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Basicranial Anatomy and Phylogeny of Primitive Canids and Closely Related Miacids (Carnivora: Mammalia)

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ABSTRACT

Selected fossil carnivorans are studied in an attempt to bridge the gap between caniform miacids and early canids, and to identify character transformations within the clade leading to canids. Several basicranial and dental features are important in characterizing the cladogenetic events that occurred and culminated in *Hesperocyon*.

Basicranial transformations from miacids to the first recognizable canids involved the formation of a rigid middle ear chamber, i.e., the ossification of an entotympanic bulla and development of a low septum from the in-bent edge of caudal entotympanic. The middle ear region is further strengthened by medial expansion of the petrosal into contact with the basioccipital and basisphenoid, the ossification of the tegmen tympani, and the closure of piriform fenestra. Another important character complex consists of the medial migration of the internal carotid artery, the loss of the stapedia artery, and the entrapment of the

internal carotid artery in an extrabullar position between the entotympanic and the petrosal. Early canids are further distinguished by their possession of a shallow suprameatal fossa. Canids successively acquired the following dental characters: presence of posterior accessory cusps on upper and lower third premolars, loss of M3, reduction of the parastyle on M1, and enlargement of the metaconid on m2 so that it equals the protoconid in size.

Although the middle ear structure of canids is relatively stable when compared with that of other families of caniform carnivorans, it does change in at least three aspects. Firstly, the low entotympanic septum varies in size and extent, and tends to be confined to the anteromedial corner of the bulla in derived forms. Secondly, the anterior loop of the internal carotid artery changes from intracranial to extracranial in position. Evidence for this latter feature is the loss of a bony signature of

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this loop in the basioccipital—an embayment on the lateral wall of the basisphenoid anteroventral to the middle lacerate foramen. Finally, a short

bony tube for the external auditory meatus develops in later canids.

INTRODUCTION

Among caniform carnivorans, the basicranial anatomy of canids has long been considered relatively stable, and canid characteristics in the middle ear region are identifiable in the earliest canid *Hesperocyon* (Hough, 1948; Tedford, 1976). This apparent stability of the middle ear of canids, together with their rather uniform dental patterns, makes canids a morphologically conservative group. Basicranially, canids can be distinguished from other families of carnivorans by possession of an inflated bulla, formed mostly from an inflated caudal entotympanic; a low septum across the inner surface of the bulla; a fully functional internal carotid artery in an extrabullar position; an external auditory meatus lacking a prominent bony tube (except derived forms); and a small mastoid process.

Cope (1877, 1883) first proposed that the ancestry of canids was to be found among the forms placed in his Creodonta. More specifically, the Miacidae was postulated as the probable ancestral stock (Cope, 1880: 81). The central theme of Cope's phylogeny revolved around a linear sequence of dental reduction from four upper and lower molars in the African bat-eared fox (*Otocyon megalotis*), to a more "normal" dental formula in *Amphicyon* (three upper and three lower molars), and to variously reduced dentitions (e.g., loss of p1, M3, and sometimes M2) in later true canids. Even though the number of upper molars in *Miacis* was not known to Cope (1883), he correctly predicted that it would be the same as in *Amphicyon*. Cope thus predicted discovery of *Otocyon*-like fossils preceding other extinct dogs.

Cope's theme of progressive dental reduction was soon challenged by Scott (1895: 74) who realized that the supernumerary teeth in *Otocyon* could be a result of character reversal: "I am by no means convinced of the impossibility of the addition of new teeth to the molar series. That modification in the mammalian lines is very generally by way of reduction in the number of teeth, is true, but

does not prove that the reverse process may not exceptionally take place, whether by reversion or otherwise." *Otocyon* was therefore removed from the basal stock in Scott's phylogeny which still recognized *Miacis* as ancestral to canids.

The miacid ancestry of canids has since been accepted by most students of carnivorans (e.g., Matthew, 1930; Clark, 1939; Tedford, 1978; Flynn and Galiano, 1982; Gustafson, 1986). Various authors, however, adopted different ways of defining the Canidae—some favored the inclusion of certain miacid genera in the Canidae consistent with their philosophy of a vertical classification (see Flynn and Galiano, 1982, for a recent review). As may be expected from such a basal group, miacoids could be claimed as ancestral to every modern family of carnivorans. Indeed, Flynn and Galiano (1982) associated certain miacoids with the phylogeny of primitive feliforms, and the rest of the miacoids were set aside in an unresolved Caniformia. In a more recent analysis (Wyss and Flynn, 1993), however, the Miacidae was removed from direct relationship to the living families of Carnivora, and placed one branch below the common ancestor of Viverravidae and Carnivora.

Among the various North American Eocene miacids, *Miacis*, with its tendency to elongate the carnassial shear and reduce the M3 (a "typical cynoid" character according to Matthew, 1909: 362), appears morphologically closest to the canids. Clark (1939), and later Gustafson (1986), went further and suggested that "*Miacis*" *gracilis* was closest to *Hesperocyon*. The proposed affinity between "*M.*" *gracilis* and *Hesperocyon* was primarily based on postcranial evidence, i.e., the advanced canidlike limb bones of "*M.*" *gracilis*; dentally, however, "*M.*" *gracilis* was little different from other species of *Miacis*.

Apart from the abovementioned attempts to link a particular taxon to the ancestry of the Canidae, the relationships between various species of miacids on the one hand, and

most primitive canids on the other, remains unresolved. Tedford (1976: 364) remarked: "The fact that very few miacoids have been identified as phyletically related to members of the modern superfamilies only increases the isolation of the archaic and modern carnivore families. In other words, there are few miacoids that possess derived characters uniquely shared with representatives of the modern families. This represents one of the largest gaps in our knowledge of the phylogeny of the Carnivora."

Recent discoveries of forms from the Vieja Group of Texas (Chadronian) intermediate between miacids and canids has significantly bridged this gap in our knowledge of canid ancestry (Gustafson, 1986). The Texas material includes the last known representatives of *Miacis* in North America, "*M.*" *cognitus* and *M. australis*. Their dental morphology is also the most derived among all *Miacis*. Another important taxon, also from the Vieja Group, is "*Hesperocyon*" *wilsoni* Gustafson (1986), which reduces, in yet another way, the morphological gap between the well-known White River *H. gregarius* and various *Miacis*. "*H.*" *wilsoni* has a fully ossified bulla with a high degree of inflation resembling that of *H. gregarius*. However, the dental morphology of "*H.*" *wilsoni* is still primitively similar to that of miacid carnivorans. It retains a primitively short shearing blade on the m1 with a relatively high trigonid and narrow talonid, and has a relatively large parastyle on the M1. The Texas material displays an interesting combination of characters, which not only offers an example of what a transitional canid may have looked like, but also raises new questions regarding the origin of canids.

The present paper describes in detail the basicranial anatomy of selected primitive caniform carnivorans that led to the emergence of the Canidae and places these taxa in a phylogenetic framework.

SCOPE, DEFINITION, TERMINOLOGY, AND ABBREVIATIONS

The term "miacoid" is usually applied to Paleocene to late Eocene carnivorans united, among other features, by their common possession of a carnassial shear fixed on the locus

of upper fourth premolar and lower first molar. Miacoids are otherwise more or less defined by the paucity of derived characters shared with advanced (mostly extant) families of carnivorans. The taxon Miacoidae is therefore one of convenience and has long been a taxonomic wastebasket waiting to be emptied. Recent phylogenetic treatments range from dividing miacoids into feliform and caniform components (Flynn and Galiano, 1982), to placing them within a multichotomy of Feliformia + Viverravidae + Miacidae + Nimravidae etc. (Flynn et al., 1988), and to postulating a sister-group relationship between Miacidae and a Viverravidae + Carnivora clade (Wyss and Flynn, 1993). In this discussion, the Miacidae includes such archaic caniforms as *Miacis*, *Uintacyon*, *Vulpavus*, etc. (roughly equivalent to Miacinae of Simpson, 1945: 108), whereas the Miacoidae includes the caniform Miacidae and the feliform Viverravidae. The present study considers only a few putative miacids, which share several derived characters, such as reduced or absent P4 parastyle, reduced P4 protocone, and internal cingulum of upper molars surrounding the protocone, in addition to various postcranial characters (Flynn and Galiano, 1982). Preservation of the basicranium is also important to the scope of this study.

As discussed in the introduction, of the known miacid genera *Miacis* seems in general closest to canids because of its tendency to elongate the carnassials and to reduce the M3. The genus was established by Cope (1872) on the type species *M. parvivorus* from the Bridger Formation (Bridgerian), Wyoming. Nearly two dozen nominal species of *Miacis* have been described from the Eocene of North America and the Old World. Considerable confusion exists regarding the taxonomic status of these forms. It is beyond the scope of this study to evaluate the taxonomic complexities among these species, and only a selected few North American taxa which have reasonably complete basicranial and dental materials are analyzed.

Unless otherwise noted, we follow Flynn et al. (1988) for taxonomic usages of major groups of carnivorans. We will enclose within quotation marks taxa that are clearly paraphyletic in this analysis, and restrict the use

of generic names to the type species, i.e., *Miacis* = *M. parvivorus*, and *Hesperocyon* = *H. gregarius*. Fortunately, these type species also contain the best known basicranial materials. For *Vulpavus*, we assumed that the type of *V. profectus*, AMNH 12626, is morphotypic for the genus. For basicranial terminology, we follow MacPhee (1981) on eutherian mammals in general, and Evans and Christensen (1979) on living *Canis* in particular.

ABBREVIATIONS

Institutions

AMNH	American Museum of Natural History, New York
CMNH	Carnegie Museum of Natural History, Pittsburgh
FMNH	Field Museum of Natural History, Chicago
F:AM	Frick Collection, American Museum of Natural History
KUVP	Museum of Natural History, University of Kansas, Lawrence
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
TMM	Texas Memorial Museum, University of Texas, Austin

Anatomical Terms

ac	alisphenoid canal
al	alisphenoid
apa	ascending pharyngeal artery
bo	basioccipital
bs	basisphenoid
cc	condyloid canal
ce	caudal entotympanic
cf	condyloid foramen
cfn	canal for facial nerve
cica	canal for internal carotid artery (or promontory artery)
eam	external auditory meatus
ec	ectotympanic
Ec	Eustachian canal
en	entotympanic
er	epitympanic recess
fc	fenestra cochleae (fenestra rotunda)
fo	foramen ovale
fs	fossa for stapedius muscle
ftt	fossa for tensor tympani muscles
fv	fenestra vestibuli (fenestra ovalis)
gf	glenoid fossa
Gf	Glaserian fissure
ica	internal carotid artery
ips	inferior petrosal sinus
irsa	inferior ramus of stapedial artery
mlf	middle lacerate foramen

mp	mastoid process
mt	mastoid tubercle
oc	occipital condyle
pa	promontory artery
pf	piriform fenestra (promontory foramen)
pgf	postglenoid foramen
pgp	postglenoid process
plf	posterior laterate foramen
pp	paroccipital process
pr	promontorium
ps	pneumatic sinus
re	rostral entotympanic
sa	stapedial artery
sf	suprameatal fossa
sica	sulcus for internal carotid artery
smf	stylomastoid foramen
smp	sulcus for major petrosal nerve (palatine ramus of facial nerve)
spa	sulcus for promontory artery
spe	suture of promontorium/entotympanic
sq	squamosal
srsa	superior ramus of stapedial artery
ssa	sulcus for stapedial artery

DESCRIPTION OF BASICRANIAL ANATOMY

Vulpavus profectus Matthew
Figures 1A, 2A

SPECIMEN EXAMINED: AMNH 12626, holotype, complete skull and mandible with partial skeleton, from unit B, Bridger Formation, Bridger Basin, Wyoming, early Bridgerian.

Both sides of the basicranium in AMNH 12626 are excellently preserved, affording confident interpretations of most osteological structures. Matthew's (1909) original description of the basicranium is brief, and he has been credited with the first proposal that two separate branches of the internal carotid artery (medial and lateral) occurred in the middle ear region (Presley, 1979; see description below). *Vulpavus profectus* is used here as an outgroup for determination of character polarities among the ingroups.

BULLA: No bulla is known for this genus. Neither is there any indication that any bullar element may have been in firm contact with the bones which make up the roof of the middle ear cavity. The lateral edge of the basioccipital and basisphenoid lacks the thickening or formation of a bony ledge usually associated with sutural contact with the caudal entotympanic. The surface of the petrosal

is smooth toward the basioccipital side rather than roughened, as it is where the bulla attaches in many carnivorans.

PETROSAL AND SURROUNDING BONES: The ventral surface of the basioccipital is flat and broad. A broad basioccipital is also present in ursids and amphicyonids, and may be a primitive character for caniform carnivorans. The lateral border of the basioccipital is constricted at the level of the sutural line between the basioccipital and basisphenoid, and has a sharp edge (i.e., it lacks the thickened and grooved edge for the inferior petrosal sinus that occurs in all canids). Anterior to the basioccipital, the lateral edge of the basisphenoid similarly lacks an embayment near the middle lacerate foramen, which houses a convoluted internal carotid artery in canids and arctoids.

The petrosal is globular in outline and is not expanded medially. This is in contrast to the viverravid *Protictis* in which there is a rugose articular surface on the medial edge of the promontorium (Gingerich and Winkler, 1985: fig. 11; personal observation of an epoxy cast). The location of this rugose area is identical to that of a rostral tympanic process of petrosal in most insectivorans and primates (MacPhee et al., 1988). In aeluroids, the anteromedial corner of the petrosal is further expanded medially to form a ventral promontorial process, an important synapomorphy for aeluroid carnivorans (Hunt, 1989).

The petrosal is completely separated from the adjacent basioccipital and basisphenoid by a 1 mm wide space (basicapsular fenestra of MacPhee, 1981: fig. 1). This space allows ample room for a large inferior petrosal sinus. The only bony signature of this sinus on the petrosal is a broad and shallow depression dorsal to a rather prominent medial ridge (fig. 2A, above the ips on cross-sectional view).

The ventral surface of the promontorium is somewhat rugose, as compared to *Hesperocyon*. It has a shallow groove (sulcus for the promontory artery) toward its lateral aspect. The groove begins posteriorly just in front of the fenestra cochleae. Traveling anteriorly, the groove slightly descends ventrally and then turns medially to lead to the free space between the petrosal and alisphenoid, here the common opening for the middle lacerate

foramen and piriform fenestra. On the posterior edge of the fused basisphenoid and alisphenoid plate is a small protuberance pointing toward the petrosal, which has a corresponding bulge closing in on the projection (better seen on the left side of the skull of AMNH 12626). These two opposing projections give hint to the initial separation of the middle lacerate foramen, or anterior carotid foramen (here continuous with the basicapsular fenestra, i.e., the open space between petrosal and basioccipital) from the piriform fenestra (fig. 1A). In the fetal stage of living eutherians, the anterior carotid foramen is separated from the piriform fenestra by an alicochlear commissure, a cartilaginous bridge continuous with the soft tissue complex inside the suture of the basisphenoid-alisphenoid (MacPhee, 1981: 21 and fig. 1). The expansion of the petrosal and basisphenoid replaces this commissure in the adult and ensures the complete separation of the anterior carotid foramen (middle lacerate foramen) and promontory foramen (piriform fenestra). The lack of ossification in this area in some fossil taxa (e.g., *Miacis parvivorus*, see description below) precludes the separation of these two foramina.

The surface between the fenestra vestibuli and the groove for the promontory artery is not clearly marked by an impression for a stapedia artery branching off the internal carotid artery, although Matthew (1909) claimed to have observed one. The only indication of a sulcus for the stapedia artery is, on the right promontorium, a slight interruption of the lateral border of the sulcus for internal carotid artery just opposite to the fenestra vestibuli (see more below).

The tegmen tympani area descends rather suddenly from the posterior edge of the alisphenoid and squamosal, leaving a large free space as the piriform fenestra. There is therefore little continuity between the tegmen tympani area and tympanic processes of alisphenoid and squamosal. This is in contrast to *Hesperocyon gregarius*, "*Miacis*" *cognitus*, and others, which have a fully ossified tegmen tympani smoothly articulated with the bones anterior to them. The opening for the facial nerve (foramen faciale) on the ventral surface of the petrosal faces anterolaterally and is slightly enlarged to house the genicular gan-

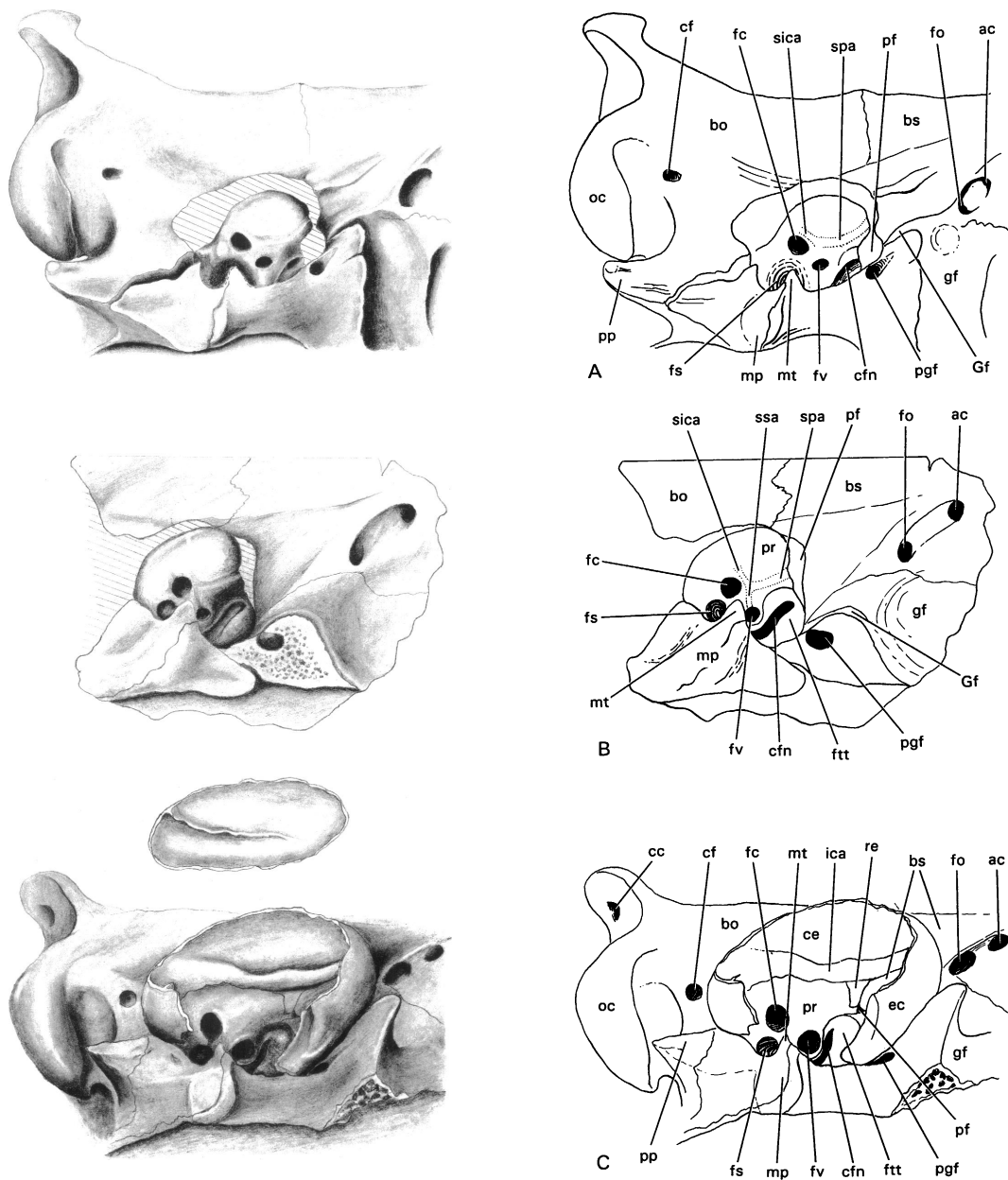


Fig. 1. Basicranium of primitive caniform carnivorans. Ventrolateral view of left middle ear region. All drawn to approximately the same size. A, *Vulpavus profectus*, AMNH 12626; B, *Miacis parvivorus*, USNM 214706, reversed from right side; C, *Hesperocyon gregarius*, F:AM 76163 (an internal view of the dissected ventral portion of the bulla is shown above with a low septum). See Definition section for abbreviations. In *Vulpavus* and *Miacis*, the piriform fenestra (pf) encompasses the middle lacerate foramen (anterior carotid foramen of MacPhee, 1981) because of the lack of preservation of the cartilaginous alicochlear commissure.

gion. Leading from this ganglion are two well-marked grooves. One leads anteriorly toward the piriform fenestra as the palatine ramus of the facial nerve (major petrosal nerve in Evans and Christensen, 1979), which may exit the middle ear cavity through the Eustachian canal as in *Canis* (Evans and Christensen, 1979: figs. 15-16). The other traverses posterolaterally to circle around the dorsal rim of fenestra vestibuli and contains the hyomandibular ramus of the facial nerve, which ultimately emerges from the middle ear cavity through the stylomastoid foramen. The entire course of the anterior and posterior branches of the facial nerve inside the middle ear cavity is thus exposed without a bony covering. Lateral to the piriform fenestra and along the petrosal/squamosal suture, there is a small canal excavated on the squamosal side of the suture, possibly for the superior ramus of the stapedial artery (see more below).

The epitympanic recess is deeply excavated laterally above a squamosal shelf, and is walled laterally by the squamosal and roofed by the petrosal. The petrosal also sends out a lateral process, better developed in the right side, toward the postglenoid foramen. This process articulates with the squamosal near the posterior base of the postglenoid process. On the dorsolateral part of the epitympanic recess, this sutural contact between the squamosal and petrosal is rather loose and filled with matrix. Toward the posterior end of the recess, there is an enlargement of this suture to form a canal with a diameter near that of the fenestra vestibuli. This canal possibly provides the exit of the superior ramus of the stapedial artery.

The tip of the mastoid tubercle is broken on both sides of AMNH 12626. Judging from the relative contribution of the squamosal and petrosal, the squamosal, rather than the petrosal, makes up the main part of the mastoid tubercle as primitively occurs in *Carnivora* (Flynn and Galiano, 1982: 19). The mastoid process is less inflated than in *Hesperocyon*, and there is no suprameatal fossa in front of the process. The paroccipital process is large and projects posteriorly.

The postglenoid process is high, and the postglenoid foramen is large and rounded.

Medial to the postglenoid process is a deep cleft—the Glaserian fissure. The well-developed Glaserian fissure of *Carnivora* has been considered suggestive of an *Insectivora-Carnivora* sister-group relationship (Wyss and Flynn, 1993). Immediately medial to the Glaserian fissure is the sutural contact between the squamosal and alisphenoid. The basisphenoid/alisphenoid suture is not clearly visible anterior to the Eustachian canal. The grooving on the alisphenoid leading to the Eustachian canal is divided by a prominent ridge and a minor ridge. In *Canis* the lateral groove carries the Eustachian tube, whereas the medial groove transmits the tendon of the tensor veli palatini muscle (and the accompanying nerve), the palatine ramus of the facial nerve, and the nerve to the tensor tympani muscle (Evans and Christensen, 1979: figs. 15-16, 19-5).

INTERNAL CAROTID ARTERY (fig. 2A): Matthew (1909: 384) described the internal carotid artery of *V. profectus* as follows, “The grooves for the tympanic and stapedial branches of the internal carotid artery are distinctly shown; beginning just anterior to the fenestra rotunda the former passes forward on the outer slope of the auditory prominence to the foramen lacerum medius while the latter descends to the fenestra vestibuli. The inner branch of the entocarotid artery is not so certainly recognizable but appears to pass into the otic depression over the lip of the basioccipital a little in front of the foramen lacerum posterius.” This short description is usually considered to be the origin of the concept of the division of internal carotid into a two-artery system in the middle ear region of primitive eutherians (Presley, 1979; Wible, 1983: fig. 1). Instead of an entocarotid artery coexisting with a promontory artery, current consensus regards the groove which Matthew interpreted as “entocarotid artery” as an impression left by the inferior petrosal sinus.

A groove on the ventrolateral surface of the promontorium, however, clearly indicates the presence of a promontory artery. As for the “distinct” impression for the stapedial artery indicated by Matthew (1909), we noted only a faint interruption of the lateral border of the sulcus for internal carotid artery, in-

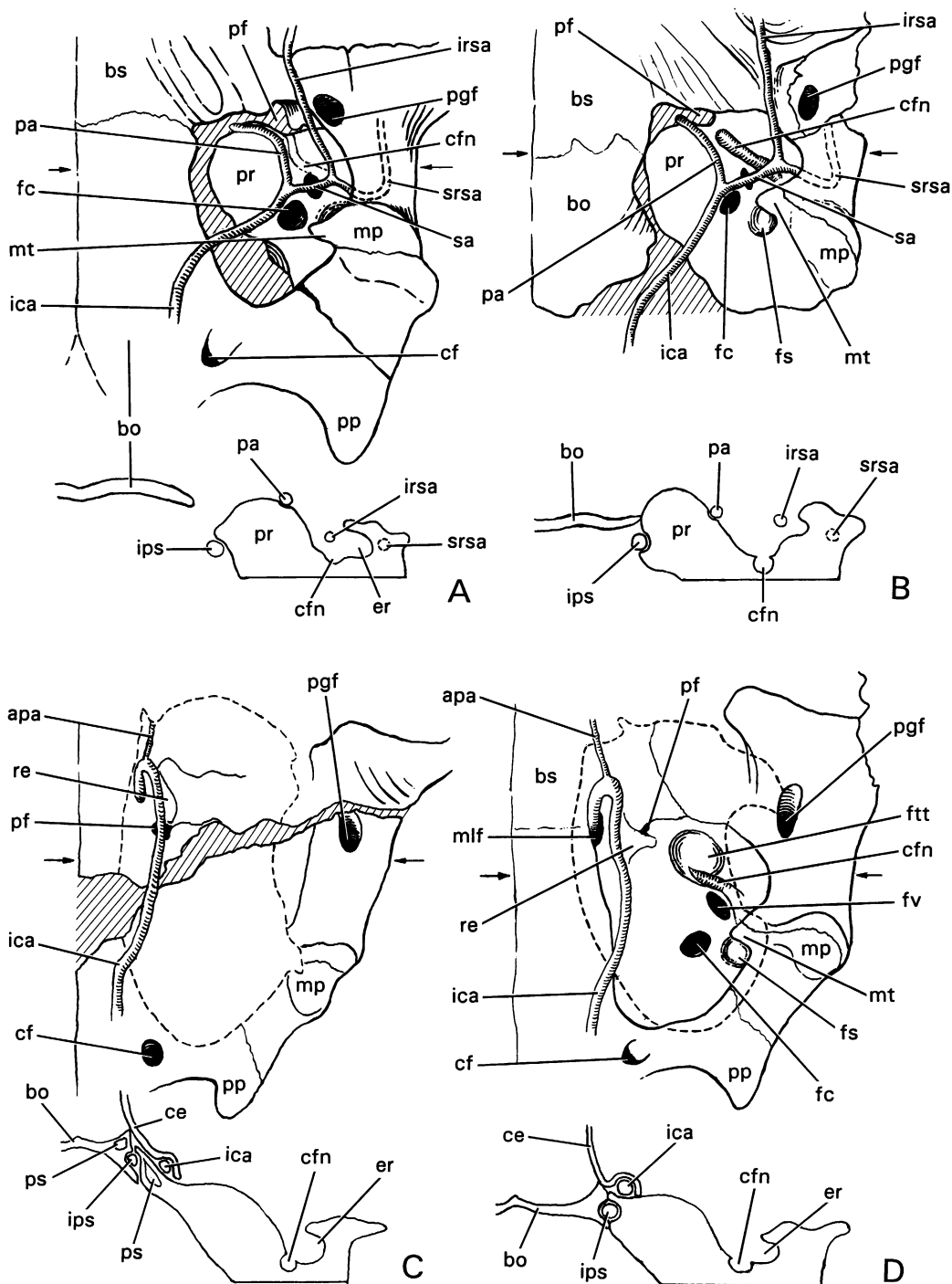


Fig. 2. Ventral (upper) and cross-sectional (lower) views of four caniform carnivorans with the hypothesized position of the internal carotid artery. A, *Vulpavus profectus*, AMNH 12626; B, *Miacis parvivorus*, USNM 214706, reversed from the right side; C, "*Hesperocyon*" *wilsoni*, TMM 40504-126, reversed from the right side, the internal structure of the posterior half of bulla not prepared, dashed

dicating a possible branch toward the fenestra vestibuli. We thus tentatively assume that there is a stapedial branch of the internal carotid artery because of its common association with a promontory artery in a number of insectivorans, primates, and other primitive eutherians (MacPhee, 1981; Novacek, 1980, 1986), as well as in primitive carnivorans, e.g., *Miacis parvivorus* (see description below), *Viverravus minutus* (Matthew, 1909), and *Protictis schaffi* (Gingerich and Winkler, 1985). Furthermore, the presence of foramina near the epitympanic recess and piriform fenestra, as well as a Glaserian fissure, also suggests that the superior and inferior rami of the stapedial artery were present, although the Glaserian fissure could be solely occupied by the chorda tympani nerve as in living dogs (Evans and Christensen, 1979).

The internal carotid artery (fig. 2A) presumably first enters the tympanic cavity in the vicinity of the posterior lacerate foramen, as in insectivorans (MacPhee, 1981; Novacek, 1986). Near the fenestra cochleae, the internal carotid artery gives rise to two branches, the promontory artery and the stapedial artery. After following the groove on the promontorium, the promontory artery enters the brain cavity through the anterior carotid foramen (middle lacerate foramen, here not fully separate from the piriform fenestra). After penetrating the obturator foramen of the stapes, the stapedial artery probably split into two branches. The ramus inferior abruptly turns anteriorly and exits the tympanic cavity through the Glaserian fissure. There are, however, two possible routes for the superior ramus of the stapedial artery. One enters the brain cavity laterally through a small canal on the posterior aspect

of the epitympanic recess as in leptictids (Novacek, 1986). The other exits anteriorly through a canal lateral to the piriform fenestra posterior and dorsal to the Glaserian fissure as in erinaceid insectivorans and tree shrews (Cartmill and MacPhee, 1980). We tentatively choose the former alternative because that seems the case in *Miacis parvivorus* (see below).

Miacis parvivorus Cope

Figures 1B, 2B

SPECIMEN EXAMINED: USNM 214706, partial skull and mandible with fragments of the postcranium, from Pinnacle Rock, unit B, Bridger Formation, Bridger Basin, Wyoming, early Bridgerian.

The genotypic species, *M. parvivorus*, was founded on a jaw fragment with a single m2 (AMNH 5019). The present description is based on USNM 214706, which has a well-preserved right ear region. USNM 214706 was briefly mentioned by Gustafson (1986) in connection with his description of "*M. cognitus*". The specimen has since been further prepared, revealing more detail in the area of tegmen tympani. A complete description of its basicranium presented below.

BULLA: Like *Vulpavus*, *M. parvivorus* does not preserve an ossified bulla. Neither is there any indication of strong bulla attachment on the petrosal, basioccipital, basisphenoid, alisphenoid, or squamosal.

PETROSAL AND SURROUNDING BONES: The basioccipital is still essentially a platelike bone as in *Vulpavus*; no thickening of its lateral edge is observed. This thin-edged plate lacks a longitudinal groove for the inferior petrosal sinus as in canids. The lateral edge of the

←

line indicating outline of bulla (as also in D); D, *Hesperocyon gregarius*, F:AM 76163. All specimens are drawn to approximately the same size. Actual arterial positions may vary from the drawings except in those segments where a bony impression is available, i.e., sulci on promontorium, Glaserian fissure, and the foramen for superior ramus of stapedial artery. Cross-sectional views are diagrammatic, and their locations of sections are indicated by short horizontal arrows to the left of midline of basioccipital and to the right of lateral border of squamosal. Diagonal hatch lines indicate areas of free spaces between bones or missing bones. In ventral views, top is anterior and right is lateral; in cross sectional views, top is ventral and right is lateral. See Definition section for abbreviations. As in fig. 1, the piriform fenestra (pf) encompasses the middle lacerate foramen in *Vulpavus* and *Miacis*.

basioccipital and basisphenoid is straight, lacking the constriction at the juncture of basioccipital/basisphenoid seen in *Vulpavus*.

The petrosal of *M. parvivorus* is primitive as in *Vulpavus* (figs. 1B, 2B). The promontorium is more medially extended toward the lateral edge of basioccipital and basisphenoid compared to that of the latter. In fact, the medial apex of the promontorium touches the lateral border of the basioccipital. The rest of the promontorium, however, is still free of any contact with the surrounding bones. On the steep, nearly vertical medial face of the promontorium, there is a conspicuous groove slightly dorsal to the level of the basioccipital. This groove is inferred to have contained the inferior petrosal sinus. The surface texture of this groove is rather uneven, possibly mirroring the irregular shape of the vein. As in *Vulpavus*, the large size of the groove for the inferior petrosal sinus and the wide space between the promontorium and the basioccipital/basisphenoid suggest a relatively large vein.

The promontorium is slightly less globular than in *Vulpavus*, especially in its less inflated anterolateral corner. The ventral surface of the promontorium is covered with irregular low ridges. Lateral to these ridges is a shallow but clear groove for the promontory artery. As in *Vulpavus*, the groove begins just anterior to the fenestra cochleae and extends anteriorly and medially toward the large open space for the combined anterior carotid foramen (middle lacerate foramen) and piriform fenestra. A transverse sulcus branches off the posterior end of the sulcus for the promontory artery. This sulcus, which must have been occupied by the stapedial artery, ends at the ventral rim of the fenestra vestibuli.

Immediately posterior to the fenestra cochleae on the posterolateral aspect of the promontorium, there is a rounded process with a flat top, presumably attached to the tympanohyoid cartilage. Lateral to this process is a deep, rounded fossa for the stapedius muscle, partially covered by the overhanging mastoid tubercle. The main body of the mastoid tubercle is made up of the petrosal, except for a small contribution from the squamosal at the base. The mastoid process is

small and less inflated than in *Hesperocyon*. There is no suprameatal fossa. The part of the basioccipital (mostly paroccipital process and the posterior rim of the middle ear region) behind the petrosal is missing along the sutural contact of the two bones, leaving the posterior face of the petrosal mostly intact. In this unobstructed view of the posterior promontorium and at the horizontal level of the inferior petrosal sinus, a small opening for the cochlear canaliculus is clearly seen facing posteromedially; this canal contains the perilymphatic duct connecting the cochlea and semicircular canals in *Canis* (Evans and Christensen, 1979: 1070).

The degree of ossification of the tegmen tympani is intermediate between that of *Vulpavus* and *Hesperocyon*. Anteriorly, the petrosal of *M. parvivorus* is in complete contact with the tympanic process of squamosal lateral to the anterior tip of the canal for the facial nerve. Medial to the canal, however, there is still a large gap, the piriform fenestra, between the petrosal and alisphenoid. The tegmen tympani floor is well-ossified so that the canal for facial nerve is mostly embedded in bone instead of being in a groove on the tegmen tympani as in *Vulpavus*. On the other hand, the ventral side of the facial nerve canal is covered by bone only at the anteriormost tip (the segment of the canal for the palatine ramus of the facial nerve, or major petrosal nerve), and the posterior part of the canal (containing the hyomandibular ramus of the facial nerve) remains open, in contrast to the complete bony coverage in "*M. cognitus*" and some *Hesperocyon*. The greater ossification of the tegmen tympani in *M. parvivorus* also helps define a rounded fossa for the tensor tympani muscle. The site for the genicular ganglion can be seen through the open facial nerve canal along the lateral border of promontorium.

The epitympanic recess is slightly less excavated than in *Vulpavus*. As in *Vulpavus*, however, the recess is laterally walled by the squamosal and roofed by the in-bent lateral margin of petrosal. On the posterior aspect of the epitympanic recess, there is a canal through the suture between the petrosal and squamosal. The opening of this canal faces directly opposite the fenestra vestibuli, and

its diameter is approximately the same as that of the latter. This combination of geometric features suggests that this canal forms the exit of the superior ramus of the stapedia artery.

In contrast to the more slitlike Glaserian fissure of *Vulpavus*, that of *M. parvivorus* is a broad trough with a gently curving floor. Immediately medial to the Glaserian fissure is the essentially anteroposteriorly oriented alisphenoid/squamosal suture. The postglenoid process is mostly broken off; the part that remains indicates a gentle crest rather than a sharp ridge as in most carnivorans.

INTERNAL CAROTID ARTERY (fig. 2B): The course of this artery is nearly identical to that in *Vulpavus*. As in *Vulpavus*, the internal carotid artery, after entering into the middle ear cavity, branches into a promontory artery and a stapedia artery. The promontory artery makes an arc along the contour of the promontorium and enters the brain cavity through the anterior carotid foramen (here continuous with the piriform fenestra). The stapedia artery branches into superior and inferior rami after passing through the obturator foramen of the stapes. The course of the superior ramus of the stapedia artery is indicated by the presence of a canal posterior to the epitympanic recess, i.e., a straight lateral exit into the brain cavity before turning forward. The inferior ramus leaves the middle ear region via the Glaserian fissure.

"Miacis" sylvestris (Marsh)

Figure 3

SPECIMEN EXAMINED: AMNH 129284, partial skull and mandible with left P2-M3, right P2-M2, left p3-m1 m3, right p3-m3, and fragments of postcranium, from south of Wamsutter, northeast Washakie Basin, Wyoming, Adobe Town Member of Washakie Formation, Bridgerian.

This specimen was recently donated to the AMNH by Mr. Joel H. Curran of Jackson, Wyoming. Except for the slightly collapsed appearance of the basisphenoid region, the right basicranium of AMNH 129284 is essentially intact; the left basicranium is missing. A complete description of the cranium and dentition is the subject of a separate report; only the basicranium is described here.

The dentition of AMNH 129284 compares favorably with two referred specimens (AMNH 13071 and 13073) from the Bridger Formation referred to "*Miacis" sylvestris* by Matthew (1909: fig. 15). Marsh's (1872) type of *Harpalodon sylvestris* (also from the Bridger Formation, Wortman, 1901: fig. 38) consists of a left ramal fragment with the p3-4 and the talonid of m1. The only diagnostic character of the holotype is the rather narrow talonid on m1 (as opposed to the wider, more basined talonid in *M. parvivorus*), and with this AMNH 129284 agrees.

BULLA: No bulla element is preserved in AMNH 129284. A slightly elevated area along the suture between the squamosal and alisphenoid, medial to the postglenoid process, suggests the site of attachment of the anterior crus of the ectotympanic.

However, on the ventral surface of the petrosal is a broad roughened area, approximately 2 mm wide, along the medial side of the promontorium (spe of fig. 3). This rugose band is laterally delineated by a distinct bony ridge, and lateral to this ridge, the ventral promontory surface is smooth. Such a sutelike surface texture along the medial promontorium is invariably left by the impression of the in-bent medial edge of the bulla in caniform carnivorans. The rather ventrally extended attachment area of the anterior crus of the ectotympanic suggests that the ectotympanic ring is in a rather erect position (large angle with the horizontal plane), and such an erect ectotympanic is often the result of inflation of the bulla due to an expansion of the caudal entotympanic. We thus assume that the rugose surface on the promontorium indicates the presence of the caudal entotympanic.

It is puzzling that such a large area for bulla attachment on the promontorium is not accompanied by the preservation of the bulla. The lack of any bullar elements in miacids is presumably due to lack of ossification with the surrounding bones. In AMNH 129284, the entotympanic attachment to the petrosal is certainly more extensive than in *Hesperocyon*, whose caudal entotympanic has only a narrow contact with the petrosal (see description below).

PETROSAL AND SURROUNDING BONES: Al-

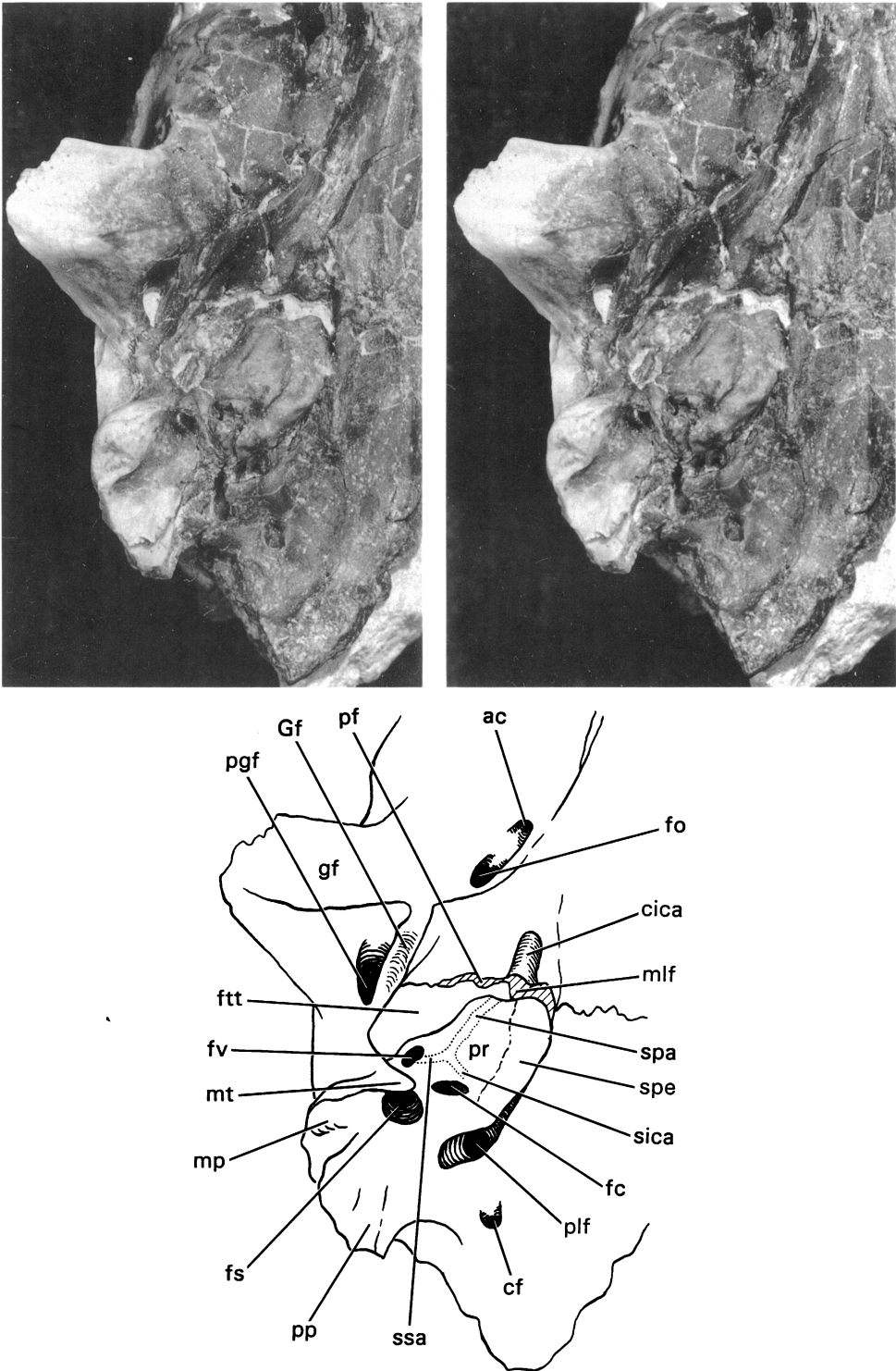


Fig. 3. Ventral view (in stereophoto and line drawing) of right basicranial region of *Miacis sylvestrus* (AMNH 129284). Top is anterior and right is lateral. See text for descriptions and Definition section for abbreviations.

though it lacks a securely attached bulla, the basicranium of AMNH 129284 is advanced in many aspects. The lateral edge of the basioccipital is fully exposed on the left side and exhibits a small, dorsolaterally extended flange to enclose the inferior petrosal sinus. This bony flange, more extensively developed in its posterior segment near the posterior lacerate foramen, is in full contact with the medial face of the petrosal. The cross sectional area of the inferior petrosal sinus is small and probably did not house a double-looped internal carotid artery as in ursids and presumably amphicyonids.

Contact between the petrosal and the other surrounding bones is similarly extensive, although the sutures are still wide, i.e., the petrosal is no longer isolated from the surrounding bones as in *Vulpavus*, and to a lesser extent in *Miacis parvivorus*. In addition to the broad rugose area described above, the petrosal is more flattened than in other miacids described above, in which it is more globular. On the ventrolateral face of the flattened petrosal surface is a shallow but distinct groove indicating the presence of a promontory artery. For its entire course, the groove is lateral to the presumed contact zone (rugose area) of the entotympanic. The sulcus of the proximal stapedia artery is less distinct and marked by a groove only near the ventral rim of the fenestra vestibuli. Aside from the grooves left by arteries, the surface of the promontorium lateral to the rugose band is rather smooth. Immediately behind the fenestra cochleae is a prominent process, which is more distinct than in *M. parvivorus*, and, together with a columnlike mastoid tubercle (composed of the squamosal), forms the attachment of the cartilaginous tympanohyoid.

The tegmen tympani area is well-ossified. The facial nerve is enclosed by bone ventrally, and the fossa for the tensor tympani muscle is well-formed. The piriform fenestra is closed and only a small promontory foramen is left. Lateral to the tegmen tympani, the epitympanic recess is shallower than in *Vulpavus* and is not excavated laterally into the squamosal wall. A small canal appears to be present between the petrosal/squamosal suture in the posterodorsal corner of the recess for the transmission of the superior ramus of stapedia artery. This suture along the epitympanic recess is otherwise tightly closed.

Anterior to the petrosal/alisphenoid suture is a deep, oval fossa in the tympanic wing of alisphenoid. This fossa is variably developed in *Hesperocyon* (e.g., F:AM 76163 and 129176) and is often surrounded anteriorly by the dorsal edge of the ectotympanic. The alisphenoid/squamosal suture lies medial to the Glaserian fissure as is common in the other taxa examined. The fissure continues posteriorly by a distinct groove, directed toward the epitympanic recess; the groove probably contained the inferior ramus of the stapedia artery. The postglenoid foramen is large. There is a shallow depression just anterior to the mastoid process in the posterodorsal wall of the external auditory meatus, which appears to be an incipient suprameatal fossa. The mastoid process is composed of the petrosal and squamosal, and is moderate in size. The tip of the paroccipital process is broken; the remaining part suggests the presence of a distinct ventral ridge, which is variably developed in many early caniforms.

INTERNAL CAROTID ARTERY: As described above, the internal carotid artery is medial to the presumed contact of the entotympanic and petrosal, i.e., retaining the primitive pattern of the transpromontorial (intrabullar) position. However, AMNH 129284 suggests that the artery had an anterior loop as in all canids and many primitive arctoids. Instead of directly entering the brain cavity through the anterior carotid foramen (middle lacerate foramen) as in some miacids, the promontory artery passes forward of the middle lacerate foramen, into a pit (cica of figs. 3 and 6) in the basisphenoid 2 mm anterior to the middle lacerate foramen. It presumably loops backward within this pit, and finally turns dorsally to enter the brain cavity through the middle lacerate foramen. This looped arrangement is further indicated by the rather shallow sulcus for the promontory artery near its anterior tip. A direct entry into the brain cavity by the artery would have left a much deeper impression on the anterior edge of the promontorium leading into the middle lacerate foramen as seen in *Vulpavus* and *M. parvivorus*.

The presence of a groove on the ventral rim of the fenestra vestibuli suggests a proximal stapedia artery. The course of the artery is identical to that in *Miacis parvivorus*. After penetrating the obturator foramen of the sta-

pes, the proximal stapedia artery branches into two rami: the superior ramus runs laterally and enters the brain cavity through a canal in the squamosal/petrosal suture near the posterior end of the epitympanic recess; the inferior ramus turns forward and exits the middle-ear cavity through the Glaserian fissure.

"Miacy" cognitus Gustafson

SPECIMEN EXAMINED: TMM 40209-200, holotype, complete skull, from upper Chambers Formation, Reeves Bone Bed locality, Little Egypt Local Fauna, Presidio County, Texas, medial Chadronian.

In the following description, we will outline only features relevant to the phylogenetic discussion; other features have been adequately described and figured by Gustafson (1986).

BULLA: No ossified bulla has been described in *"M." cognitus*, although an ectotympanic ring was reconstructed by Gustafson (1986: fig. 24B). Medial to the left postglenoid process, there is a low platform of bone on the tympanic process of squamosal; this bone is clearly part of the squamosal rather than a floating piece of ectotympanic.

PETROSAL AND SURROUNDING BONES: Aside from its lack of an ossified bulla, the overall structure of the basicranium is more advanced than that of the miacids described above. The promontorium is flattened and considerably expanded so that it is in contact with the basioccipital, basisphenoid, alisphenoid, and squamosal, although there is still a large, triangular space at the anteromedial corner of the petrosal that forms the middle lacerate foramen. The tegmen tympani is completely ossified and the facial nerve is enclosed by bone which forms the floor of the fossa for the tensor tympani muscle. Anterior and medial to the middle lacerate foramen, there is a clear impression of a looped internal carotid artery on the thickened lateral wall of basisphenoid. No suprimeatal fossa is present. The mastoid tubercle is formed from petrosal.

INTERNAL CAROTID ARTERY: A medially positioned internal carotid artery is firmly

established by the presence of the embayment on the basisphenoid, the unambiguous turn-around point of the artery. There are no grooves on the promontorium for branches of the internal carotid artery.

"Miacy" gracilis Clark

SPECIMEN EXAMINED: CMNH 11900, holotype, crushed skull and mandible with most of the limb bones. CMNH 12063, partial skull and mandible with most of the upper teeth except incisors and less well-preserved lower teeth; an epoxy cast of the dentition is available for examination. Both specimens are from Horizon C of Uinta Formation, Uinta County, Utah, late Uintan.

The following brief discussion of the basicranium was based on a stereophotograph of the type.

BULLA: Clark (1939: 352) described the holotype (CMNH 11900) of *"M." gracilis* as having "a large, extraneous piece of bone adhering to the right alisphenoid just anterior to the inner part of the glenoid fossa," which he interpreted as "a portion of the rim of the tympanic." This he cited as an important characteristic linking miacids, without an ossified bulla, and *Hesperocyon*, with its fully ossified entotympanic. Clark's observation cannot be confirmed in our photograph. However, a distinct band of rough area on the medial edge of the petrosal is present, indicating the attachment area of the entotympanic, as also occurs in *"M." sylvestris*.

PETROSAL AND SURROUNDING BONES: The promontorium is generally flat on its ventral surface and it is in contact with the lateral border of the basioccipital. The tegmen tympani area appears to be well-ossified. A shallow suprimeatal fossa may have been present on the anterior face of the mastoid process.

INTERNAL CAROTID ARTERY: Presence of a transpromontorial artery cannot be ascertained from the available photographs. A pit in the basisphenoid for the turn-around of the internal carotid artery, however, can be observed although the pit is partially obscured by the lateral edge of the basisphenoid in the photograph.

COMMENTS: In addition to his single cranial character (bulla ossification), the remaining

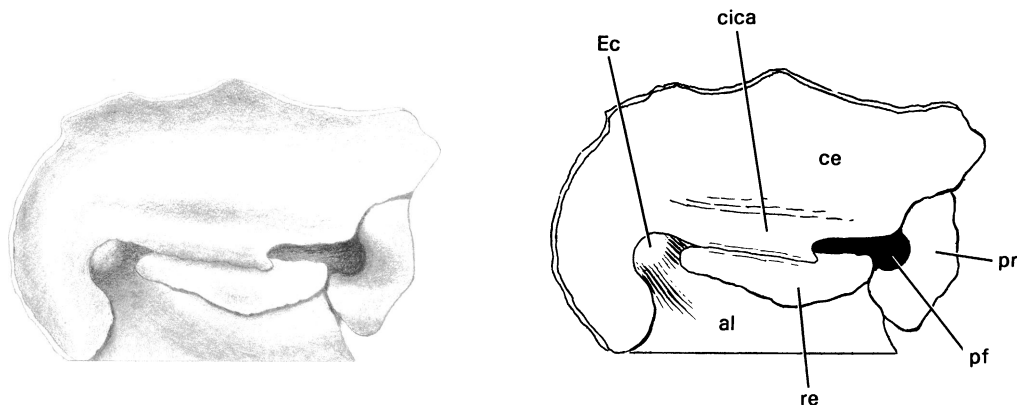


Fig. 4. Internal view (bulla partially removed) of the anterior part of right middle ear region of "*H. wilsoni*", TMM 40504-126, showing the rostral entotympanic, the internal carotid canal, and the promontory foramen. Anterior is toward the left and lateral is toward the bottom of the illustration. The breakage line on the right side corresponds to a natural break of the middle ear region (see fig. 2C, ventral view) and thus only the anteromedial corner of the promontorium is shown in the figure. See Definition section for abbreviations.

"cynodictoid" (canid) characteristics (five) of "*M. gracilis*" cited by Clark (1939: 360) are entirely postcranial, and are mainly related to its slender, straight limb bones that contrast with the more robust limbs of most miacids. The postcranial adaptation toward increased cursoriality is one of the important transformations from miacids to primitive canids (Tedford, 1978; Wang, 1993). The poorly known postcrania of miacids, however, are of limited use in a detailed phylogenetic analysis.

"Hesperocyon" wilsoni Gustafson
Figures 2C, 4

SPECIMEN EXAMINED: TMM 40504-126, holotype, partial skull and mandible, from Airstrip Local Fauna, Capote Mountain Tuff, in southern part of the Sierra Vieja area, Presidio Co., Texas (Wilson et al., 1968), early Chadronian.

Gustafson's (1986) original description dealt with only the external morphology of the bulla. Further preparation during the present study reveals details inside the bulla described below.

BULLA: "*H. wilsoni*" is the most primitive canid with a fully ossified bulla. Although areas of the bulla wall have suffered diage-

netic losses, particularly on the left side, the overall shape of the bulla is still intact because of the well-preserved endocast. The bulla wall is generally thinner than those in *H. gregarius* and some portions of the bulla are nearly transparent. The bulla in "*H. wilsoni*" has a canidlike shape, although the suture between ecto- and entotympanic is not readily discernible externally. The bulla is highly inflated (presumably mainly by the entotympanic) and anteroposteriorly elongated. The anterior apex of the bulla extends anterior to the posterior wall of the glenoid fossa. To accommodate the anterior expansion of the bulla, the external opening of the foramen ovale is shifted forward toward the alisphenoid canal. There is no trace of a bony external auditory meatus.

There is a diagonal break across the middle section of the right bulla, affording an opportunity to examine the cross section of the bulla wall. No trace of a low septum can be detected on either side of the break, which crosses the region where a low septum is found in *H. gregarius*. Further preparation posteriorly did not reveal a septum, although a significant amount of matrix was left intact for fear of damage to the extremely delicate bulla wall. In the anterior half, no septum is present at the junction between rostral (see

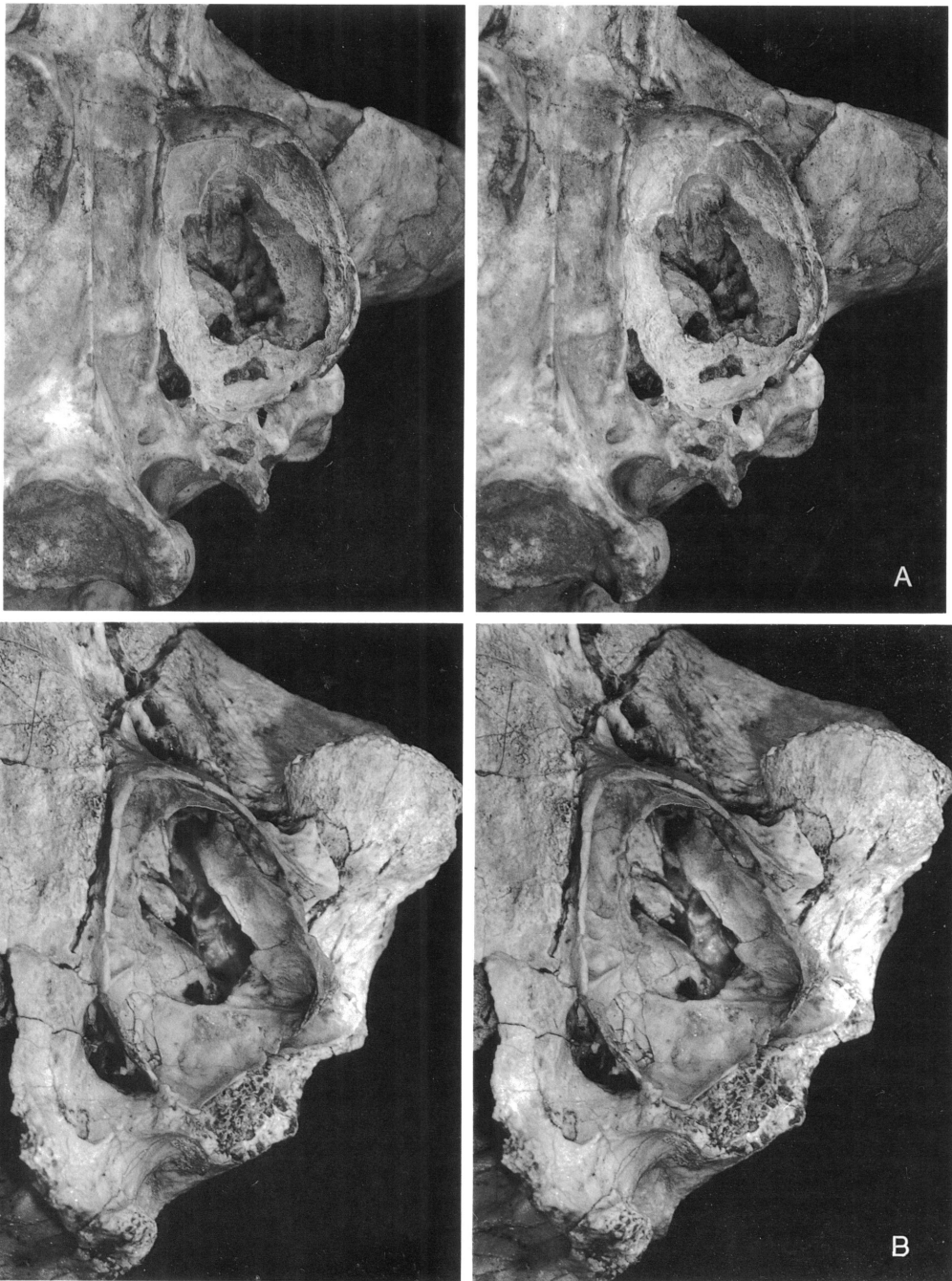


Fig. 5. Ventral views (in stereo) of dissected left basicranial region in A, "*Mesocyon*" *josephi* (MCZ 2102) and B, *Enhydrocyon pahinsintewakpa* (CMNH 13588), showing developments of bullar septa. Arrows in the line drawings indicate the extent of septum. Top is anterior and right is lateral. See Definition section for abbreviations.

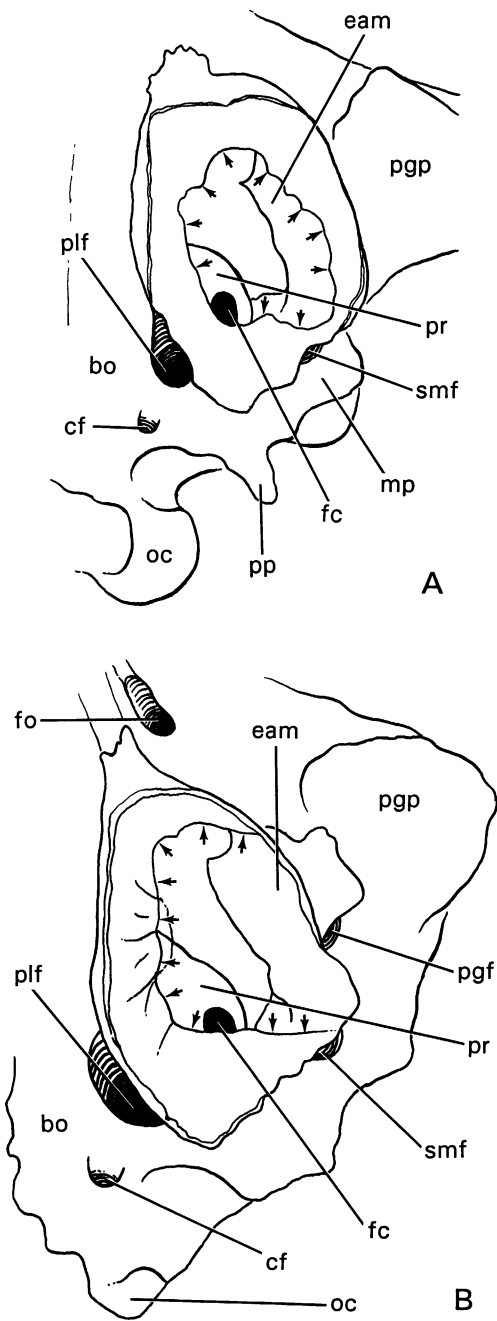


Fig. 5. Continued.

panic: the rostral and caudal entotympanics (Hunt, 1974). The rostral entotympanic in living *Canis*, which ossifies only after birth (Wible, 1984), is usually a small triangular bone at the anteromedial corner of the bulla that forms the roof of the internal carotid artery (Hunt, 1974: pl. 7). In the anterior half of the right bulla of "*H.*" *wilsoni*, there is a slender bone that is nearly continuous with the in-bent edge of the caudal entotympanic, immediately anterior to the promontory foramen and along the lateral edge of the internal carotid canal (fig. 4). This small bone is here interpreted as a rostral entotympanic. The contact zone between the rostral and caudal entotympanic is a narrow area of overlap, slightly wider than the thickness of the individual bones. The rostral entotympanic is covered slightly on its ventrolateral edge by the caudal entotympanic. Although not fused, the rostral/caudal entotympanic suture is not filled with dark-colored matrix as occurs between more loosely attached bones, and this suture is best seen near the posterior segment of the rostral entotympanic. The topographic position of the rostral entotympanic is rather typical of canids as seen in living *Canis* (Hunt, 1974), i.e., the internal carotid artery lies near the junction of the caudal and rostral entotympanic. Near the posterior lacerate foramen, the opening for the internal carotid artery is defined by a small groove on the external surface of the entotympanic. More anteriorly, near the petrosal/basisphenoid suture, the course of the internal carotid artery is recognized as a canal beneath the in-bent edge of the caudal entotympanic.

PETROSAL AND SURROUNDING BONES: Much of the relevant information is obtained from the cross section afforded by the breakage of the right auditory region, and can be partially verified by the exposed anterior half of the bulla.

The lateral border of the basioccipital in "*H.*" *wilsoni* is thick and deep, instead of being thin-edged as in *Vulpavus* and *M. parvivorus*. This lateral edge is divided into dorsal and ventral lips, thus enclosing a groove that housed the inferior petrosal sinus. The thickened basioccipital is filled with a small pneumatic sinus isolated from the inferior petrosal sinus by a thin bony wall (fig. 2C).

below) and caudal entotympanic. We thus infer that "*H.*" *wilsoni* lacks a septum.

All living carnivorans have at least two separate ossification centers for the entotym-

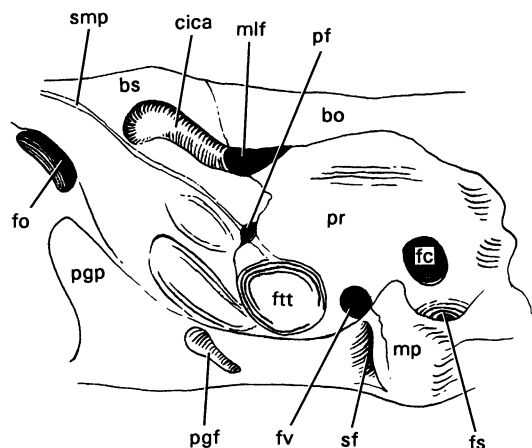


Fig. 6. Ventrolateral view of the anterior part of right middle ear region of *H. gregarius*, F:AM 76160. All bullar elements are removed, showing the impression of a loop of the internal carotid artery on the basisphenoid. Anterior is toward the left side and lateral is toward the down side. See Definition section for abbreviations.

The promontorium of "*H.*" *wilsoni* is candidlike in its low and flattened appearance, as opposed to the primitive globular promontorium of miacids. The promontorium has expanded medially and its medial edge reaches to the lateral border of the basioccipital. However, the medial edge of the petrosal does not appear to fully surround the lateral side of the inferior petrosal sinus. Instead, the entotympanic forms a thin strip of the ventrolateral wall of the sinus. (TMM 40504-126 is slightly distorted in this area and there is a possibility that the original relationship of the bones is obscured.) As in the lateral edge of basioccipital, the medial extension of the petrosal is also pneumatic with a small sinus just inside the medial edge.

Due to its medial expansion, the ventral surface of petrosal in "*H.*" *wilsoni* is more flattened than in *Vulpavus* and *M. parvivorus*. In cross section, there is an oval space (somewhat more compressed in the anterior segment due to crushing) between the overlapping the entotympanic and petrosal. This space is for the medially positioned internal carotid artery (fig. 2C).

The petrosal is also anteriorly expanded and in contact with the tympanic process of

alisphenoid and squamosal. The piriform fenestra is fully closed between these bones, leaving only a small promontorium foramen at the petrosal/alisphenoid suture directly above the internal carotid canal (fig. 4).

Another derived character of "*H.*" *wilsoni* is a small suprimeatal fossa in front of the mastoid process. It is a shallow, rounded pit on the squamosal half of the mastoid process, just like that of *H. gregarius*. The mastoid tubercle is broken, but judging from the remaining basal portion, it was composed of the petrosal as in *H. gregarius*.

INTERNAL CAROTID ARTERY (figs. 2C, 4): Although slightly more laterally positioned than in *H. gregarius*, particularly in the anterior segment, the internal carotid artery in "*H.*" *wilsoni* is in a truly medial, extrabullar position. The internal carotid canal is floored by the dorsal flange of the caudal entotympanic posteriorly and by the caudal and rostral entotympanic anteriorly (thus extrabullar in topography). It is roofed by the medially expanded petrosal. Entry into the internal carotid canal is marked by a small indentation in the caudal entotympanic immediately below (outside) the posterior lacerate foramen as in *H. gregarius* (see below). After entering the internal carotid canal, the artery travels forward following the contour of the ventral surface of petrosal. As in "*M.*" *cognitus* and *H. gregarius*, it probably makes a U-turn within the bony confinement of basisphenoid and caudal entotympanic (not exposed in this area in TMM 40504-126) and finally enters the brain cavity through the middle lacerate foramen.

Hesperocyon gregarius (Cope)

Figures 1C, 2D, 6

SPECIMENS EXAMINED: AMNH 39442, skull without bullae, from south of Scenic, Pennington County, South Dakota, Brule Formation, Orellan; F:AM 50345, complete skull and mandible, left bulla removed, from Quinn Draw, Washington County, South Dakota, near top of lower nodular zone, Brule Formation, Orellan; F:AM 63942, skull, right bulla dissected, from middle fork of Lone Tree Gulch, Natrona County, Wyoming, 10

ft below ash F, White River Formation, Chadronian; F:AM 76160, basicranial part of skull without bullae, from Morton Ranch highway area, 6½ mi. southeast of Douglas, Converse County, Wyoming, middle nodular zone, Brule Formation, Orellan; F:AM 76163, partial skull, left bulla dissected, from W. R. Silver Ranch, Converse County, Wyoming, middle part of a nodular zone, Brule Formation, Orellan; F:AM 129176, endocast plus basicranium without bullae, from west of the Anthill, Niobrara County, Wyoming, 40 ft above the purplish white layer, Brule Formation, Orellan; FMNH UC495, complete skull and mandible, left bulla dissected, from Cedar Creek, Sioux County, Nebraska, Brule Formation, Orellan.

Various aspects of the skull, dental, and postcranial morphology of *Hesperocyon* have been well-known from descriptions in Scott (1898), Matthew (1901), Scott and Jepsen (1936), and Wang (1990, 1993, MS). Abundant specimens are available for examination of nearly every detail of the basicranium and their individual variations. Our knowledge of the *Hesperocyon* middle ear region is thus relatively secure compared to that of other fossil carnivorans that are known from more limited materials. Existing descriptions of its basicranium (e.g., Hough, 1948; Mitchell and Tedford, 1973), however, are inadequate for the present comparisons, and a detailed description is thus necessary to identify the relevant features.

BULLA: The external morphology of the bulla of *H. gregarius* is little different from that of "*H. wilsoni*" other than the slightly greater inflation of the latter. No bony external auditory meatus is present. The bulla is made up of the ectotympanic, caudal entotympanic, and rostral entotympanic components as it is in living canids (Hunt, 1974). Fusion between the ecto- and entotympanic, however, occurred early in the ontogeny of *Hesperocyon*, and inferences about the individual components must be based on subtle external surface features of the bulla (a line of minute pits along the ventral apex), and on a low septum on the internal surface. By these criteria it can be recognized that the inflation of the bulla is mostly caused by the expansion of the caudal entotympanic which

encompasses the entire medial half of the bulla. A Chadronian individual (F:AM 63942) shows an appreciably smaller bulla than those in the Orellan sample. Its caudal entotympanic, whose lateral edge can be observed to terminate in a low septum (see below), is less expanded on the medioposterior aspect of the bulla, and consequently its ectotympanic ring is inclined toward the medial side. No definite trend of increased inflation of the bulla through time can be established because of the relatively small Chadronian sample of *Hesperocyon* compared to that from the Orellan.

In F:AM 76163, a triangular rostral entotympanic, similar to that in "*H. wilsoni*", is visible on the dorsal side of the internal carotid canal (figs. 1C, 2D). This rostral entotympanic is slightly posterior of the anterior end of the bulla, and straddles the petrosal/alisphenoid suture. Anterior to the rostral entotympanic, there is no bullar element on the dorsal side of the internal carotid canal, in contrast to living *Canis*, in which the rostral entotympanic reaches the anterior end of the bulla (Hunt, 1974). Although no suture is seen, the rostral entotympanic presumably joins the caudal entotympanic along the internal carotid canal, as in "*H. wilsoni*" (fig. 4). A similarly shaped, narrow rostral entotympanic can be seen in FMNH UC495 and F:AM 63942, and is similarly positioned across the petrosal/alisphenoid suture. In F:AM 63942, the internal carotid canal is broken near the middle of the rostral entotympanic region, affording a limited view of the relationship between rostral and caudal entotympanic; the ventral portion of the bony canal (presumably mostly made of caudal entotympanic as in "*H. wilsoni*") appears continuous with the more dorsal rostral entotympanic, i.e., the suture is indistinct. In all individuals, the rostral entotympanic tapers toward the anterior end.

A low, anteromedial septum inside the bulla has long been considered unique to canids (Flower, 1869). The presence of a septum in *Hesperocyon* was first mentioned by Tedford (1976). In the present study, a low septum was found in all *Hesperocyon* specimens in which the internal surface of the bullae was prepared (F:AM 50345, 76163 and FMNH

UC495) or in specimens preserved as endocasts of the bullae so that the septum can be seen as embedded within the endocasts (e.g., F:AM 63942, a Chadronian individual with uninflated entotympanic). The septum lies along the ecto-/entotympanic suture, and may taper off toward the anterior end (fig. 1C). In FMNH UC495, the septum is rather low and frequently interrupted by tiny notches, whereas in F:AM 50345, it is higher and forms a continuous thin blade.

Within hesperocyonines, the most primitive subfamily of Canidae, there is a tendency toward increasing the length and depth of the septum. Thus, in KUVVP 85067, a larger *Hesperocyon*, the septum runs the entire length of the ecto-/entotympanic suture instead of only part of the length as in some *H. gregarius* specimens. Furthermore, in *Mesocyon coryphaeus* (AMNH 6859, holotype) and "*M.*" *josephi* (MCZ 2102, holotype of *M. hortuliroae*, fig. 5A), the septum becomes much deeper, and may also develop a septumlike low ridge along the in-bent dorsal edge of the caudal entotympanic (fully exposed in MCZ 2102). These two septa, one formed along the ventral edge of entotympanic (ecto-/entotympanic suture) and the other along its dorsal edge (rostral/caudal entotympanic suture, or a free edge in the posterior half of caudal entotympanic), join at their anterior tips and form a complete ring inside the bulla. In some derived hesperocyonine canids (e.g., *Enhydrocyon*, CMNH 13588, fig. 5B); in borophagines: (*Tomarctus*, F:AM 49088, 62300; *Aelurodon*, F:AM 61755, 67025; *Epicyon*, F:AM 61475); and in canines (personal observations on representatives of all living genera), however, the septum is mostly confined to the anterior end of the bulla, and is at an angle with the parasagittal plane. This limited septum sits on the anteriormost part of the internal carotid canal, in parallel or at a small angle with the canal, and stretches ventrolaterally toward the tympanic membrane.

Hunt (1974) emphasized the nonhomologous nature of the unilaminar canid septum to the bilaminar, complete septum of most living feliform carnivorans. The canid septum is composed of the entotympanic alone rather than by both ento- and ectotympanics as in feliforms. More importantly,

Hunt stressed the different topographic relationships of the septa: "A tympanic [ectotympanic] contribution can be definitely excluded in the Canidae in which the septum develops from the edge of the caudal entotympanic nearest the rostral entotympanic, that is, from the dorsal edge. In felids and viverrids, the *septum bullae* develops from that part of the caudal entotympanic farthest from the rostral entotympanic, that is from the ventral or opposite edge which is in contact with the tympanic" (Hunt, 1974: 38–39, original italic, brackets added).

Although not easily verified in *H. gregarius*, the morphology in some fossil canids appears to agree with part of Hunt's description, i.e., the entotympanic forms the septum. Although composition of the septum cannot be ascertained because of the advanced stage of fusion, the development of a dorsal segment of the septum, posterior to the presumed contact with the rostral entotympanic (e.g., in MCZ 2102, "*Mesocyon*" *josephi*, fig. 5A) clearly involves an in-bent margin of caudal entotympanic, i.e., the free edge of caudal entotympanic grows toward the empty space of the middle ear cavity. We thus assume that the ventral septum seen in all early canids is similarly formed by the same ontogenetic process in the expansion of the in-bent caudal entotympanic.

Hunt's (1974) claim that the canid septum is formed by the dorsal edge of caudal entotympanic only, however, is in contradiction to the present observations on early canids. In *Hesperocyon*, a dorsal septum is absent along the rostral and caudal entotympanic suture; instead, a ventral septum is invariably present between the ectotympanic and the caudal entotympanic. In more derived hesperocyonines such as "*Mesocyon*" *josephi* and *Enhydrocyon pahinsintewakpa*, a dorsal septum begins to develop due to the expansion of the caudal entotympanic, but the ventral septum is even more pronounced (fig. 5). It appears that the anteriorly limited occurrence of the septum in most canids (all extant canines, some borophagines, and derived members of hesperocyonines) is a derived condition from a more ubiquitous presence of the septum along all edges of the caudal entotympanic in early canids. In fact, the septum may not be limited to the area of contact

between the rostral and caudal entotympanic in living *Canis* either. The septum in adult *Canis* can be seen to reach down as far as the ventral apex of the bulla, far exceeding the range of the rostral entotympanic.

PETROSAL AND SURROUNDING BONES: The basioccipital is essentially the same as in "*H. wilsoni*"; it has a thickened lateral border surrounding a small inferior petrosal sinus. The medial border of petrosal forms a corresponding groove to surround the lateral half of the sinus. The inferior petrosal sinus is thus completely embedded within a bony tube formed by the basioccipital and petrosal, in contrast to the condition in ursids and amphyconids where the sinus is housed within a large embayment formed in the medial side of the basioccipital.

The petrosal is in full contact with the surrounding bones. Its anterior edge is in smooth transition with the tympanic processes of alisphenoid and squamosal; there is no sudden drop of the tegmen tympani floor from the posterior edge of the alisphenoid as in *Vulpavus* and to a lesser extent in *Miacis*. The Eustachian tube and the tendon for the tensor vela palatine muscle enter through the Eustachian canal (musculotubal canal of Evans and Christensen, 1979). Contrary to the finding in Hough (1948: 94), there is a bony partition between the Eustachian tube and the anterior "carotid foramen" (= foramen lacrum medium of Hough, 1948), i.e., the ascending pharyngeal artery is fully enclosed by the entotympanic (see description below).

The promontorium is flattened rather than globular in shape as it is in *Vulpavus* and *Miacis*. In all specimens, the ventral surface of the promontorium is very smooth and devoid of any indication of artery or nerve impressions. The piriform fenestra is completely closed, leaving only a small promontory foramen, from which the palatine ramus of facial nerve (major petrosal nerve) emerges from within the petrosal (Evans and Christensen, 1979: fig. 15-16). This ramus of the facial nerve immediately turns forward and leaves the middle ear cavity through the Eustachian canal. In most specimens, a very thin, but distinct groove is left by the nerve on the alisphenoid floor between the promontory foramen and the Eustachian canal (fig. 6, smp). There is also a groove between the

promontory foramen and the anteromedial rim of the fossa for the tensor tympani (fig. 6). The occupant of this groove is unknown. The hyomandibular ramus of the facial nerve is still partially exposed near the posterior half of the tensor tympani fossa in some individuals (AMNH 39442; F:AM 76160, 76163) and is fully covered by a thin layer of bone in others (FMNH UC495). In the single Chadronian specimen (F:AM 63942), the facial nerve is more exposed than in the Orellan individuals, following the general tendency toward a better ossified tegmen tympani in later taxa. The course of the nerve is stable among carnivorans—passing dorsolaterally around the fenestra vestibuli and emerging from the middle ear region via the stylo-mastoid foramen.

Mitchell and Tedford (1973) noted the presence of a small suprameatal fossa in *Hesperocyon*. This fossa is only at an incipient stage of development, and is far from reaching the size or varied locations it does in musteloids (Schmidt-Kittler, 1981). As in *M. parvivorus*, the tip of the mastoid tubercle is composed of the petrosal rather than the squamosal as in *Vulpavus*.

INTERNAL CAROTID ARTERY (fig. 2D): There is little doubt as to the course of the internal carotid artery in *Hesperocyon*, not only because of the clear presence of its canal preserved by the surrounding entotympanic, which is consistently observed in all individuals, but also because of the well-known anatomical details in living *Canis* of the gross anatomy of adults (Evans and Christensen, 1979), the osteology of neonatal individuals (Hunt, 1974), and the ontogenetic transformations of early embryonic stages (Wible, 1984).

From the internal view of the bulla, the position of the internal carotid artery is clearly marked by a prominent bony welt formed by the entotympanic. On specimens (F:AM 76163, 129176) that are fortuitously broken, this crest can be seen as a column of matrix surrounded by the petrosal dorsomedially and the entotympanic ventrolaterally. This column is the endocast of the internal carotid artery, and can be traced in its entire course along the medial wall of the bulla.

In most specimens, the posterior entrance of the internal carotid canal is at the same

level as, or slightly ventral to, the caudal entotympanic/basioccipital suture. A small, short groove on the external bullar surface is usually seen ventral to the posterior lacerate foramen. The posterior opening of the internal carotid canal is thus visible from outside of the bulla. This is slightly different from the condition in most canids in which the internal carotid artery first enters into a common recess for the posterior lacerate foramen and the internal carotid canal, then turns anteriorly into the internal carotid canal; therefore, no posterior carotid foramen can be seen on an unbroken specimen. The more ventral entrance of the internal carotid artery in *Hesperocyon* may represent the morphotypic condition for Caniformia. From this primitive condition, two directions of change may occur. In more derived canids, the posterior entrance of the internal carotid canal moves dorsally into the recess for posterior lacerate foramen. In arctoids, however, the entrance moves ventrally and anteriorly and becomes an opening on the bullar wall anterior to the posterior lacerate foramen.

After entering the carotid canal, the internal carotid artery follows the contour of the ventral surface of the petrosal, i.e., turning dorsally slightly and then maintaining a rather straight course forward. Within the confinement of the internal carotid canal, the artery turns medially toward the lateral margin of basisphenoid at a level slightly anterior to the middle lacerate foramen. It then immediately turns posteriorly when contacting the basisphenoid, and finally enters the middle lacerate foramen. This tight U-turn is clearly imprinted on the surrounding basisphenoid, which exhibits a tightly coiled sulcus (fig. 6). Such a landmark is a bony signature that is often correlated with a medially positioned internal carotid artery.

The peculiar looped-back internal carotid artery occurs in living *Canis* (e.g., Evans and Christensen, 1979: figs. 11–16). This loop can now be similarly traced in *Hesperocyon*. There is, however, an important distinction between living canids and their archaic relatives. The actual looping occurs in an extrabullar fashion in *Canis*, i.e., the internal carotid artery emerges from the anterior tip of the bulla through the anterior carotid foramen and then turns back immediately to

enter the brain cavity through the middle lacerate foramen. In contrast, this loop occurs within the contact zone between the entotympanic and basisphenoid in *Hesperocyon*. This is also reflected in the relatively small, anteriorly restricted “carotid foramen” of *Hesperocyon*, which is much smaller in diameter than the adjacent Eustachian canal. Not only is it impossible for this small opening to accommodate the volume of a doubled artery, the “bottleneck” will not even permit the passage of a single internal carotid artery with its original volume. In comparison, the opening of the anterior carotid foramen in *Canis* is enlarged relative to the thickness of internal carotid canal and is larger than the nearby Eustachian canal. Consequently, the thickened lateral wall of the basisphenoid in *Canis* is free of any marks left by the internal carotid artery because the artery is not even in contact with the basisphenoid in this region. A sheet of entotympanic bone separates the artery from such contact.

In *Hesperocyon*, the short segment of the canal formed by the basisphenoid and the entotympanic just anterior to the loop of the internal carotid artery is the site of union of the internal carotid and the slender ascending pharyngeal arteries (fig. 2D). In living *Canis* the latter branches off the internal carotid artery *outside* (anterior to) the bulla (Evans and Christensen, 1979: figs. 11–16). This intracanal condition of the ascending pharyngeal artery in *Hesperocyon* suggests that the ascending pharyngeal canal in *Hesperocyon* (as dictated by the enclosed vessel) is converted to house the looped internal carotid artery in *Canis*.

Wible (1984: 124) documented the disappearance of the stapedia artery early in the ontogeny of *Canis familiaris*. The proximal stapedia artery gives rise to the inferior and superior rami after penetrating through the stapes at the 14.5-mm stage. This vessel is reduced in calibre by the 17-mm stage, and completely degenerated by the 25-mm stage. At this stage, the internal carotid artery becomes extrabullar because of the newly formed ossification center of the caudal entotympanic lateral to the artery. The adult *Hesperocyon* has apparently reached this same stage of middle-ear arterial circulation as in living *Canis*.

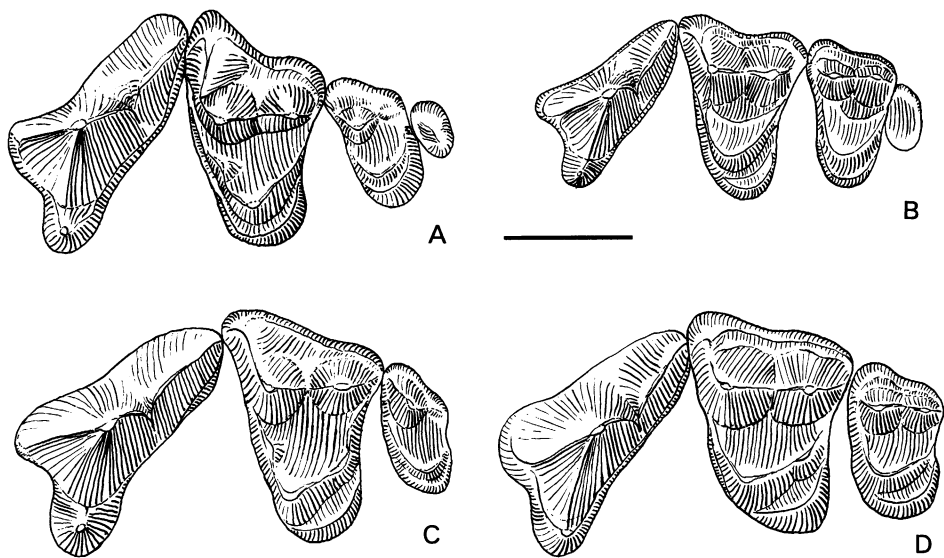


Fig. 7. Upper P4-M2 (or M3) of *Miacis* and *Hesperocyon*. A, "*M.*" *gracilis*, CMNH 12063; B, "*M.*" *cognitus*, TMM 40209-200; C, "*H.*" *wilsoni*, TMM 40504-126; D, *H. gregarius*, F:AM 63930. Scale = 5 mm.

CHARACTER ANALYSIS

Basicranial characters as well as dental characters were incorporated in the following analysis (character numbers correspond to those in the character matrix in table 1). Polarities were determined by outgroup comparison. The primitive feliform viverravids, commonly considered the sistergroup of miacids, are here used as the primary outgroup. Recent study by Hunt and Tedford (1993), however, suggests that the caniform-feliform (i.e., miacid-viverravid) dichotomy may be traced as far back as the Cretaceous *Cimolestes*, and considerable independent evolution may thus have occurred within the two separate lineages by the time of their first appearances in the fossil record. More problematic is the supposed ancestral status of creodont to the carnivorans, despite its popularity as a hypothetical ancestor among carnivore systematists (Flynn et al., 1988; Wozencraft, 1989; Wyss and Flynn, 1993). In cases of polarity conflicts, we use the Creodonta as the next outgroup outside the Carnivora. Based on these polarity assessments, the basicranium of *Vulpavus* is quite close to a primitive morphotype of the Caniformia, even though its quadrate upper molars and the low

trigonids of lower molars clearly indicate specialized tendencies toward hypocarnivory (i.e., "cercoleptoid" omnivores of Matthew, 1909). In most instances, the presumed plesiomorphic conditions in *Vulpavus* are consistent with such primitive viverravids as *Protictis*.

1. REDUCTION OF PARASTYLE ON P4: Caniforms have a reduced parastyle on the P4 in

TABLE 1
Character Matrix for Selected Miacids and Primitive Canids

Numbers of characters correspond to those listed under Character Analysis. Question marks represent missing data. See text for discussions of polarities.

	11111111
characters:	12345678901234567
taxa:	
Outgroup	0000000000000000
<i>Vulpavus</i>	110000000000?1000
<i>Miacis parvivorus</i>	111111000000?0000
" <i>Miacis</i> " <i>sylvestris</i>	112111111000?0000
" <i>Miacis</i> " <i>cognitus</i>	112111100010?1?00
" <i>Miacis</i> " <i>gracilis</i>	11?11?1111?0?0001
" <i>Hesperocyon</i> " <i>wilsoni</i>	12211111111100001
<i>Hesperocyon gregarius</i>	12211111111111100
<i>Daphoenus</i>	112111100010?1010

contrast to the primitive retention of such a parastyle in feliforms (Flynn et al., 1988).

Polarity: 1(0), presence of a well-developed parastyle on P4; 1(1), reduction or absence of the parastyle.

2. LINGUAL CINGULAE ON UPPER MOLARS: Presence of a complete lingual cingulum to be continuous with the pre- and postcingulum of the upper molars is apomorphic for the Caniformia (Flynn et al., 1988). Reduction of anterior segment of the internal cingulum of M1 and enlargement of its posterior segment, resulting in an asymmetrical arrangement of internal cingulum, are characteristic of early hesperocyonine canids. In most individuals of *Hesperocyon*, the anterior segment is completely lost, leaving a peculiar, posteriorly swung appearance of the internal cingulum (fig. 7C, D); the protocone is consequently exposed anteriorly.

Polarity: 2(0), absence of a complete lingual cingulum; 2(1), presence of a complete lingual cingulum on upper molars; 2(2), reduction or loss of anterior segment of internal cingulum.

3. CLOSURE OF PIRIFORM FENESTRA AND OSSIFICATION OF TEGMEN TYMPANI: Primitively the piriform fenestra opens widely and the tegmen tympani is poorly ossified, i.e., lacks an ossified floor for the facial nerve. In canids, the piriform fenestra is closed except for a small promontory foramen, and the tegmen tympani is fully ossified, i.e., the facial nerve becomes fully enclosed in the tensor tympani region.

Polarity: 3(0), wide open space for a piriform fenestra between petrosal and alisphenoid/squamosal, facial nerve exposed ventrally; 3(1), narrowing of the piriform fenestra, facial nerve partially embedded within tegmen tympani and floored in anteromedial segment; (2), complete closure of the piriform fenestra leaving only a small promontory foramen, facial nerve beneath a bony sheath which defines the fossa for tensor tympani muscle.

4. CONTACT OF PROMONTORIUM AND BASIOCCIPITAL: Primitively, the promontorium is separated from the basioccipital on the medial side. The free space between the promontorium and basioccipital is partially closed in *Miacis parvivorus* and further fused in all canids. Although it may be apparent

that a globular (Character 9) and isolated (Character 4) promontorium is primitive for caniform carnivorans, this is not so evident if feliform miacoids are taken into consideration. For example, the Tiffanian *Protictis* and Bridgerian *Viverravus* (both members of the Viverravidae) have flat promontoria, which are medially expanded to be in full contact with the basioccipital (Gingerich and Winkler, 1985; Matthew, 1909). The primitive condition for Carnivora remains to be settled. Among taxa examined here, however, an isolated, globular promontorium is primitive.

Polarity: 4(0), promontorium isolated; 4(1), promontorium in contact with basioccipital.

5. REDUCTION OR LOSS OF M3: The nearly universal absence of M3 in living carnivorans (except in isolated cases of secondary acquisition of three molars, e.g., *Otocyon*) was a convenient synapomorphy for Carnivora in Wozencraft's phylogeny (1989). This character is similarly used by Wyss and Flynn (1993) in support of their hypothesis that Miacidae (the contents of which were not explicitly stated) lies outside of a Viverravidae + Carnivora clade. Loss of the posterior molars is a repeated trend throughout the history of the Carnivora, especially among various hypercarnivorous lineages which minimize grinding (molars) and maximize shearing (carnassials) dentitions. Data in fossil samples are often sufficiently dense to show gradual reduction and loss of the last molars. In the case of canids, it is likely that the M3 was lost within the canid clade, as suggested by the occasional presence of M3 in Chadronian *H. gregarius* (Wang, MS). We did not further divide the reduction of M3 into multiple character states as would be desirable to aid in the resolution of different lineages of miacids; this will have to wait for more detailed analysis of the group.

Polarity: 5(0), presence of a relatively large M3; 5(1), reduction and loss of M3.

6. COMPOSITION OF MASTOID TUBERCLE: Flynn and Galiano (1982: 19) suggested that a mastoid tubercle (= process hyoideus, attachment for the cartilaginous tympanohyoid) composed of the squamosal may be a synapomorphy for Carnivora. The mastoid tubercle is composed of the squamosal in *Vulpavus* but is made up of the petrosal in

the remaining taxa examined in this study (fig. 2).

Polarity: 6(0), mastoid tubercle formed by squamosal; 6(1), mastoid tubercle formed by petrosal.

7. ANTERIOR LOOP OF INTERNAL CAROTID ARTERY: In derived miacids ("*Miacis*" *sylvestris* and "*M.*" *cognitus*), canids, and amphicyonids, the internal carotid artery makes an anterior loop before entering the brain cavity through the middle lacerate foramen, in contrast to a direct entry without this loop as in *Vulpavus* and *Miacis parvivorus*. The derived condition is readily recognized in fossils by a sigmoid or oval fossa on the tympanic wing of the basisphenoid. In living *Canis*, the loop becomes extrabullar in position.

Polarity: 7(0), lack of an anterior loop of the internal carotid artery; 7(1), presence of the loop.

8. SUPRAMEATAL FOSSA: A small suprameatal fossa is found in *H. gregarius* and "*H.*" *wilsoni*. The only canid that has a well-developed suprameatal fossa is "*Cynodesmus*" *cooki* Macdonald, which is an extremely aberrant borophagine. A small fossa is present in the primitive ursid *Cephalogale*, in addition to its well-known occurrences in musteloids (Schmidt-Kittler, 1981), but it is lost in the amphicyonids.

Polarity: 8(0), absence of a suprameatal fossa; 8(1), presence of a small suprameatal fossa.

9. SHAPE OF PROMONTORIUM: In *Vulpavus* and *Miacis parvivorus*, the promontorium is globular. From this primitive condition, the canid promontorium becomes flattened; whereas the amphicyonids appear to have retained the primitive condition.

Polarity: 9(0), promontorium globular; 9(1), promontorium flattened.

10. POSTERIOR ACCESSORY CUSPS ON PREMOLARS: In primitive canids (most hesperocyonines and borophagines), a posterior accessory cusp is present on the P3 and p3 in addition to the anterior and posterior cingular cusps. This is in contrast to many miacids that have a posterior accessory cusp only on the p4 and no accessory cusps present on the upper premolars (e.g., *M. parvivorus*, "*M.*" *cognitus*). "*M.*" *gracilis* possessed the advanced condition as in *Hesperocyon*.

Polarity: 10(0), absence of posterior acces-

sory cusps on P3 or p3; 10(1), presence of posterior accessory cusp on these premolars.

11. POSITION OF INTERNAL CAROTID ARTERY: Presence of a promontory artery lying along a groove on the ventral surface of the promontorium and a stapedia artery penetrating the stapes is a widespread condition among mammals (e.g., MacPhee, 1981; Novacek, 1986). Ontogenetic evidence suggests that this may be the derived state among eutherians (Wible, 1983). The taxa in the present study suggest that the transpromontorial position of the internal carotid artery (promontory and stapedia arteries) is primitive for caniform carnivorans (e.g., *Vulpavus profectus*, *Miacis parvivorus*, "*M.*" *sylvestris*). This view is further strengthened by similar arterial configurations in some living feliform families (Hunt, 1977), in the archaic feliform *Protictis schaffi* (Gingerich and Winkler, 1985) and *Viverravus* (Matthew, 1909), and possibly in nimravids (Neff, 1983; Bryant, 1991; but see Hunt, 1987, and Flynn et al., 1988, for an alternative view). This primitive intrabullar condition contrasts with the extrabullar state of canids, in which the internal carotid artery travels within a bony canal between the caudal entotympanic ventrally and the petrosal/rostral entotympanic dorsally (Hough, 1948; Hunt, 1974; Tedford, 1976).

Flynn et al. (1988: 77) stated that "all living carnivorans are derived in the lack of a stapedia artery," because of the absence or weak development of a groove leading toward the fenestra vestibuli. In caniform carnivorans, the primitive condition is likely the presence of a proximal stapedia artery (Wang and Tedford, 1991). In *Miacis parvivorus* and "*M.*" *sylvestris*, not only is there a clear groove on the promontorium for a stapedia artery, there is also a corresponding foramen near the posterior part of the epitympanic recess for the exit of the superior ramus of the stapedia artery (the presence of a wide Glasierian fissure may also indicate the presence of a inferior ramus of the stapedia artery). These latter structures are found in *Vulpavus profectus* except for the lack of a clear groove leading to the fenestra vestibuli.

Wible (1984: 119) described an ontogenetic sequence for the transformation of the cranial artery systems in *Canis familiaris* that is similar to the phylogenetic series in the

present study. The internal carotid artery displays an "indifferent position" early in ontogeny. During late-fetal to neonatal stages, the artery shifts to an extrabullar position because of the appearance of the caudal entotympanic forming the ventral lateral border of the internal carotid artery. Finally, in postnatal stages, the artery becomes trapped within the canal formed by the expanding caudal and rostral entotympanic.

Polarity: 11(0), internal carotid artery laterally positioned, transpromontorial, presence of a promontory artery and stapedia artery, as well as superior and inferior rami of the stapedia artery; 11(1), internal carotid artery medially positioned, extrabullar, inside a bony canal formed by the caudal entotympanic and the petrosal/rostral entotympanic, stapedia artery lost.

12. OSSIFICATION OF ENTOTYMPANIC BULLA: An ossified entotympanic bulla is unknown in available miacid skulls. Beginning with "*Hesperocyon*" *wilsoni*, a fully ossified bulla is present. Its degree of inflation, which is comparable to that of *H. gregarius*, suggests significant contribution from the entotympanic. In *H. gregarius*, the ossified bulla clearly consists of ecto- and entotympanic elements as confirmed by the presence of a low septum inside the bulla.

Flynn et al. (1988: 100) noted the negative aspect of the character "bulla ossification," i.e., miacoids may have had an ossified bulla although none are preserved. Recent cladistic analysis by Wozencraft (1989) on living families postulated a unique synapomorphy of an ossified bulla for all extant carnivorans except *Nandinia*. A similar conclusion was reached by Wyss and Flynn (1993), who reasoned that the possibility still exists that an ossified entotympanic may eventually be found in miacoids. In their data matrix, however, Viverravidae and Miacidae are still coded as lacking an ossified bulla, thus lending support to their phylogeny which excludes these fossil families from the Carnivora. Perhaps more radical is their suggestion that the cartilaginous caudal entotympanic in *Nandinia*, and the lack of an ossified entotympanic in primitive amphicyonids, may be secondarily derived from a primitively fully ossified condition. In any case, this would

still leave the attachment of an ossified bulla to the basicranium (strong enough to be preserved in fossils) as a derived condition, and the known distribution of this condition continues to be a useful character to diagnose advanced caniforms.

Polarity: 12(0), absence of an ossified entotympanic bulla; 12(1), presence of an ossified entotympanic bulla.

13. LOW ENTOTYMPANIC SEPTUM IN BULLA: Generally considered to be nonhomologous with the bilaminar, complete septum of felids, hyaenids, and viverrids, in which both the ectotympanic and caudal entotympanic contribute to the septum (Hunt, 1974); the low, incomplete septum of canids is here inferred to derive from the caudal entotympanic only. The low septum tends to be formed around all edges of the caudal entotympanic in *Hesperocyon* and primitive hesperocyonines (sensu Wang, MS), but is restricted to the anteromedial corner of the bulla in derived hesperocyonines and in living canids (fig. 5).

Polarity: 13(0), absence of a low septum; 13(1), presence of a low septum.

14. SIZE OF PARASTYLE OF M1-M2: Presence of a long, transversely oriented parastyle on M1-M2 is primitive for all miacoids (fig. 7A). Accompanying this large parastyle is the more medially placed paracone so that the metacone has a more lateral position relative to the paracone. In *Hesperocyon* (fig. 7D) and more so in later canids, the parastyles of the upper molars are reduced to a labial cingulum, sometimes swelling slightly and the labial cusps lie in tandem. The condition in "*H.*" *wilsoni* is only slightly advanced toward the canid type (fig. 7C). On the other hand, "*Miacis*" *cognitus* (fig. 7B), *Daphoenus*, and other amphicyonids have a very reduced parastyle and side-by-side paracone and metacone much like that of *Hesperocyon*.

Polarity: 14(0), large, ridgelike parastyle of M1-M2; 14(1), reduced parastyle.

15. SIZE OF METACONID ON M2: In *Hesperocyon* and most early canids the metaconid of m2 is nearly equal to or larger than the protoconid, in contrast to the more dominant protoconids in all *Miacis* and in "*H.*" *wilsoni*. Although shown as an autapomorphy under the Phylogeny (below), this character is syn-

apomorphous for the Canidae (excluding "*H.*" *wilsoni*).

Polarity: 15(0), protoconid of m2 larger than metaconid; 15(1), protoconid subequal to metaconid.

16. INFERIOR PETROSAL SINUS: As demonstrated by Hunt (1977), amphicyonids are characterized by an enlarged embayment of the basioccipital, presumably to house a looped internal carotid artery within the inferior petrosal sinus as a counter current heat exchange mechanism as seen in living ursids. Such a large sinus is also found in primitive ursoids such as hemicyonines and amphiodontines (Tedford et al., in press).

Polarity: 16(0), inferior petrosal sinus small; 16(1), inferior petrosal sinus greatly enlarged.

17. RELATIVE SIZE OF METACONE TO PARACONE OF M2: The M2 metacone is about the same size as the paracone in *Hesperocyon* (fig. 7D), "*Miacis*" *cognitus* (fig. 7B), and later canids, whereas it is very reduced or nearly absent in "*M.*" *gracilis* (fig. 7A) and "*H.*" *wilsoni* (fig. 7C).

Polarity: 17(0), metacone of M2 subequal to paracone; 17(1), metacone much smaller than paracone.

Some of the basicranial characters described above may be correlated with one another. For example, the expansion and increased ossification of the petrosal may be linked to the closure of piriform fenestra (anterior expansion of the petrosal), the articulation of the petrosal with the basioccipital (lateral expansion of petrosal), and the ossification of the floor of facial nerve. Until the basicrania of a larger series of miacids are known, all of these are treated as individual characters in the present analysis. Merging of these characters does not affect the topology of the phylogeny.

In addition to above characters, some dental autapomorphies of *H. gregarius* and others useful for discussion within Canidae are not listed above, because they do not contribute to the resolution of phylogeny at this level of analysis. Other potentially useful characters are excluded from the present analysis primarily because of the paucity of materials. These include some soft anatomy or postcranial characters for the Caniformia

(Flynn et al., 1988), and some cursorial adaptations of the postcranial skeleton in *Hesperocyon* (Tedford, 1978; Wang, 1990) and in "*M.*" *gracilis* (Clark, 1939).

PHYLOGENY

One shortest tree (fig. 8) was found by the Hennig86 program (version 1.5, written by J. S. Farris), with a total length of 20 steps, a consistency index of 80, and a retention index of 82 (all calculated after the autapomorphies are removed). The character matrix is listed in table 1 and all characters are nonadditive.

That "*H.*" *wilsoni* is closest to *Hesperocyon* is supported by the present analysis (Characters 12 and 2), even though its teeth are still largely primitive. In addition to the external bullar morphology noted by Gustafson (1986), the anatomy inside the bulla further supports this relationship. The lack of a low septum in "*H.*" *wilsoni*, however, is interesting, with its two alternative implications: nonpreservation (lack of ossification) of a septum in "*H.*" *wilsoni*, or acquisition of a septum beginning in *H. gregarius*. The first possibility cannot be ruled out until more and better preserved bullae are found. The second, a canid septum independently derived from those of feliforms, is a tentative conclusion reached in this analysis.

The tree in figure 8 is in general agreement with Clark's (1939) contention of a close affinity between "*M.*" *gracilis* and *Hesperocyon*; support for such a relationship is based on the presence of a posterior accessory cusps on the third premolars (Character 10). As pointed out by Clark (1939), the postcranial skeleton of "*M.*" *gracilis* offers the best evidence for affinity with *Hesperocyon*. Increased cursoriality (elongated limbs and other associated structures) appears to be one of the key evolutionary innovations by canids (Wang, 1993), that contrast with the relatively stout, plantigrade limbs in most arcitoids. Within the limits of current knowledge, "*M.*" *gracilis* appears to be close to the base of the canid clade.

"*Miacis*" *sylvestris* is most interesting in its transitional characteristics of the basicran-

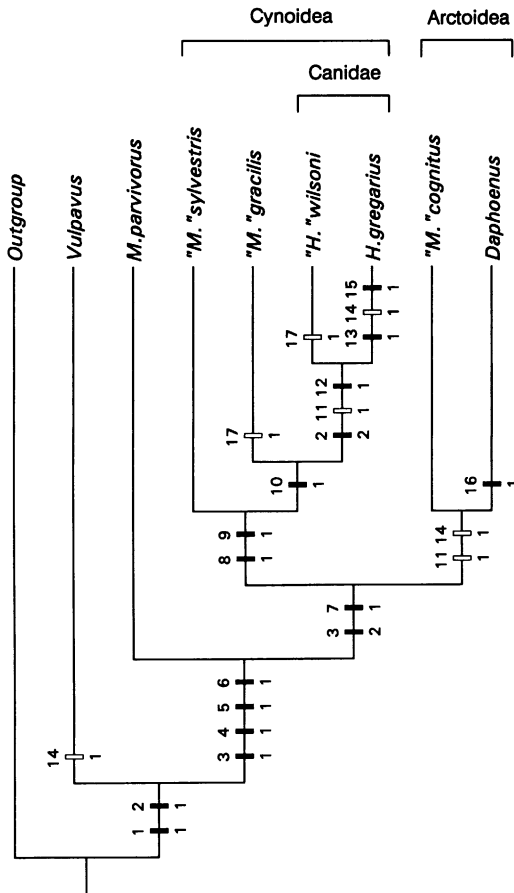


Fig. 8. A shortest tree found by the Hennig86 program (version 1.5) based on a 9 taxa by 18 character matrix in table 1. Tree statistics are (after removing the autapomorphies): tree length = 20 steps, consistency index = 80, retention index = 82. The program settings are: all characters are nonadditive to avoid preconceived assumptions of character transformations with multiple states; calculations of trees are in the ie (implicit enumeration) option, a search procedure certain to find all trees of minimal length. Solid bars represent unique synapomorphies; open bars represent homoplasies. Character numbers above the bars correspond to those listed in the Character Analysis section and table 1; numbers below the bars represent character states.

ium and its rather primitive teeth. Although still retaining a lateral (intrabullar) position of the internal carotid artery, it has a fossa to accommodate an anterior loop of the artery in front of the middle lacerate foramen,

a character most often associated with a medial position of the artery in advanced caniforms. "*M.*" *sylvestris* is here linked to the cynoid clade by its flattened promontorium (Character 9) and presence of a suprameatal fossa (Character 8).

We included the amphicyonids in the analysis to indicate a possible position of the arctoids within the present phylogenetic framework. We assumed that amphicyonids (here *Daphoenus*) represent a close approximation to the primitive arctoid morphotype as suggested in recent studies by Flynn et al. (1988) and Tedford et al. (in press). Basicranially, the amphicyonids retain the primitive conditions of a rather globular promontorium and the lack of a bulla. The position of the internal carotid artery is not certain; the lack of a transpromontorial groove on the promontorium suggests a medial position of the artery (in advanced amphicyonids which have ossified entotympanics, the artery is trapped in a bony tube within the entotympanic). In addition, the amphicyonids possess an enlarged basioccipital embayment (Character 16) for a presumed "ursid loop" of the internal carotid artery within the inferior petrosal sinus, a unique arterial cooling system found in living ursids (Hunt, 1977). Whether or not this character is present in "*Miacis*" *cognitus* will be a further test of the present phylogeny which links it to the amphicyonids. Dentally, primitive amphicyonids (e.g., *Daphoenus*) are little different from primitive canids (e.g., *Hesperocyon*); the fact that members of the Amphicyonidae were consistently included in the Family Canidae (e.g., Matthew, 1930; Simpson, 1945) further testifies to this primitive resemblance. However, one dental character presently recognized as a synapomorphy of the amphicyonid/arctoid clade (i.e., reduced parastyles of upper molars, Character 14) was independently acquired by canids.

With regard to the broader question of caniform phylogeny, the presence of a sulcus on the basisphenoid that is indicative of an anterior loop of the internal carotid artery (Character 7) seems to be a synapomorphy for the common ancestors of the Cynoidea and Arctoidea. The ossification of the tegmen tympani is another character [3(2)] that unites these two clades.

Given the current confusion surrounding the systematics of miacids, the present characterization of the genotypic species *Miacis parvivorus* serves by default as a morphotype for the paraphyletic family Miacidae. Among the miacids in the present study, *M. parvivorus* is too plesiomorphic to be included in any derived caniform family. Basicranially, it is more derived than *Vulpavus* in that it has a better ossified tegmen tympani [Character 3(1)] and there is a contact of the promontorium and basioccipital (Character 4). A mastoid tubercle (processus hyoideus) made up of the petrosal (Character 6) first appears in *M. parvivorus* and may be a synapomorphy at some level within the caniform clade [assuming the primitive condition is a squamosal process which occurs in *Viverravus*, *Vulpavus* and *Didymictis* (Flynn and Galiano, 1982)], although its distribution in various clades of carnivorans has yet to be clarified.

A partial classification that is consistent with the present phylogeny is indicated in figure 8. Most species of "*Miacis*" are obviously in need of generic reassessment, a task beyond the scope of this study.

PHYLOGENETIC HISTORY

If we regard the cladogram as a hypothesis of phylogeny, it bears clear implication of the historical relationships between the forms studied. It can be translated into a phylogenetic diagram by setting the temporal ranges of the taxa involved into a time scale (fig. 9). The cladistic relationships of the taxa can now be calibrated. The resulting hypothesis about the history of the group will embody predictions about the timing of cladogenetic events that can be tested as knowledge of the temporal ranges of the taxa involved improves and other sister taxa are recognized.

In this example the temporal ranges of the taxa are determined as follows: *Vulpavus* spp. has a generic range extending from its first appearance at the beginning of the Wasatchian (Kristalka et al., 1987) to its documented last record in Bridger B, early Bridgerian (Matthew, 1909). *Miacis parvivorus* is recorded only from Bridger B, early Bridgerian (Matthew, 1909). "*Miacis*" *sylvestris* occurs in Bridger C in the Bridger Basin (Matthew,

1909) and in the lower Adobe Town Member of the Washakie Formation equivalent to Bridger C-D (Turnbull, 1978) as recorded in this paper. "*Miacis*" *gracilis* has been identified only in the late Uintan (Uinta C, Clark, 1939). "*Hesperocyon*" *wilsoni* is known only from the Chadronian strata in the Sierra Vieja approximately 35–36 Ma (Emry et al. 1987). *Hesperocyon gregarius* (with its synonym *H. paterculus*, Wang, MS) occurs in early Chadronian strata (Emry, 1992) and the genus extends well into the Duchesnean (Bryant, 1992). "*Miacis*" *cognitus* is known only from early Chadronian rocks in the Sierra Vieja, approximately 36–37 Ma (Prothero and Swisher, 1992). *Daphoenus* spp. has been recorded within the Duchesnean (Bryant, 1992) and the generic range is here extended to the beginning of that age.

These data provide minimum ages for the initiation of the taxa considered in this paper, which in turn can be used to postulate minimum divergence dates for the clades recognized. The time of divergence of the Caniformia from other Carnivora (fig. 9A) is constrained by the range of *Vulpavus* whose first appearance in Holarctica is at the beginning of the Eocene (Savage and Russell, 1983). The divergence of the Cynoidea and Arctoidea from their sister taxon *Miacis parvivorus* (fig. 9B) occurred during the later Wasatchian as did the appearance of those superfamilies (fig. 9C), both events constrained by the early Bridgerian presence of the *Miacis* species involved. The late Bridgerian presence of *Miacis sylvestris* indicates initiation of the clade that includes the Cynoidea (fig. 9D) in the early Bridgerian close to 50 Ma. This is in agreement with DNA hybridization data compiled by Wayne et al. (1989) and calibrated by an estimate of 40 Ma for the divergence of modern caniform families. Our revised divergence estimate of the Canidae from "*Miacis gracilis*" (fig. 9E) in the Uintan at approximately 45 Ma is younger than the 50 Ma estimate for the origin of the family obtained by Wayne et al. (1989) but close to the 40 Ma estimate they adopted for the appearance of living carnivore families from previously available data. Although the record of the Arctoidea does not extend beyond the Duchesnean, its sister relationship with the Cynoidea and the temporal constraints

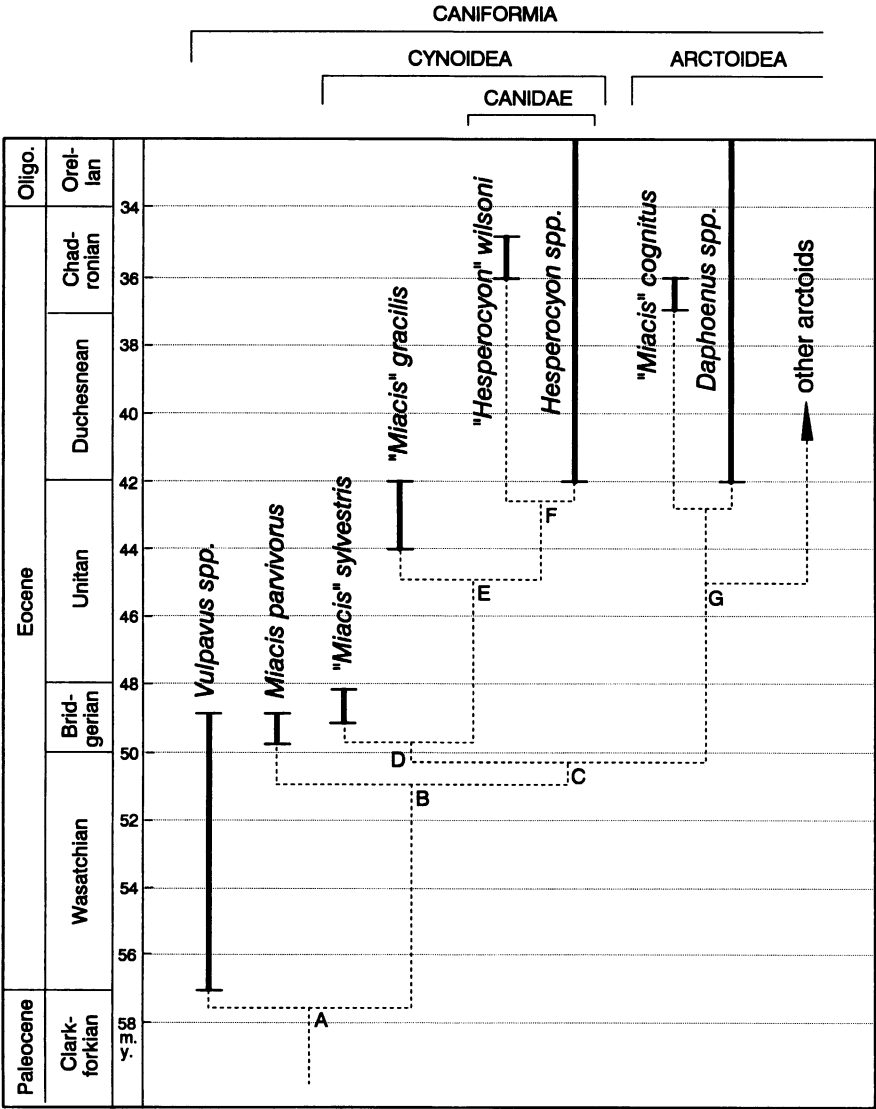


Fig. 9. Phylogenetic history of the Caniformia and related taxa obtained by calibrating the cladogram (fig. 8) using the known temporal ranges of the taxa studied. Lettered branch-points are explained in the text.

placed on the history of that group, predicts a Bridgerian and Uintan record during which time other arctoid families may have arisen (fig. 9G). This revised estimate places initial cynoid and arctoid differentiation in the late Wasatchian or early Bridgerian at about 50 Ma. The Canidae do not appear in this analysis to be markedly older than other living caniforms as claimed by Wayne et al. (1989).

CONCLUSIONS

This study was initiated to investigate the large gap in our knowledge between the known basicranium morphology of canids and those of the little known miacids. An attempt was made to arrange a series of miacids into a morphological sequence leading to the emergence of the well-known early canid, *Hesperocyon*. A number of trends may be sum-

marized along the transformation series from miacids to primitive canids:

1. Ossification of an entotympanic bulla. The nearly simultaneous (geologically speaking) occurrences of a completely ossified bulla in various families of carnivorans suggest the functional importance of a rigid middle ear space rather than the homology of this feature across the order Carnivora as recently proposed by Wyss and Flynn (1993), i.e., fossil evidence indicates independent appearance of a bony bulla in nimravids and amphicyonids, in addition to canids. The canid bulla, however, has a unique development of a low septum through the in-bent edge of caudal entotympanic, that is distinguished from the bilaminar septum in the bulla of the feliforms.

2. Anterior and medial expansion of the petrosal. The petrosal promontorium is transformed from a globular structure isolated from the surrounding bones (except the lateral side), to a flattened, pear-shaped structure in full contact with the adjacent basioccipital, basisphenoid, alisphenoid, and squamosal. Perhaps correlated with the petrosal expansion is the ossification of tegmen tympani, the flooring of the canal for facial nerve, and the closure of piriform fenestra.

3. Medial migration of the internal carotid artery and loss of the proximal stapedia artery. The promontory branch of the internal carotid artery in the primitive miacids shifts toward the medial side to become extrabullar in position and the primary carrier of arterial blood to the brain. The stapedia artery, on the other hand, is completely lost. This loss of the stapedia artery is often seen in medium to large-size mammals, presumably to avoid the physical constraint of a small obturator foramen of the stapes (Fleischer, 1978).

In addition to the above trends in the basicranium, canids can be distinguished from miacids by the better developed accessory cusps on the premolars, the reduction of the M1 parastyle, and the loss of the third upper molar.

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