogs as the most aberrant dental types and little variation of any sort in the limbs. If, however, selection were relaxed and the geography of the country inhabited by the Canidae broken in more isolated habits than are found in Europe and North American today, a radiation similar to that in the Miocene might occur. Competition also, of course, plays a great part in preventing or at least limiting such radiation, and the absence of any competing groups probably has a greater evolutionary effect in this regard than the geography.

The Procyonidae and Ursidae present a rather different problem and one which at present we do not have the material to solve. The Procyonidae are in some respects more uniform than the Canidae (there are relatively few species and still fewer distinct races, to the hundreds of canid types), and in others much less so. There is more difference, for example, between *Bassariscus* and *Procyon*, to say nothing of *Potos* and *Ailurus*, if they are considered members of the family, than between any of the Canidae. Because of this a dual or even triple origin of the Procyonidae has been suggested. The modern Canidae, on the other hand, have almost certainly all been derived from one species and that, in the writer's opinion, rather recently, geologically speaking, middle Miocene at the earliest.

SUMMARY AND CONCLUSIONS

There are three central types of auditory region in the Carnivora, the procyonid, canid, and viverrid. These seem to have been established very early in the history of the order. Specimens are known from the lower Oligocene of Europe and North America in which the structures characteristic of the living Procyonidae, Canidae, and Viverridae are well developed. *Plesictis robustus* of the Phosphorites of Quercy, France, represents the procyonid type; *Pseudocynodictis* of the White River Oligocene, the canid type; and *Daphoenus* of the White River and *Paleoprionodon* of the Phosphorites represent the viverrid.

These differ, however, from their modern counterparts in (1) the lack of a tubular auditory meatus in the procyonids, and (2) the lack of ossification of the posterior chamber of the bulla in the viverrid type. *Nandinia*, a living viverrid related to the paradoxures, has a similar type of bulla.

Ursid, felid, and mustelid types of auditory region are not certainly known as early as the procyonid, canid, and viverrid and may have been derived from them. The ursid type has the same arrangement of the blood vessels and nerves as the procyonid, and the same relative size of the parts. It could be derived from the procyonid by a flattening of the bulla, extension of the hypotympanic sinus along the sides of the meatus, and the ankylosis of the meatus with the postglenoid and mastoid processes. Young bears have an auditory region much more procyonid-like than older bears. The mustelid characters are also derivable from the procyonid.

The canid type is altogether different and in essential structure more like the felid than has sometimes been supposed. The position of the carotid canal in the canid, i.e., between the roof of the bulla and the periotic, is altogether unlike its position in the procyonid where it occupies a large tube in the wall of the tympanic. In the Canidae there is no extension of the auditory meatus into the tympanic cavity. The tympanic membrane is very near the porus acusticus externus. Consequently there is no possibility of the extension of the hypotympanic cavity along the sides of an internal tubular meatus as in the bears and the mustelids. A long bony external meatus also develops rather early in the procyonids and mustelids, and never develops in the canids, felids, or viverrids. At most in the canids the lip of the porus may be somewhat prolonged, and a similar specialization takes place in a few of the Viverridae.

The canid structure would seem to be easily derivable from a demi-bulla such as that of *Paleoprionodon* by the overgrowth of the ectotympanic and the suppression of the entotympanic. It follows that the division of the bulla into chambers may not be so important a means of classification, at least among fossils, as Flower supposed.

Relative Stability of the Auditory Region

The auditory region seems certainly to be more stable than the limbs or dentition. The essential features were established in the Canidae and Procyonidae very early and have continued unchanged, especially in the Canidae, to the present time. There are no aberrant types of auditory region in living canids, although the dentition ranges from the cyonine reduction of the molars to the insectivorous specialization with an increase of tooth number, in *Otocyon*. In the lower Miocene apparently there were also frugivorous specializations similar to those found in living viverrids and a tendency towards the elongation of the molars and the broadening of the cingulum characteristic of the Mustelidae.

The limb structure also underwent a minor adaptive radiation in the Miocene, producing parallels of the wolverine and hyena as well as the more typically canid structure.

The basicranial region generally would seem, therefore, to be more reliable as a means of tracing phylogeny than the dentition or limbs.

Significance of the Auditory Region in Classification

Although the basicranial region seems to preserve ancestral characters to a greater extent that the more adaptive structures, it

would nevertheless be a mistake to depend
wholly upon it, or upon any one feature, in
determining relationships. There are theoreti-
cal as well as practical reasons why this is so.
The use of any feature, such as the presence
or absence of a septum bulla, to determine
superfamily relationships implies that these
structures arose by a mutation which at once
produced a division of the species in which
they occurred into two mutually exclusive
sections, that these in turn divided dichoto-
mously by a similar mutation, and so on.
There is nothing in the paleontological record
or in evolutionary histories of living popula-
tions to support this idea. Instead there is
every evidence that the characters later to
become diagnostic of species or of higher
categories appear first as individual variations
and persist as such for a long period. It is
only by the accumulation of large numbers of

differences under conditions of isolation that
one group becomes sufficiently differentiated
from another genetically to produce a new
species. Characters that are diagnostic of
species, or even of genera and families among
living forms, may not have the same value
in the earlier history of the order. For this
reason it is unreal to carry such terms as
Aeluroidea, Canoidea, etc., back to the
Oligocene (or perhaps even the Miocene),
since at this period no such division as char-
acterizes modern Carnivora existed. *Daphoen-
us* is certainly not an "aeluroid" in the strict
definition of the term, nor are the saber-tooth
cats canoids, although they have many of the
characteristics of the living families usually
included under that section. These terms
may be useful in a discussion of living forms,
but they are not valid and are even mislead-
ing as implying descent.

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