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Evolution of the Aeluroid Carnivora: Viverrid Affinities of the Miocene Carnivoran *Herpestides*

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ABSTRACT

Although the time of origin of viverrid and hyaenid carnivorans has not been clearly documented in the fossil record, their theater of evolution has long been established by a mid-Cenozoic fossil distribution entirely confined to the Old World. Recent examination of the basicranial morphology of important early aeluroid crania from Europe and Asia significantly alters earlier views of viverrid and hyaenid origins. The early Miocene carnivoran *Herpestides antiquus*, considered a potential ancestral hyaenid or herpestid in earlier studies, is identified as a true viverrid on the basis of a large sample of skulls of both juveniles and adults from Aquitanian sediments of the Allier basin, France. The basicranial morphology of *Herpestides* has attained the modern

viverrid grade of development in the early Miocene (European Neogene mammal zone MN2a), and suggests that diversification of the Viverridae was in progress by this time. In ongoing work to be published elsewhere, the mid-Miocene Asian carnivoran *Tungurictis spocki*, long regarded as a viverrid, is identified as an early hyaenid, following preparation and restudy of the auditory region of the genoholotype cranium from Tung Gur, Mongolia. These discoveries indicate that separation of the modern aeluroid families as discrete lineages had been accomplished by the beginning of the Neogene in the Old World, and that diversification within these families must have been initiated in the early to mid-Miocene.

INTRODUCTION

Among the superb carnivoran fossils recovered from the Aquitanian deposits of the Allier basin, France, are abundant cranial and postcranial remains of a small civetlike aeluroid, originally described by Blainville (1842) under the name "*Viverra*" *antiqua*. As additional remains were discovered, they were placed by later European students (Pomel, 1853; Filhol, 1879; Schlosser, 1890; Virot, 1929) in several species allocated to the extant genus *Herpestes*. However, in a thorough, recent review of this material, Beaumont (1967) affirmed its distinctness from *Herpestes* and created the genus *Herpestides* for this Aquitanian carnivoran lineage, recognizing only a single species highly variable in size and dental morphology, *Herpestides antiquus* (Blainville).

Herpestides is the oldest Eurasian or African aeluroid carnivoran represented by numerous skulls with intact basicrania, including auditory bullae (fig. 1). A number of these fossil skulls retain osseous basicranial structure as well preserved as in the living animal, and both juveniles and adults are represented. My intent was to examine an adequate sample of the crania of *Herpestides* in order to determine its basicranial and bullar morphology; to discuss the ontogenetic pattern of bulla formation; and to attempt to establish the higher-level systematic relationships at the family level. In September 1989, I was given the opportunity to study the sample of

complete and partial crania of *Herpestides* at the Musée Guimet d'Histoire Naturelle in Lyon, and at the Naturhistorisches Museum, Basel, representing about 12 individuals, which forms the basis for this report.

I did not examine the question of the number of species attributable to *Herpestides* from the St.-Gérard region. It is sufficient to note that Beaumont (1967), who has studied the nature of dental variation in this carnivoran, determined that dental and cranial materials suggest a range of variation somewhat greater than that found in most living aeluroid species (fig. 2). The amount of variation in dental and cranial dimensions, however, is in keeping with geographically variable populations of a lineage sampled over a short interval of time, as pointed out by Beaumont. Significantly, the degree of variation observed in the dentition, both in terms of morphology and size, is not evident in the basicranial morphology, which displays a high degree of uniformity. Thus, regardless of the number of species of *Herpestides* finally determined from the Aquitanian sediments of the Allier basin, the fossils indicate a morphologically uniform, closely related assemblage referable to a single genus.

ACKNOWLEDGMENTS

I wish to express my appreciation to Dr. Michel Philippe for the numerous courtesies

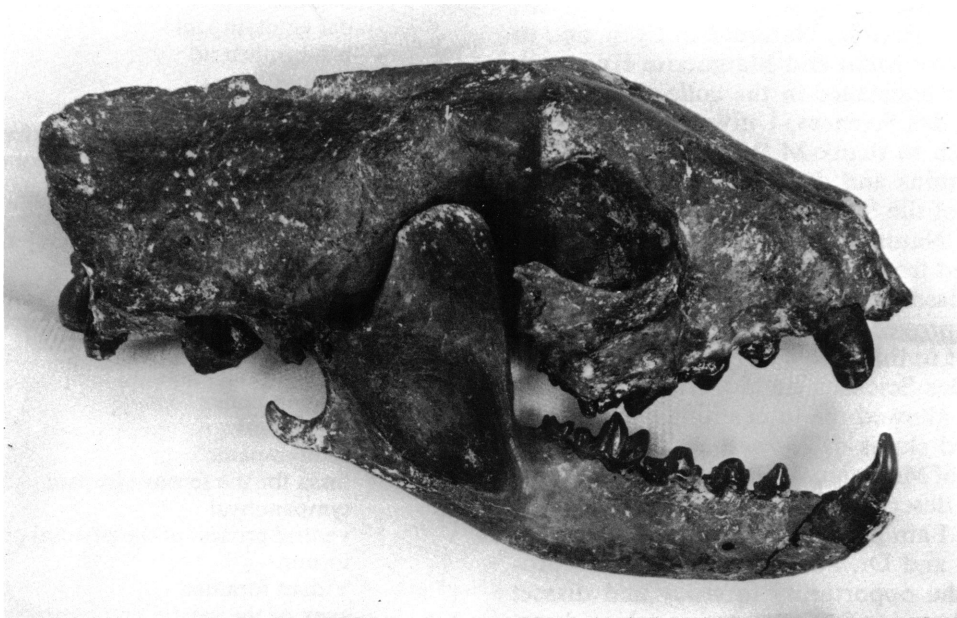


Fig. 1. Cranium and associated lower jaw of the viverrid *Herpestides antiquus* (Blainville), MGL St.-G. 3066, from the Aquitanian, Allier basin, France. Natural size.

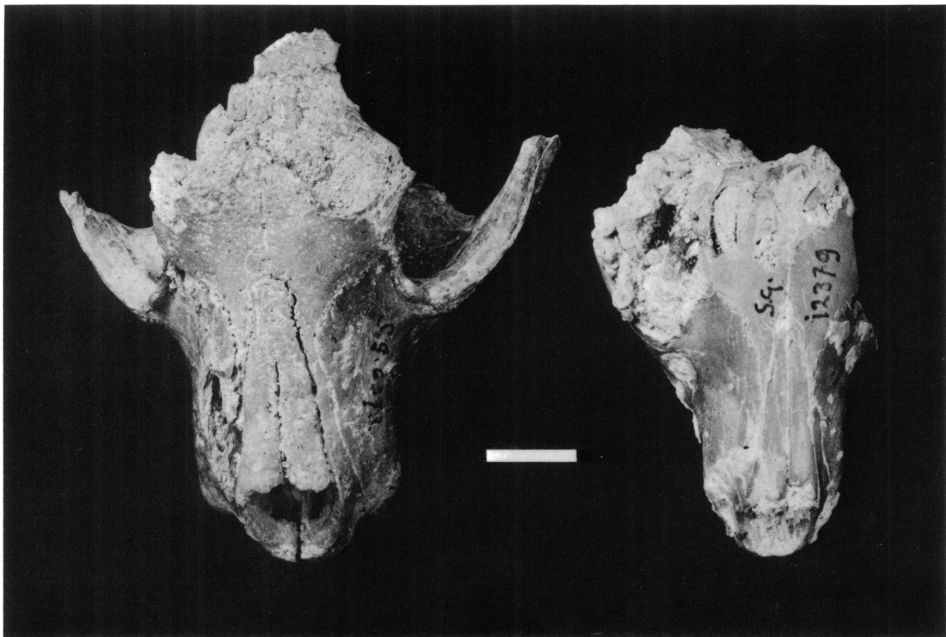


Fig. 2. Rostra of a large (left, NMB 6373) and a small (right, NMB 12379) individual of *Herpestides* from Montaigu-le-Blin, Allier basin, France, demonstrating the range in size attributed to *H. antiquus* by earlier workers. On dental traits, both are adults. Scale bar in this and all subsequent figures is 1 cm in length.

extended me during my research at the Musée Guimet d'Histoire Naturelle in Lyon, and to Drs. Pierre Mein and Marguerite Huguency for their assistance in the collections of the Faculté des Sciences, Université de Lyon. I also wish to thank M. Huguency for recent publications and discussion of the geologic setting of the St.-Gérard deposits. My work at the Naturhistorisches Museum, Basel, benefited from conversations with Dr. Burkart Engesser and Prof. Dr. Johannes Hürzeler that improved my comprehension of issues relevant to this study. M. Francois Escuillie, Dépt. des Sciences de la Terre, Lyon, generously allowed me to examine two recently collected skulls of *Herpestides* from the localities of Montaignu-le-Blin and Gepiac which he will describe in his work on these carnivorans. I am particularly grateful to Dr. Guy Musser and Dr. Patricia Freeman who provided the opportunity to study and dissect the basicrania of representative aeluroid carnivorans in collections in their care. Reference casts of basicrania used in this study were produced by Head Preparator Gregory Brown, University of Nebraska State Museum. My thanks to R. M. Joeckel, Harold Bryant, and Cliff Lemen for review of the manuscript.

ABBREVIATIONS

A	alisphenoid
a	epitympanic wing of alisphenoid
ac	alisphenoid canal
b	epitympanic wing of basisphenoid
BO	basioccipital
bof	basioccipital flange
BS	basisphenoid
c	canal for the facial (VII) nerve
Ca	pit in squamosal for anterior crus of ectotympanic
d	depression in alisphenoid for anterior limb of ectotympanic
EO	exoccipital
E	caudal entotympanic
e	epitympanic recess
ee	epitympanic wing of exoccipital
f	flange of septum bullae contacting promontorium anterior to round window
fo	foramen ovale
g	postglenoid foramen
h	hypoglossal (condyloid) foramen
ica	tube for internal carotid artery
L	middle lacerate foramen
M	mastoid process

m	depression in mastoid produced by caudal entotympanic
OS	orbitosphenoid
P	petrosal
p	epitympanic wing of petrosal
PC	groove in entotympanic for internal carotid artery, leading to posterior carotid foramen
plf	posterior lacerate foramen
Pp, pp	paroccipital process of exoccipital
PT	pterygoid
R	rostral entotympanic
rc	basioccipital attachment for rectus capitis ventralis
S	suprameatal fossa
sb	septum bullae
SQ	squamosal
T	ectotympanic
t	fossa for the tensor tympani
th	tympanohyal
V	ventral process of the petrosal promontorium
vf	Vidian foramen
x	apex of the caudal entotympanic fused to the posterior edge of rostral entotympanic

AMNH	American Museum of Natural History, Mammalogy
FSL	Faculté des Sciences, Université de Lyon, France
MGL	Musée Guimet d'Histoire Naturelle, Lyon, France
NMB	Naturhistorisches Museum, Basel, Switzerland
UNSM	University of Nebraska State Museum, Zoology

GEOLOGIC AND GEOGRAPHIC SETTING

The remains of *Herpestides* discussed herein were found in nonmarine early Miocene (Aquitanian) sediments of the St.-Gérard region, Limagne d'Allier, central France. The Limagnes are Cenozoic fault-bounded basins ("fosses d'effondrement") within the Massif Central of France that developed contemporaneously with Alpine tectonism. The Limagne d'Allier that contains the fossiliferous Aquitanian sediments of the St.-Gérard sub-basin is a complex graben fill of late Eocene to early Miocene age, dissected by the modern Allier River flowing northward from the Massif Central. Aquitanian sediments in the vicinity of St.-Gérard-le-Puy have been

commercially exploited for over a century for limestone, resulting in a network of quarries that produce the vertebrate fauna. The distribution of the principal localities in the region has recently been illustrated by Bucher, Ginsburg, and Cheneval (1985), and a map of the quarries in the St.-Gérard sub-basin near the villages of Montaigu-le-Blin, St.-Gérard, and Langy appears in Cheneval and Hugueney (1985).

Fossils of *Herpestides* that I have studied in the Museum at Lyon are simply attributed to "St.-Gérard," and lack a more specific locality designation. As is well known, fossils designated by the term "St.-Gérard" could have been found in any of the limestone quarries of the region (Viret, 1929; Cheneval and Hugueney, 1985). However, the crania from the Naturhistorisches Museum, Basel, are all attributed to Montaigu-le-Blin, with the year of collection appended. Today several active as well as inactive quarries occur near the village of Montaigu-le-Blin (Cheneval and Hugueney, 1985), but it is uncertain at which of these sites the crania were found. Recent studies of the Aquitanian sediments near Montaigu-le-Blin allow an improved understanding of their depositional environment (Bucher et al., 1985; Hugueney, 1984; Don-simoni and Giot, 1977).

The depositional setting of the vertebrate remains are described in a recent study of "Les Pérards" quarry near Montaigu-le-Blin by Bucher, Ginsburg, and Cheneval (1985), and my subsequent remarks are based on their illuminating publication and an excursion guide by Cheneval and Hugueney (1985). Depositional environments are primarily fluvio-lacustrine, and record the waxing and waning of local carbonate-rich lakes within the Allier basin. Terrestrial vertebrates (including viverrid carnivorans) occur in green marls with abundant shells of the pulmonate gastropod *Cepaea moroguesi* deposited between columnar lacustrine stromatolites (phryganid algal bioherms). These green marls lack internal stratification and have been interpreted as mudflows that swept littoral debris (including vertebrate bones) downslope onto the floor of these lakes, surrounding and influencing the growth pattern of the stromatolite community. Vertebrates within the green marls include both aquatic and terres-

trial reptiles and birds; there are abundant remains of diverse terrestrial mammals (didelphid marsupials; insectivores; bats, lagomorphs and rodents; viverrid, felid, and mustelid carnivorans; small artiodactyls).

Of particular interest is the occurrence of vertebrate bones in brown marls with hydrobids. These brown marls are similar to the green marls in that they also infiltrate between stromatolitic mounds, but in the brown marls the associated vertebrates are primarily aquatic (freshwater fishes and aquatic birds); mammals are represented only by abundant remains of viverrid carnivorans, a situation not understood at the present time. However, similar lack of diversity appears in contemporaneous fluvio-deltaic biocalcarene in which only partial skeletons of a single family of aquatic birds have been found. Such situations reflect local ecologic and taphonomic biases.

Vertebrate bones have been found within the stromatolites themselves, but are rare. In "Les Pérards" quarry near Montaigu, only aquatic vertebrates have been found within these structures.

Bentonites composed of montmorillonitic clay associated with these deposits indicate contemporaneous volcanism, but volcanogenic crystals for radiometric dating have not been recovered from the bentonites (Bucher et al., 1985).

Was *Herpestides* an aquatic carnivoran? How can the abundance of its remains be explained in these deposits? Its skeletal structure does not possess any evident specialization that might indicate restriction to an aquatic setting; the animal may have been a capable swimmer but this assumption is probably not necessary to account for its good representation in lacustrine sediments. Rather, the abundance of *Herpestides* suggests that it frequented lake margins, and its dental morphology and postcranial skeleton indicate that it was an active predator, probably taking small terrestrial and aquatic vertebrates living in these perilacustrine environments.

BASICRANIA OF *HERPESTIDES*

Complete or partial crania of 12 individuals were examined in the collections at Lyon

and Basel. Of these, four are represented by complete skulls (two with associated lower jaws), seven are posterior crania (only one with associated upper teeth), and one is the skull of a small individual lacking only the occiput. These fossils comprise the hypodigm under study and are listed and briefly described below:

(1) MGL St.-G. 3065. – Complete skull (basilar length, 89.6 mm) without lower jaws, but retains in the maxillae both right and left P3–4 and M1. This is the only skull in the MGL collection that preserves a complete and intact auditory bulla. The complete left bulla includes both ectotympanic and caudal entotympanic; the rostral entotympanic is not visible. The right bulla lacks only the ventral part of caudal entotympanic. Length of the complete bulla from the anteriormost part of ectotympanic to posterior limit of the caudal entotympanic is 19.4 mm (exclusive of the paroccipital process).

(2) MGL St.-G. 3066. – Complete skull (basilar length, 102.8 mm) associated with both lower jaws. Upper dentition includes right C, P2–4, M1–2; left C, P3–4, M1–2 (rarely does a maxilla retain M2). Lower dentition includes right c, p2–4, m1–2; left c, p3–4, m1. A well-preserved skull with intact basicranium, in which the auditory bullae lack only the ventral parts of the caudal entotympanics.

(3) MGL St.-G. 3067. – Posterior cranium, including part of the frontal region but lacking rostrum and dentition. The left auditory region (including the petrosal) and the occiput are missing; the petrosal and ectotympanic chamber of the right auditory region are preserved. Of interest because it represents the largest individual in the MGL sample (estimated basilar length, ~110 mm).

(4) MGL St.-G. 3068. – Juvenile posterior cranium (indicated by an open basisphenoid-basioccipital suture), without rostrum or dentition. Both auditory bullae are absent, suggesting that in juveniles ecto- and entotympanic elements are loosely attached to the basicranium. Both petrosals are present and well preserved.

(5) MGL St.-G. 2009. – Nearly complete skull (estimated basilar length, ~80 mm), lacking occiput and basicranium, representing a very small individual. Caution should be exercised in designating this specimen as one individual because, although the rostrum

has been attached to the posterior cranium with plaster, there is no certain contact between the two parts. The rostrum includes the left P3–4.

(6) FSL unnumbered. – Complete skull with basicranium and both auditory bullae intact, currently undergoing preparation and study by M. Escuillie, Université de Lyon.

(7) NMB S.G. 11583. – Posterior cranium, lacking rostrum and dentition. Basicranium with right and left auditory regions very well preserved. Auditory bullae are represented only by the right anterior ectotympanic and rostral entotympanic, and the left rostral entotympanic; caudal entotympanics on both sides are missing. Montaigu-le-Blin, 1921.

(8) NMB S.G. 12377. – Partial posterior cranium, with left auditory region only, but with most of bulla missing. Only a dorsal remnant of caudal entotympanic remains in place. Associated with left and right maxillae with P2–4 present on each side. Montaigu-le-Blin, 1921.

(9) NMB S.G. 6890. – Posterior cranium, lacking rostrum and dentition, but with both auditory regions preserved. Bullae are absent except for a small caudal entotympanic fragment on the right, and a detached ectotympanic. Montaigu-le-Blin, 1913.

(10) NMB S.G. 2935. – Posterior cranium, lacking rostrum and dentition, but with both auditory regions well preserved. Bullae are entirely lacking. A juvenile with open basisphenoid-basioccipital suture. Montaigu-le-Blin, 1913.

(11) NMB S.G. 7244. – Posterior cranium, lacking rostrum and dentition, and without the occiput. Both petrosals are present, but bullae are absent. A juvenile with open basisphenoid-basioccipital suture. Montaigu-le-Blin, 1932.

(12) NMB S.G. 11407. – Complete skull and associated lower jaws. Both auditory regions are present, but only the left auditory bulla is exposed. Skull somewhat crushed. Montaigu-le-Blin, 1920.

AUDITORY REGION OF *HERPESTIDES*

The sample of *Herpestides* crania from the St.-Gérard region represents an age spectrum from juveniles to mature adults (neonatal individuals are not present). The morphology of the auditory region can be determined at

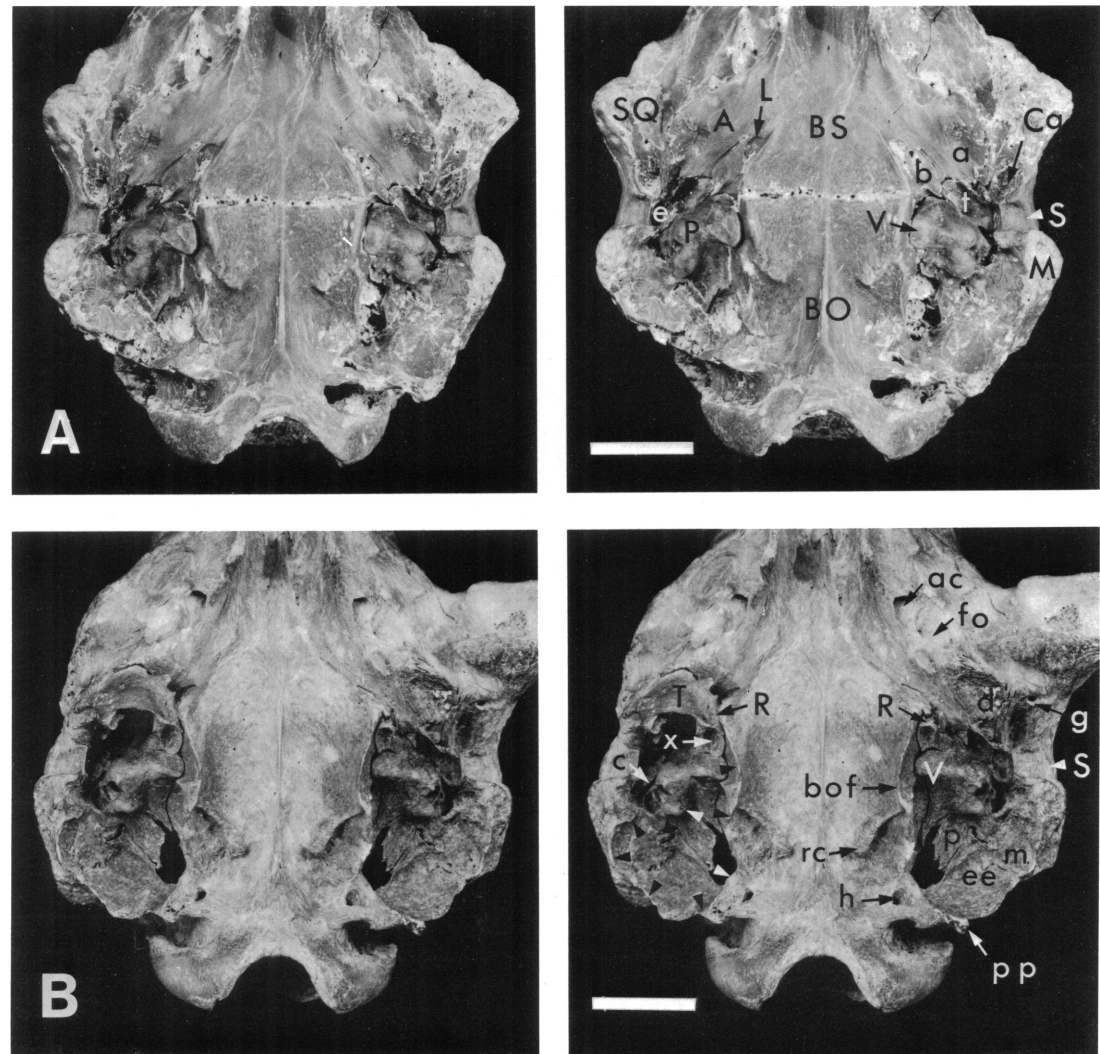


Fig. 3. Basicrania of *Herpestides* juvenile (A, NMB 2935) and adult (B, NMB 11583) from Montaigne-Blin in ventral view. In B, small triangles indicate the perimeter of attachment for the caudal entotympanic in the right posterior auditory region; both right and left caudal entotympanics have been removed from the basicranium. Note that in the adult (B) the ectotympanic and rostral entotympanic are not fused to surrounding bones, and the sutures between epitympanic elements forming the roof of the posterior auditory region remain open. For abbreviations in this and all subsequent figures, see p. 4. Stereopairs.

several ontogenetic stages by examining a series of these basicrania in which the auditory bullae range from complete, to broken open, to fully detached from the skull. As a result, the internal structure and geometry of the middle ear and the composition of the bulla can be studied in detail. Several skulls also possess intact auditory regions for which external basicranial morphology can be determined. In all respects, the auditory regions

observed in this sample of *Herpestides* crania demonstrate a morphology typical of extant Viverridae.

PETROSAL-MASTOID

In both juveniles (figs. 3A, 4A) and adults (figs. 3B, 4B) the petrosal displays a characteristic form most similar to that of living viverrid carnivorans such as *Civettictis civet-*

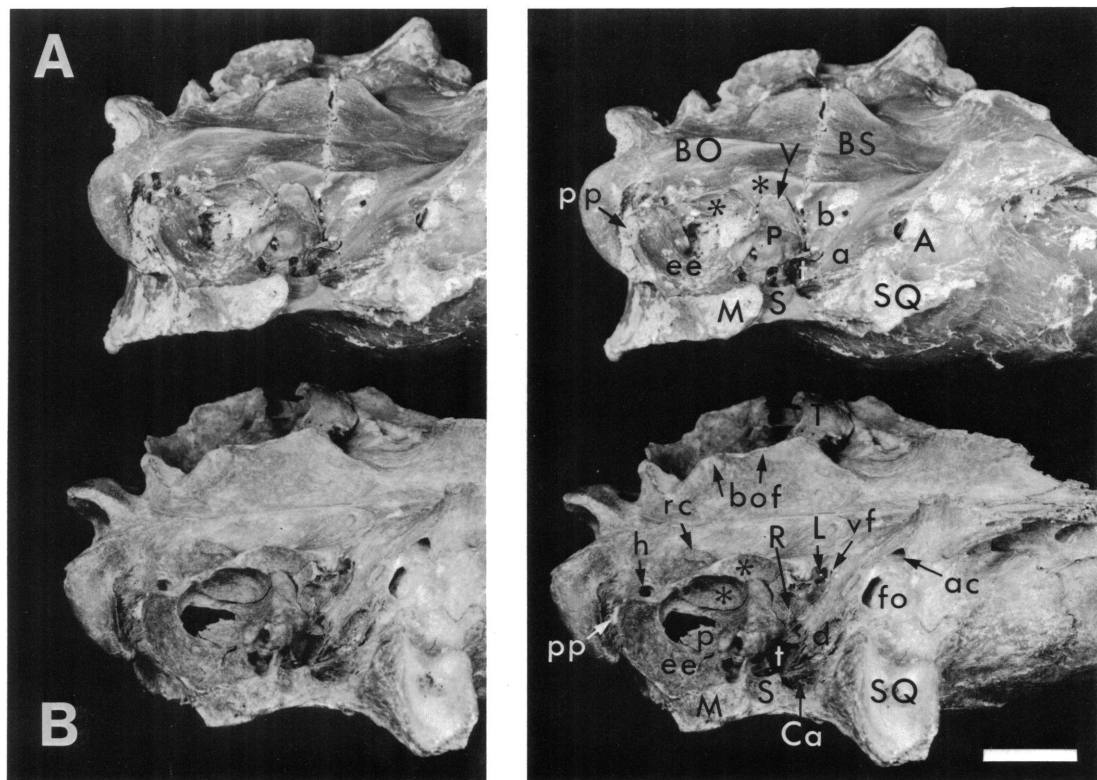


Fig. 4. Comparison of juvenile (A, NMB 2935) and adult (B, NMB 11583) auditory regions of *Herpestides* in ventrolateral view, same individuals as in figure 3, both from Montaigu-le-Blin. Note the basioccipital flange (bof) and the pocketing of the lateral part of basioccipital (asterisks) that develop in adults during ontogeny. Stereopairs.

ta. The structural geometry of the middle ear region, including the configuration of the bulla elements, is largely determined by a robust promontorium that forms a transverse ridge dividing the middle ear into anterior and posterior chambers. A prominent ventral process of the promontorium forms a medial extension of this ridge, buttressing the lateral face of the basioccipital immediately posterior to the basisphenoid-basioccipital suture (fig. 3A). This process is as well developed in *Herpestides* as in living aeluroid carnivorans, in which it is a key synapomorphy of the group (Hunt, 1989).

Both the anterior and posterior faces of the promontorium slope steeply dorsad away from the transverse ridge that forms the promontorial apex. On the anteromedial face of the promontorium rests an ossified rostral entotympanic element that contributes to the

bulla's medial wall. The posteromedial face of the promontorium is deeply impressed by an inflated caudal entotympanic element in juvenile and adult. Lateral to this pronounced indentation the promontorium bulges outward behind the round window as a knoblike rugose process. The posterior edge of the petrosal is prolonged as one or two thin sheetlike epitympanic processes of bone that contribute to the roof of the posterior chamber; the thin dorsal surface of the caudal entotympanic element is closely applied to these epitympanic processes.

The tegmen tympani is identified as a prominent bony shelf of the petrosal that extends anterior and lateral to the promontorium; its ventral surface bears a sharply demarcated tensor tympani fossa, epitympanic recess, and facial canal, described by Beaumont (1967). Whether the tegmen is in fact

a composite structure formed by both a true tegmen and by additional epitympanic processes of the petrosal, as described in some eutherians by MacPhee (1981), is unknown, but for descriptive purposes the entire shelf anterior as well as lateral to the promontorium is herein termed the tegmen. In juveniles, an unfused suture between the petrosal, sphenoid, and squamosal clearly defines the limits of the tegmen (fig. 3A). The anterior portion of the tegmen is deeply pocketed by a medially placed tensor tympani fossa and a laterally placed epitympanic recess. The petrosal-squamosal suture runs anteroposteriorly through the epitympanic recess, hence its lateral part lies in the squamosal and its medial portion in the tegmen. Posteromedial to the epitympanic recess the facial canal emerges dorsal to the oval window in the lateral portion of the tegmen; the nerve follows a groove in the petromastoid, turning laterad to exit the cranium via the stylomastoid foramen. A prominent fossa lies posteromedial to the facial canal and dorsolateral to the round window in the posterior part of the tegmen.

In several juveniles a suture between the mastoid and tegmen may be present (fig. 3A), as in certain living viverrids. In *Viverricula* and *Civettictis* there is a persistent suture between the lateral face of petrosal and what appears to be a fused squamosal-mastoid plate lateral to it. In herpestids, felids, and hyaenids a distinct mastoid is present that becomes attached to the petrosal in early development, the mastoid later fusing to squamosal. In viverrids, it seems probable that the squamosal-mastoid fusion occurs first, forming a squamous lamina that covers the petrosal without fusing to it.

SQUAMOSAL

In the basicranium the sutural boundaries of the squamosal are well defined, particularly in juveniles (fig. 3A). The basicranial portion of the squamosal posterior to the postglenoid process contributes the anterolateral part of the auditory region to which the ectotympanic crura are attached. On the posterior slope of this process near its base is a reduced postglenoid foramen which, although variable in diameter in different in-

dividuals, is always quite small, indicating a vestigial postglenoid vein. Posterodorsal to this foramen is a deep pit for insertion of the anterior crus of ectotympanic. Medial to the pit the squamosal is grooved by the Glaserian fissure for the chorda tympani branch of the facial nerve. The fissure is situated immediately lateral and parallel to the anteroposteriorly aligned alisphenoid-squamosal suture.

The squamosal forms the roof of the bony external auditory meatus directly posterior to the pit for the anterior crus of ectotympanic. In juveniles and adults the roof of the meatus is impressed by a deep suprimeatal fossa, as well developed as those observed in living procyonids, presumably incorporating a prominent pars flaccida of the tympanum. Dorsal to the suprimeatal fossa the medial face of the squamosal is pocketed by the epitympanic recess (there were no auditory ossicles preserved in any of the crania under study). The suprimeatal fossa is excavated entirely in the squamosal; its posterior wall is formed by the posttympanic process of the squamosal applied against the anterior face of the mastoid, the two bones uniting to form the mastoid process. The mastoid-squamosal suture must fuse early in ontogeny because, even in juveniles, a distinct sutural contact between the mastoid bone and the posttympanic process is difficult to identify, despite an open sutural contact between squamosal and tegmen.

ALISPHEOID-BASISPHEOID

The epitympanic wings of alisphenoid and basisphenoid contribute the roof of the auditory region anterior to the petrosal. In juveniles a visible basisphenoid-alisphenoid suture demonstrates that the basisphenoid wing completes the roof medial to the tensor tympani fossa and a somewhat larger alisphenoid wing is situated anterior to the fossa. The basisphenoid wing closes the anteromedial corner of the auditory region; the rostral entotympanic is applied against its lateral face, and it is perforated in its anterior part by the middle lacerate foramen for entrance of the internal carotid artery into the cranial cavity. The pterygoid (Vidian) canal for the Vidian nerve (made up of the greater super-

ficial and deep petrosal nerves) can be seen as a narrow channel on the surface of the basisphenoid wing (fig. 4B).

The ectotympanic's anterior part indents the epitympanic wing of alisphenoid, forming a prominent elliptical depression in adults. The size, depth, and orientation of impressions in alisphenoid and squamosal made by the anterior face of ectotympanic and the tip of its anterior crus, respectively, provide important information on the configuration of the anterior bulla chamber in a variety of fossil carnivorans in which the ectotympanic has been lost from the skull.

The basisphenoid-basioccipital suture is open in juveniles and young adults, and is fused in mature animals (compare fig. 3A, B).

BASIOCCIPITAL-EXOCCIPITAL

The basioccipital buttresses the greater part of the medial wall of the auditory bulla, whereas the exoccipital supports its posterior wall. During ontogeny in *Herpestides*, these two bones are significantly modified to a greater degree than any other basicranial bones bordering the auditory region. This modification results from progressive ontogenetic growth and encroachment of the caudal entotympanic on the basi- and exoccipital.

Figures 3 and 4 indicate the extent of this modification during bulla growth. In the juvenile (figs. 3A, 4A) the lateral edge of basioccipital is not produced, but in the adult (figs. 3B, 4B) this edge is greatly extended ventrad, and the rugosities on the basioccipital's ventral surface for attachment of the rectus capitis ventralis muscles are much more developed. When seen in lateral view (fig. 4), the edge of basioccipital that borders the middle ear cavity can be divided into an anterior part in direct association with the ventral promontorial process of the petrosal, and a posterior part behind this process. In the juvenile (fig. 4A), the anterior and posterior parts are not deeply indented by the caudal entotympanic, nor is the edge of basioccipital strongly extended ventrad. However, in the adult (fig. 4B), the anterior part is indented by the forwardly growing apex of caudal entotympanic; the posterior part shows a prom-

inent elliptical depression for a medial expansion of caudal entotympanic into basioccipital; and the edge of the basioccipital is ventrally extended to buttress the enlarging caudal entotympanic chamber. There is no epitympanic wing of the basioccipital; instead the basioccipital is entirely involved in supporting the medial wall of the bulla, and in consequence its lateral margin becomes modified by contact with the growing caudal entotympanic element.

Similarly, the exoccipital is also in contact with the expanding caudal entotympanic and becomes modified in shape during the process of ontogenetic growth. The exoccipital forms the posterior wall of the auditory region, extending ventrad as the paroccipital process (fig. 3). This posterior wall becomes thinned and tightly appressed against the rapidly inflating caudal entotympanic chamber of the bulla. The expansion of caudal entotympanic is so pervasive that the adjacent mastoid bone becomes impressed and slightly displaced by caudal entotympanic growth. Furthermore, the exoccipital develops an epitympanic wing that extends dorsal to the caudal entotympanic and fills in the roof of the posterior chamber. This epitympanic wing retains an open sutural contact with the mastoid and with the posterior epitympanic wing of the petrosal, even in adults (fig. 3B).

ROSTRAL ENTOTYMPANIC

The rostral entotympanic in adults (figs. 3B, 4B) is situated in the anterointernal corner of the auditory region, where it forms a small wedge of bone between the anterior face of the petrosal promontorium and the epitympanic wing of the basisphenoid. Approximately triangular in lateral view, its apex is directed dorsad toward the tensor tympani fossa. Its anterior edge fits against the basisphenoid where a small ridge separates it from the pterygoid canal, and its posterior edge is applied to the petrosal. The ventral margin of rostral entotympanic is in contact and fused to the ectotympanic and caudal entotympanic (fig. 4B), but even in adults it does not fuse to either petrosal or basisphenoid; these sutures remain open. The medial edge of the ectotympanic contacts and fuses to the ven-

tral edge of rostral entotympanic (thictic state, Hunt, 1987). The anterior apex of the forward-growing caudal entotympanic element contacts and fuses to the posteroventral corner of rostral entotympanic (fig. 4B). The ventral margin of rostral entotympanic is exposed on the bulla surface and can be recognized even after it has fused with ectotympanic (fig. 3B).

The anteroventral corner of rostral entotympanic borders on the middle lacerate foramen. The foramen is entirely within the basisphenoid and transmits the internal carotid artery to the cranial cavity. Directly in front of the middle lacerate foramen is a tiny Vidian foramen for the nerves of the pterygoid (Vidian) canal.

ECTOTYMPANIC

Relations of the chambered ectotympanic are demonstrated in figures 3B, 5A, B. In figure 3B the posterior half of the right ectotympanic in an adult is missing, thus it is possible to observe the relation of the anterior crus and limb of ectotympanic where they contact squamosal and alisphenoid bones. Note the inflated volume of the anterior chamber of the auditory bulla formed by ectotympanic, in contact with the small rostral entotympanic and petrosal, and the location of the suprameatal fossa outside the tympanic cavity proper. The crista tympanica is slightly inclined inward from the parasagittal plane, indicating the near-vertical orientation of the tympanum. The crista is in direct linear continuity with the medial edge of the suprameatal fossa, thus the fossa is properly situated to receive the pars flaccida of the tympanum.

The medial rim of ectotympanic is in contact with and fused to the rostral entotympanic (thictic condition, Hunt, 1987). The external auditory meatus of the ectotympanic is not laterally prolonged as a bony tube, thus it conforms to the pattern found in living viverrids, and differs from that in most herpestids and hyaenids in which a bony meatal tube develops.

The complete ectotympanic bone (fig. 5) is known in two large individuals with basilar skull lengths of ~10–11 cm. In figure 5A the

ectotympanic is shown in relationship to the petrosal, the entire caudal entotympanic having been removed. In figure 5B the ectotympanic appears in relation to the dorsal part of the caudal entotympanic (and the petrosal).

Note in figure 5A the relatively inflated or expanded ectotympanic with robust anterior crus seated in the squamosal, and a more gracile posterior crus resting on the posttympanic process of the squamosal. Internal to the tip of the posterior crus the triangular end of the tympanohyal can be seen entering the auditory region where it fuses with the crista parotica of the petrosal. Closure of the posterolateral wall of the ectotympanic chamber is accomplished by a prominent septum bullae. The bilaminar nature of the septum formed by both ectotympanic and caudal entotympanic contributions is evident in figure 5A where a thin entotympanic was applied to the ectotympanic surface.

The dorsal edge of the septum bullae is produced into a flange that rests on the ventral surface of the petrosal promontorium. The thickened flange makes a strong promontorial contact (fig. 5B) that produces a facet on the surface of the petrosal immediately anterior to the round window. The linear contact of the septum with the promontorium is an aeluroid trait (Hunt, 1989), and is the result of the spatial relationship of the ectotympanic's posterior limb to the promontorium in early ontogeny (see subsequent discussion).

The close apposition of ectotympanic and petrosal, together with the fusion of ectotympanic to rostral entotympanic, segregate an anterior chamber of the auditory bulla from a posterior chamber formed by caudal entotympanic. The relative volume and dimensions of the two chambers are illustrated in the adult of figure 5B. By analogy with living viverrids of nearly identical bulla configuration, the posterior chamber of the *Herpestides* bulla grew forward into the anterointernal corner of the auditory region (fig. 5B), migrating along the medial wall of the ectotympanic, and thereby extended the length of the septum bullae cranially. This pattern of ontogenetic growth, in which caudal entotympanic penetrates into the anterointernal

corner of the auditory region, is typical of viverrids and felids, not hyaenids or herpestids.

CAUDAL ENTOTYMPANIC

The caudal entotympanic gradually enlarges during ontogeny to produce a voluminous posterior chamber of the auditory bulla (figs. 5B, 6). This process of growth and remodeling causes the caudal entotympanic to impinge upon and indent the adjacent surfaces of the basioccipital, exoccipital, mastoid, and petrosal. The floor and sidewalls of caudal entotympanic expand to form a large hypotympanic cavity. As growth progresses, the ventral process of the petrosal (V) becomes enclosed and hidden from view between the caudal entotympanic and basioccipital (fig. 5B), and hence is not visible in figure 6C (left auditory region).

The external form of the caudal entotympanic is typical of viverrids (fig. 6). The principal axis of inflation runs from the anteromedial to posterolateral surface in ventral view. The direction of ontogenetic growth is forward into the anterointernal corner of the auditory region (fig. 6A, C). It is particularly noteworthy that overgrowth of the ectotympanic by the caudal entotympanic takes place in the same manner as observed in living viverrids (fig. 6A, B). This degree of anterior penetration by caudal entotympanic, and its overgrowth of ectotympanic, is not observed in any herpestid or hyaenid. In hyaenids and herpestids the caudal entotympanic is restricted to the posterior part of the auditory region.

INTERNAL CAROTID ARTERY

The path of the internal carotid artery as it travels through the auditory region is fortuitously preserved in several *Herpestides* crania in which the bulla has been broken to reveal the internal anatomy of the middle ear cavity. In the adult (fig. 6A, C) the artery enters the auditory region behind the ventral process of the petrosal, immediately lateral to the prominent ridge on the basioccipital for attachment of the rectus capitis ventralis muscle. The artery passes between the lateral edge of basioccipital and the caudal entotympanic, and is enclosed in a conspicuous bony

tube formed by the caudal entotympanic element. It travels anterolaterad within the entotympanic tube, which opens on the ventral apex of the promontorium (figs. 5B, 6C). From this point the artery ascends the anterior face of the promontorium (the promontorium is slightly grooved), travels forward along the lateral face of rostral entotympanic, and then descends to enter the middle lacerate foramen in the basisphenoid (figs. 4B, 7B).

This U-shaped arterial course and its relationship to surrounding bullar and basicranial bones are typical of viverrids (fig. 7). In figure 7A the path of the internal carotid through the auditory region of the bush civet *Civettictis civetta* exemplifies the viverrid condition (Hunt, 1987, 1989). In *Herpestides antiquus* the artery follows the same course (fig. 7B), and manifests the same relationships to surrounding basicranial structures. This arterial pattern distinguishes *Herpestides* from living and fossil herpestids in which the internal carotid follows a straight anteroposterior course within the medial wall of the auditory bulla (perbullar course, Hunt, 1989: fig. 4). The herpestid character state is derived, a synapomorphy uniting the genera of that family. The construction of the petrosal, auditory bulla, and surrounding basicranial architecture in *Herpestides* thus differs from the basicranial morphology of living and fossil herpestids, but conforms closely to that of the Viverridae.

COMPARATIVE MORPHOLOGY OF THE AELUROID MIDDLE EAR

In order to adequately evaluate basicranial morphology in *Herpestides*, it is necessary to describe and analyze two particularly diagnostic attributes of the auditory region in the living aeluroid families: (a) the ontogeny of the auditory bulla, especially the relationship between ectotympanic and petrosal in early ontogeny, and (b) the stage of evolution of the ossicular chain, as demonstrated by the form and orientation of the auditory ossicles. In the first case, the relationship of ectotympanic to petrosal promontorium determines the geometry of the anterior bulla chamber, and also appears to influence the final structural relationship between caudal entotym-

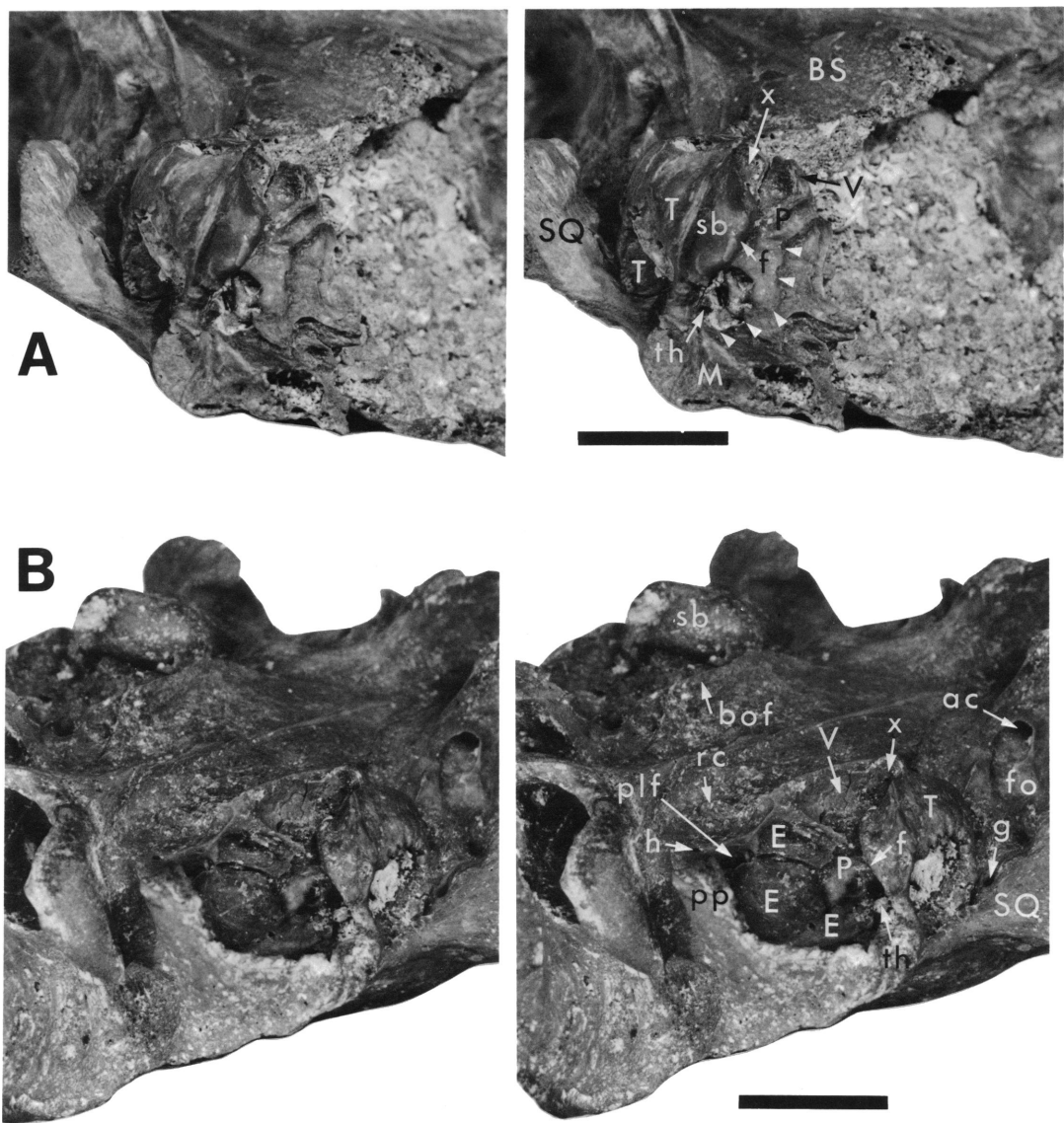


Fig. 5. Relationship of ectotympanic to petrosal in *Herpestides*: **A**, posterolateral view of right auditory region (MGL St.-G. 3067) of large individual; caudal entotympanic, basi- and exoccipital removed; white triangles indicate line of attachment of caudal entotympanic to petrosal and mastoid; **B**, posterolateral view of left auditory region (MGL St.-G. 3066, see also fig. 1) of another large individual in which the dorsal part of caudal entotympanic is in place. Note contact between the ectotympanic flange and the promontorium just anterior to the round window in both individuals; this contact produces a small characteristic facet on the promontorium. Stereopairs.

panic and ectotympanic. In the second, the morphology of the auditory ossicles of viverrids and felids reflects a more primitive stage of evolution than the ossicles of herpestids and hyaenids. As a result, the viverrid and

herpestid auditory patterns are sharply defined, and *Herpestides*, in its adult morphology and in what can be determined of its auditory ontogeny, is identifiable as a true viverrid.

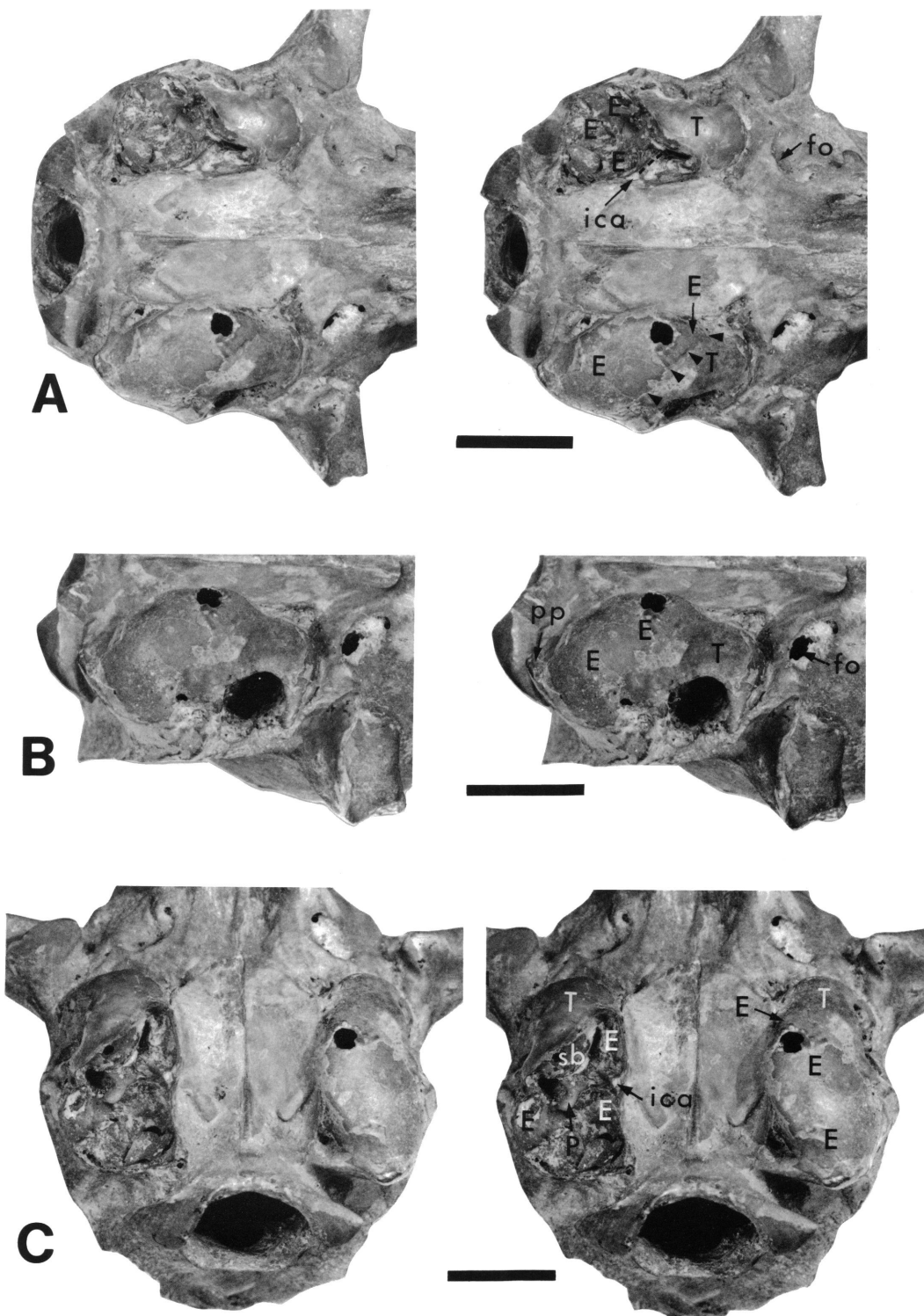


Fig. 6. The auditory bulla of *Herpestides* (MGL St.-G. 3065): **A**, high lateral oblique view of basicranium, showing intact left bulla (black triangles indicate the line of fusion between ectotympanic and caudal entotympanic), and broken right bulla opened to show internal structure of the posterior chamber, including course of internal carotid artery (dashed line) as it enters the middle ear; **B**, lateral view of auditory bulla showing inflation of caudal entotympanic relative to ectotympanic as in viverrids; **C**, posteroventral view of the basicranium, demonstrating penetration of caudal entotympanic into the anterointernal corner of the auditory region. Stereopairs.

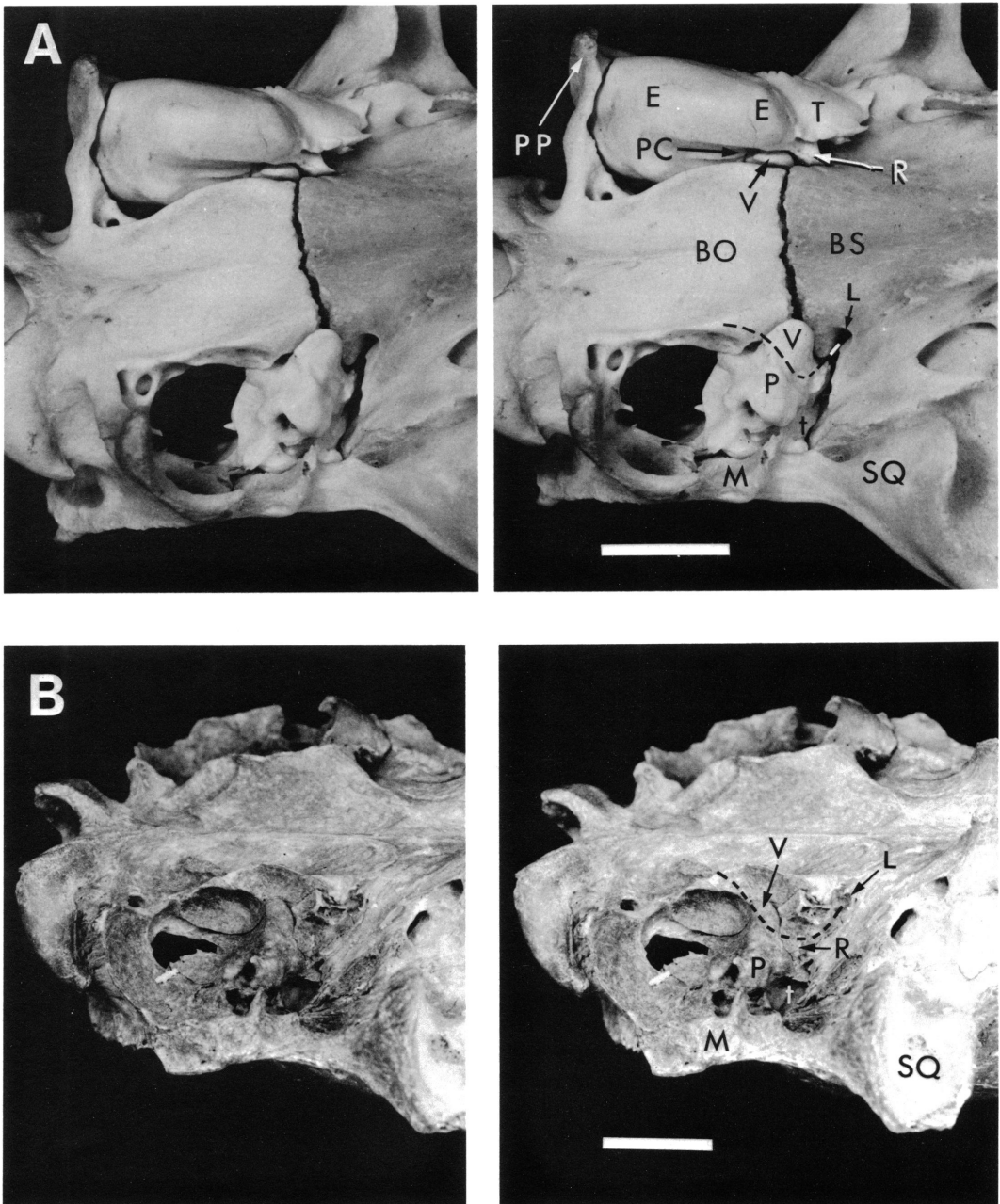


Fig. 7. Comparison of the auditory regions of (A) the viverrid *Civettictis civetta* (UNSM 14114), Kibwezi, Kenya, and (B) *Herpestides antiquus* (NMB 11583), Montagu-le-Blin, France. Dashed lines in A and B indicate the path of the internal carotid artery from its point of entrance into the auditory region until it enters the cranial cavity at the middle lacerate foramen. Stereopairs.

The course of ontogenetic development in the auditory region of aeluroids is perhaps best understood in terms of the different ontogenetic pathways adopted by viverrids and herpestids: I intend to describe a sequence of

early ontogenetic stages from a representative viverrid and herpestid in order to explore the developmental basis for these differences.

Because the felid pattern of bulla development is nearly identical to that of viver-

rids, and has been previously described at length (Hunt, 1974, 1987, 1989), I will not review it here. The pattern of felid bullar ontogeny differs from that of viverrids only in the more elaborate inflation of the caudal entotympanic and its diagnostic encroachment on surrounding basicranial bones. As part of this process, the felid caudal entotympanic penetrates into the anterointernal corner of the auditory region, inserting itself between ectotympanic and rostral entotympanic (bradyothitic state, Hunt, 1987); this insertion does not occur in viverrids. In the Aquitanian sediments of the Allier basin, both viverrid and felid patterns can be recognized. Comparison of these contemporaneous forms indicates that *Herpestides* is not an early felid.

Insight into the development of the hyaenid bulla and ossicular chain is limited by lack of knowledge of early ontogenetic stages. However, following discussion of viverrid and herpestid morphologies, I review what is known of the hyaenid auditory region, and argue that there is sufficient knowledge of hyaenid bulla and ossicular structure to confidently exclude *Herpestides* from the Hyaenidae.

BULLA ONTOGENY IN HERPESTIDAE

In an ontogenetic series of crania of *Herpestes* (*Xenogale*) *naso* from various localities in Zaire, a progression from an incipient stage of bulla formation to the fully formed adult bulla defines the herpestid pattern of development.

The earliest available ontogenetic stage is a skull (AMNH 51092, Niangara, Zaire) with basilar length of 30.9 mm in which the tips of the principal cusps of DP3–4 are just forming in the dental crypts, and the only ossified bulla element is the ectotympanic (fig. 8C). The ectotympanic crescent lies in the horizontal or frontal plane parallel to the basicranial axis. Its anterior and posterior crura are attached to the squamosal. The ventral edge of the squamosal between the two crura is bent inward as a lamina forming a floor for a large epitympanic recess. The recess contains the robust heads of malleus and incus (a deeply pocketed epitympanic recess within the squamosal is typical of herpestids). The anterior ectotympanic crus is anchored

to the edge of the squamosal, directly lateral to the gonial process of the malleus, whereas the posterior crus simply overlaps its lateral surface at the level of the posttympanic process of the squamosal.

Because the ectotympanic is essentially horizontal, its anterior limb is pressed against the roof of the tympanic cavity, which is formed by the epitympanic wings of basi- and alisphenoid. Its posterior limb is applied to the petrosal promontorium slightly posterior to the round window. At this stage, the posterior part of the tympanic cavity is closed by a sheet of connective tissue attached to the posterior margin of ectotympanic, and extending from that margin to the edges of the basioccipital, exoccipital, and mastoid bones.

The malleus and incus within the epitympanic recess are relatively large and already ossified, and the posterior process of the incus and anterior process of the malleus that jointly determine the axis of rotation are developed (the rotational axis of the carnivoran malleus-incus complex is a straight line drawn through the posterior process of the incus and the tip of the anterior process of the malleus). In this and all subsequent developmental stages, even in adults, a line drawn parallel to the manubrium of the malleus intersects the rotational axis of the malleus-incus at a high angle. Furthermore, the axis of ossicular rotation is nearly horizontal (here defined as a line parallel to the basicranial axis), and is not markedly inclined. The tensor tympani fossa at this stage remains open and has no bony floor.

In the next available stage of development, a skull (AMNH 51093, basilar length, 42.7 mm) from Faradje, Zaire, the DP3–4 crowns are fully formed and partially erupted, and the three separate bulla elements are present as unfused ossifications. The ectotympanic crescent has widened considerably, especially in its medial part, tilting the crescent (and eardrum) slightly laterad. Although the ectotympanic's posterior limb rests on the posterior slope of the promontorium, the promontorium remains largely within the circumference of the ectotympanic (hence within the bulla's anterior chamber). The rotational axis of the auditory ossicles does not alter its alignment, and remains nearly per-

pendicular to the manubrium of the malleus. At this stage the tensor tympani fossa now is largely encapsulated by bone, and the external auditory meatus between the ectotympanic crura has begun to close by progressive ossification of the rim of the aperture. Appressed against the posterior margin of ectotympanic and the posterior surface of the promontorium is a small caudal entotympanic chamber, only weakly ossified and slightly inflated, enclosing a volume that is perhaps half that of the anterior chamber.

At this early stage of development the entrance of the internal carotid artery into the middle ear cavity is already blocked by ossification of the bulla wall. Subsequently, the artery becomes isolated within a bony tube in the medial wall of the bulla (perbullar state, Hunt, 1987), a condition found in all living herpestids but in no other living aeluroids.

A slightly more advanced stage of auditory development (fig. 8B) is present in two skulls (AMNH 51609, basilar length, 46.1 mm; AMNH 51089, basilar length, 45.2 mm) from Medje, Zaire, in which DP3-4 are erupted to a somewhat greater degree than these same teeth in the 42.7 mm stage. The bulla shows the initiation of caudal entotympanic inflation, enlarging in ventral and medial directions, whereas the ectotympanic is about the same size. The amount of inclination of the ectotympanic crescent and eardrum remain the same, but closure of the external auditory meatus by bone has progressed, and this process continues during ontogeny until the meatal aperture is completely filled (or nearly so) by bone in the adult. This new bone forms a ventral floor below the eardrum. The rostral entotympanic has increased in size, following its initial appearance between the 30.9 and 42.7 mm stages discussed above.

Dissection of the bulla reveals a bilaminar septum bullae that will fuse into a single partition in the adult. The plane formed by the septum bullae at the juncture of ectotympanic and caudal entotympanic is somewhat posteriorly inclined (see Hunt, 1989: fig. 5). The caudal entotympanic chamber of the bulla is confined to the posterior part of the auditory region behind the promontorium and it remains so in the adult.

In adult herpestids the caudal entotympanic chamber continues to inflate relative

to the anterior chamber, however the direction of inflation is primarily ventrad, and the caudal entotympanic does not penetrate the anterior part of the auditory region as it does in viverrids and felids. In a number of herpestid species the ectotympanic crescent and eardrum remain nearly horizontal; in other species such as *Herpestes auropunctatus*, the ectotympanic plane rotates outward, but the pronounced anterolateral tilt found in viverrids (and felids) never occurs.

BULLA ONTOGENY IN VIVERRIDAE

Using an ontogenetic series of skulls of *Viverricula indica*, it is possible to examine equivalent stages of basicranial development in a typical viverrid (fig. 8A), and identify differences relative to herpestid ontogeny. At the earliest available stage, the skull (AMNH 59935, Hainan, China, basilar length 38.2 mm) shows the tips of DP3-4 cusps just forming in the alveolar crypts. The only ossified bulla element is the ectotympanic. The ectotympanic crescent does not lie in the horizontal (or frontal) plane parallel to the basicranial surface as in herpestids. The plane of the ectotympanic is tilted forward and outward (anterolaterad) relative to its orientation in herpestids, the result of displacement of the ectotympanic's posterior limb by ventral protrusion of an enlarged petrosal promontorium. Because the ectotympanic crescent is unable to fully surround the enlarged petrosal, its posterior limb is captured by the ventrally extended promontorium. This displacement causes the posterior limb to lie across the apex of the promontorium, slightly anterior to the round window. As a result, a substantial part of the promontorium lies behind the posterior limb, where it is covered by connective tissue forming the posterior wall of the tympanic cavity (in herpestids, more of the promontorium is enclosed by the ectotympanic). This connective tissue sheet is attached at the posterior margin of ectotympanic and extends to the mastoid and occipital bones just as in herpestids.

In a later developmental stage (AMNH 60065, Hainan, China, basilar length 51.8 mm) in which DP3-4 are formed but unerupted, the ectotympanic has been enlarged by the addition of bone to its medial margin,

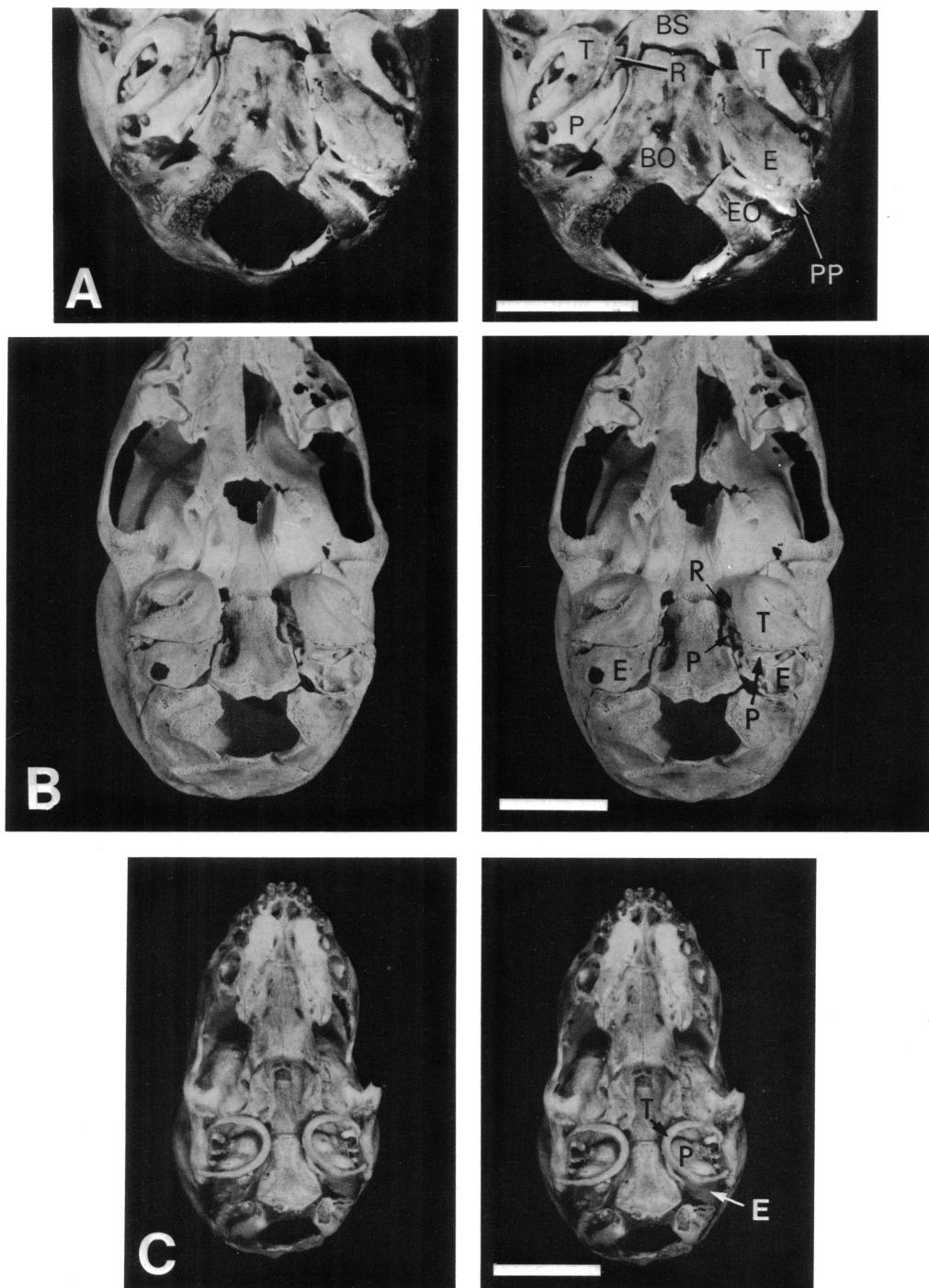


Fig. 8. Petrosal-ectotympanic relationship of a viverrid and herpestid in early ontogeny. A, Basicranium in ventral view of viverrid *Paradoxurus hermaphroditus* (AMNH 59933, female neonate, Hainan, China). The caudal entotympanic has been removed from the right auditory region to demonstrate the petrosal-ectotympanic relationship: note large amount of petrosal exposure posterior to ectotympanic (compare fig. 8B); B, Basicranium in ventral view of herpestid *Herpestes (Xenogale) naso* (AMNH 51609, male neonate, Medje, Zaire). The caudal entotympanic has been opened on the left side to show petrosal nearly completely overlapped by ectotympanic: there is almost no petrosal exposure posterior to ectotympanic (compare A); C, Basicranium in ventral view of herpestid *Herpestes (Xenogale) naso* (AMNH 51092, male neonate, Niangara, Zaire). The ectotympanic nearly encompasses the petrosal promontorium at this very early developmental stage in herpestids.

creating an anterior bulla chamber. A small but well-defined rostral entotympanic ossification has appeared on the anterior slope of the promontorium, and has made contact with the medial rim of ectotympanic by a narrow isthmus of bone. Ossification of caudal entotympanic has progressed about three-quarters of the distance from the rear of the bulla element toward the anterointernal corner, migrating along the tympanic membrane medial to ectotympanic. The ossification front is a smooth convex margin that has reached a point just anterior to the ventral process of the promontorium. In front of this margin (and posterior to the ectotympanic-rostral entotympanic complex), a small portion of the tympanic membrane remains unossified.

Two skulls (AMNH 45504, Fukien, China; AMNH 107605, Bali; basilar lengths about 52–54 mm), with DP3–4 nearly fully erupted, indicate a slightly later stage in which the three ossified bulla elements have joined, but fusion is only incipient, so that the boundaries of each element remain evident. There is no significant change in orientation or inflation of the ectotympanic or anterior chamber, and the posterior limb of ectotympanic remains in contact with the surface of the promontorium anterior to the round window. As a consequence, the posterior part of the enlarged promontorium containing the round window continues to protrude into the posterior chamber of the bulla (fig. 8A).

The caudal entotympanic has completed its anterior growth and is entirely ossified. Its rounded anterior margin has made contact and fused with rostral entotympanic and the medial edge of ectotympanic, and its degree of inflation is visibly greater than in the previous developmental stage. The application of caudal entotympanic to the posteromedial rim of ectotympanic has produced a bilaminar septum bullae about 1.5 mm in height.

In all developmental stages of *Viverricula indica*, the manubrium of the malleus is “bent forward” (strongly inclined anteromesad), placing the long axis of the manubrium at a very low angle relative to the rotational axis of the auditory ossicles (I refer to the inclination of the manubrium in the plane of the ossicular rotational axis in lateral view, not to medial deviation of the manubrium which can occur independently in mammals). This arrangement occurs in other viverrids and in felids, but contrasts with the herpestid con-

dition in which the long axis of the manubrium maintains a high angle ($>60^\circ$) relative to the rotational axis. This difference between the neonatal mallei of herpestids and viverrids persists in the adults, and its origin and explanation are of considerable interest.

We can determine that the “bent” viverrid manubrium does not result from the change in orientation of the ectotympanic during ontogeny because, in prenatal stages in which the ectotympanic lies nearly in the horizontal plane, the manubrium has already adopted its alignment relative to the rotational axis. In fact, the “bent” manubrium is plesiomorphic for aeluroids, and probably for Carnivora (see below); it is an attribute of the primitive therian malleus.

Furthermore, in viverrids the rotational axis of the malleus-incus complex is tilted slightly upward (i.e., the attachment of the incus to the posterior wall of the epitympanic recess is dorsal to the point of attachment of the anterior process of the malleus), deviating from the horizontal to a greater degree than the herpestid axis of rotation.

Felids display the same ectotympanic-caudal entotympanic growth pattern as viverrids during ontogeny, including displacement of the posterior limb of ectotympanic by an enlarged promontorium and, as a result, application of the posterior ectotympanic limb to the promontorium anterior to the round window (fig. 9). Felids and viverrids also share the “bent” orientation of the manubrium, and the slightly tilted ossicular rotational axis. In these aspects of bulla ontogeny, and ossicle form and orientation, the two families are extremely similar. These features were confirmed in an ontogenetic series of the domestic cat, and also in a comparable series of the African wild cat, *Felis silvestris*, and in juveniles and adults of almost all living felids.

BULLA ONTOGENY IN HYAENIDAE

The hyaenid auditory region is distinguished by a unique ontogenetic pattern of bulla development in which the ectotympanic contributes an enlarged anterior bulla chamber that extends backward, ventral to the more confined posterior chamber formed by caudal entotympanic (Hunt, 1974, 1987, 1989). The earliest known hyaenid basicrania from the mid-Miocene of Asia already have developed this bulla configuration (Qiu et al.,

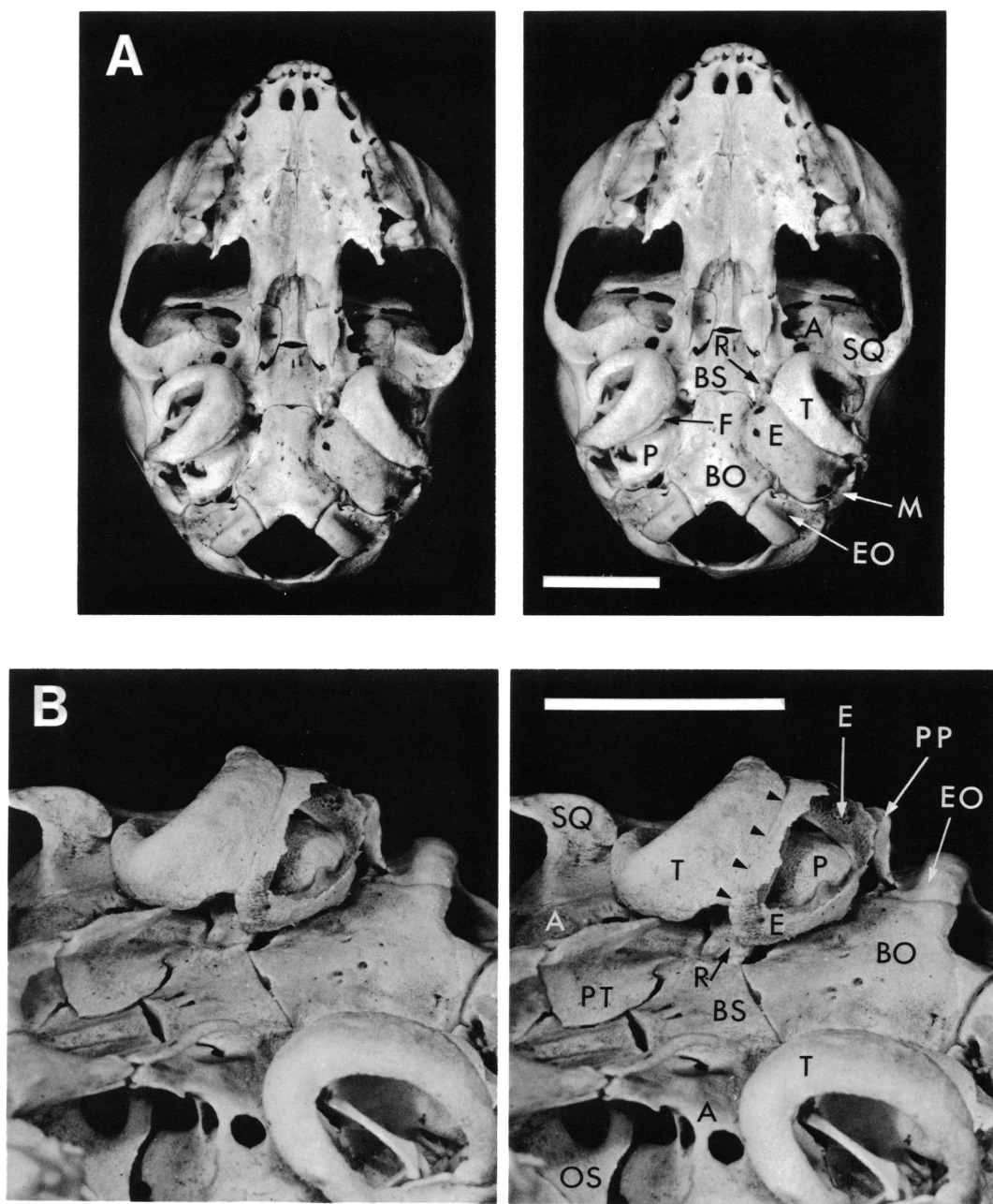


Fig. 9. Petrosal-ectotympanic relationship of a felid in early ontogeny. **A**, Basicranium in ventral view of newborn domestic cat *Felis*, demonstrating the large portion of the petrosal promontorium posterior to the ectotympanic, as in viverrids (compare fig. 8A); **B**, same specimen as A, medial view of auditory bulla, showing the considerable exposure of the promontorium posterior to the ectotympanic. Black triangles indicate ectotympanic-caudal entotympanic suture.

1988; Hunt, 1989). I know of no representative ontogenetic series of the hyaenid basicranium; however, the few juvenile stages of living hyaenids that have been studied dem-

onstrate that the fundamental hyaenid bulla pattern was already developed in the earliest ontogenetic stages presently identified (e.g., Hunt, 1974: fig. 35). It seems likely that the

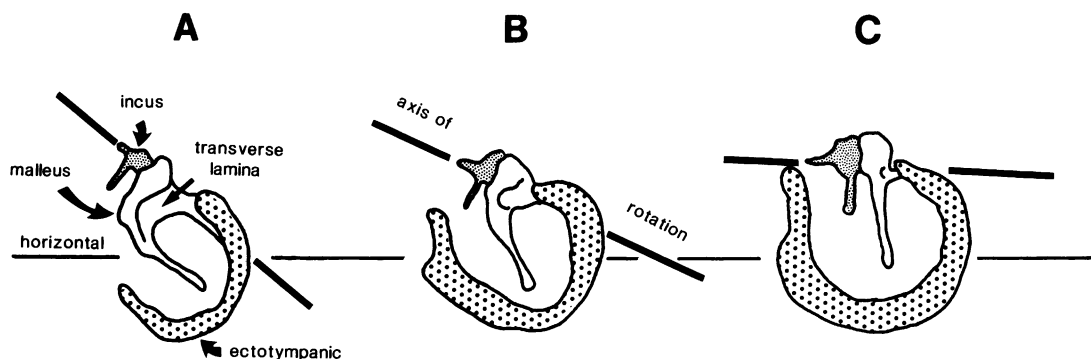


Fig. 10. Evolution of the malleus-incus complex in therian mammals: **A**, primitive therian; **B**, transitional stage; **C**, derived. Diagrams depict right ossicular complex in lateral view, dorsal to top, anterior to right. Key trends include change in inclination of rotational axis, reduction of malleal attachment to ectotympanic, reorientation of the manubrium, and relative size increase of the incus. Living aeluroid carnivorans belong to stages B and C.

hyaenid bulla ossifies in the neonatal animal in much the same configuration seen in young juveniles. Even in the aberrant hyaenid *Proteles*, the basic morphology of the hyaenid bulla can still be recognized, despite the failure of the anterior chamber to extend backward under the posterior chamber (Hunt, 1974).

Hyaenids share with viverrids and felids a "bent" manubrium and an inclined ossicular rotational axis. However, hyaenids and herpestids lack the prominent pocketed anterior lamina of the malleus found in viverrids and felids that connects the neck of the malleus with the anterior process. The anterior lamina of herpestids and hyaenids is strongly reduced.

AUDITORY OSSICLES IN AELUROIDS

OSSICULAR ORIENTATION IN MAMMALS

Ossicular patterns contribute an additional dimension to an understanding of auditory evolution in Carnivora. In living aeluroid carnivorans, morphology and orientation of the auditory ossicles are closely correlated with bulla morphology, particularly with ectotympanic placement. This information allows a reasonable prediction of the morphology and orientation of the auditory ossicles in *Herpestides antiquus*, and also supplies evidence for a hypothesis describing the evolution of the ossicular system in aeluroids.

Incorporation of the mammalian postden-

tary bones into the auditory region has been much better understood in recent years (Allin, 1975; Kermack and Mussett, 1983). The orientation and probable functional relations of the angular (ectotympanic), articular (malleus), quadrate (incus), and stapes in primitive therians have been determined both from fossils and from anatomical studies of living eutherians and metatherians. Fleischer (1973, 1978) has proposed a series of stages in the evolution of the auditory ossicles and ectotympanic that progresses from a primitive therian morphotype (Ausgangstyp) via a transitional arrangement (Übergangstyp) to a final derived condition in which the ossicles are freely mobile within the middle ear space (fig. 10). All these stages can be found among living therian mammals, and their functional and anatomical attributes have been the object of extensive investigation (Fleischer, 1978; Hunt and Korth, 1980).

From my observations of eutherians and metatherians, and those of Segall (1969, 1970, 1971), it is possible to identify three properties of the ossicular chain that change through time. Each of these properties seems to be able to evolve independently of the others:

(1) *Altered orientation of the rotational axis of malleus-incus.* — The plesiomorphic orientation of the ossicular rotational axis in early mammals is slightly tilted or inclined (fig. 10A), having an approximately antero-posterior alignment (Allin, 1975: pl. 3, fig. 10; Segall, 1969: fig. 1; Fleischer, 1973: fig.

58B). The axis passes forward and downward from the point at which the incus (quadrate) contacts the periotic bone, thence through the gonial process of the malleus (articular) along its line of attachment to the ectotympanic (angular). This primitive orientation of the ear ossicles is seen in marsupials such as *Didelphis* and *Caenolestes*, where the axis of rotation makes an angle of about 20 to 23° with the horizontal (Segall, 1969), and is also known in placentals with primitive ossicular configurations, where one finds similar amounts of axial inclination, ranging from about 20 to 42° (Segall, 1971). In living marsupials and placentals, the rotational axis either is maintained in an inclined orientation, or has transformed by rotation into a more horizontal alignment (fig. 10B, C). Thus an inclined axis of rotation reflects a more plesiomorphic ossicular alignment relative to derived states that approach or attain the horizontal.

(2) *Loss of malleal attachment to ectotympanic.* – The plesiomorphic mammalian ossicular chain (fig. 10A) incorporates a large U-shaped malleus (one leg formed by the manubrium, the other by the gonial process) firmly attached to the ectotympanic, and a relatively small incus (Allin, 1975: pl. 3, figs. 10, 11; Fleischer, 1978: figs. 1, 8). This type, or a close approximation, is known in living marsupials, monotremes, and placentals, and its ontogenetic development (for example, in certain marsupials) shows a clear correspondence to the postdentary bones of cynodont reptiles and early mammals (Kermack and Mussett, 1983). An ossicular chain of this kind exhibits considerable torsional stiffness due to the plesiomorphic bony fusion of malleus to ectotympanic. As the ossicular apparatus evolves from primitive (fig. 10A) to more advanced states (fig. 10B, C), the malleus often becomes more loosely attached to ectotympanic, and as a result the degree of stiffness is proportionately reduced. This looser attachment is achieved by reduction of the bony process anchoring the malleus to ectotympanic to either a ligamentous connection, or if osseous, one that is very thin and flexible (living aeluroid carnivorans all maintain a thin, flexible, bony attachment). Thus a primitive eutherian malleus will have a prominent gonial process firmly attached

to ectotympanic, and a well-developed transverse lamina (fig. 10A); both the process and the lamina become much reduced in derivative eutherian mallei (fig. 10B, C).

(3) *Realignment of the manubrium relative to the axis of rotation.* – Fleischer (1978) indicated that the long axis of the manubrium can alter its alignment relative to the rotational axis of the malleus-incus complex. In primitive therians the manubrium is generally aligned parallel to the rotational axis (fig. 10A). In many modern lineages with freely mobile ossicular chains, the long axis of the manubrium is nearly perpendicular to the rotational axis (fig. 10C), a derived character state in therian mammals.

Thus we can identify plesiomorphic and derived morphological states of the auditory ossicles involving orientation of the rotational axis, nature of the attachment of malleus to ectotympanic, and orientation of the manubrium. We can apply this knowledge to the ossicular morphology and orientation of the living aeluroids. As a result, we find that ossicular patterns are apparent at the family level, and that both plesiomorphic and derived conditions exist among aeluroids that can be used to constrain evolutionary hypotheses.

OSSICULAR ORIENTATION AND MORPHOLOGY IN AELUROIDS

Viverrids and felids have an ossicular orientation and geometry that reflect a transitional stage of ossicular development (fig. 10B). The axis of rotation is tilted forward and downward (fig. 11C, D), inclined 25 to 30° from the horizontal (determined as a line drawn parallel to the basicranial axis). Thus the viverrid-felid alignment approximates the axial orientation found in a living therian such as *Didelphis*. The manubrium is oriented at an angle of about 15 to 25° relative to the ossicular rotational axis (fig. 12C, D), hence similar to primitive manubrial alignments that parallel this axis, and unlike derived manubria that lie nearly perpendicular to the axis.

The malleus of viverrids and felids is firmly yet delicately attached by thin, flexible bone to the ectotympanic in both neonates and adults. The lamina of the malleus is well de-

veloped, and its lateral face is characteristically pocketed (fig. 12C, D); viverrids and felids preserve this plesiomorphic configuration of the lamina, whereas the lamina is strongly reduced or lost in herpestids and hyaenids (figs. 12A, B). The pocketed lamina is a vestige of the well-developed transverse lamina of the malleus found in primitive therians (fig. 10A).

Alignment and morphology of the ossicles in viverrids and felids thus appear to differ from a primitive eutherian ossicular pattern (fig. 13) only in (a) reduction of the gonial process of the malleus to produce a more flexible bony attachment (the anterior process, fig. 12C, D) of malleus to ectotympanic; (b) a slightly greater deviation of the long axis of the manubrium from the axis of ossicular rotation; (c) size increase of incus relative to malleus. There also may have been a small (but uncertain) amount of declination of the rotational axis toward the horizontal, based on the supposition that the primitive therian axis was more steeply inclined, but there is no reason why the present inclination in viverrids and felids might not closely approximate the primitive state for carnivorans.

Herpestids on the other hand have an ossicular arrangement similar to the freely mobile type of Fleischer (fig. 10C). The axis of rotation is anteroposteriorly aligned without significant deviation from the horizontal (figs. 11B, 13E). The manubrium is more nearly perpendicular to the axis of rotation (60° to 80° , fig. 12B). The malleus is delicately attached to the ectotympanic by a fragile, much reduced anterior process (a bony connection, however, still persists in neonates and adults). The lamina is strongly reduced, and only a minute vestige of a pocket remains (fig. 12B). Herpestids appear to have evolved the most derived ossicular geometry and orientation among the living aeluroid carnivorans (fig. 13).

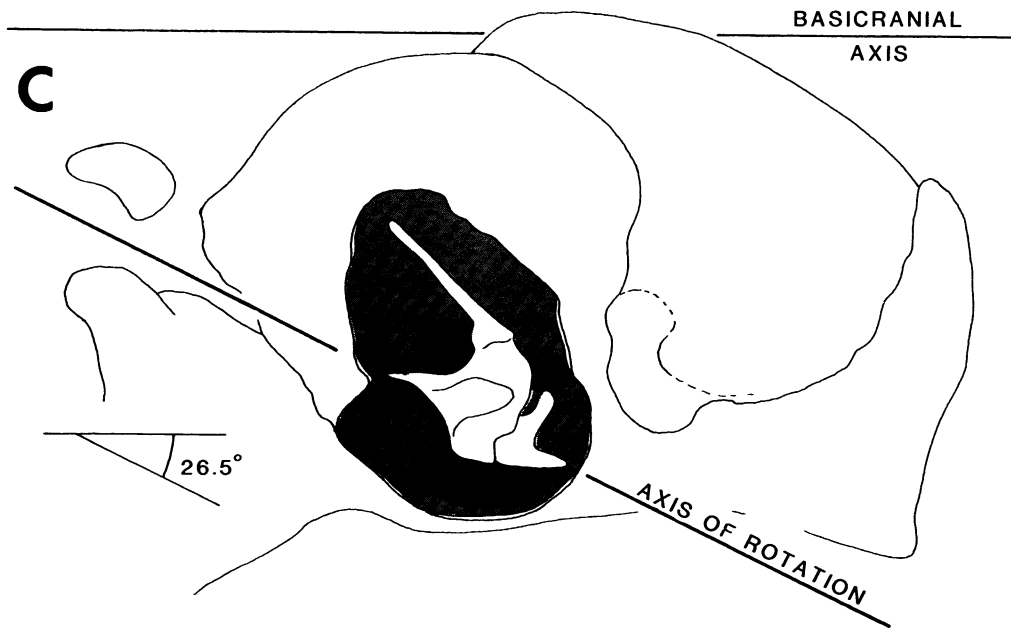
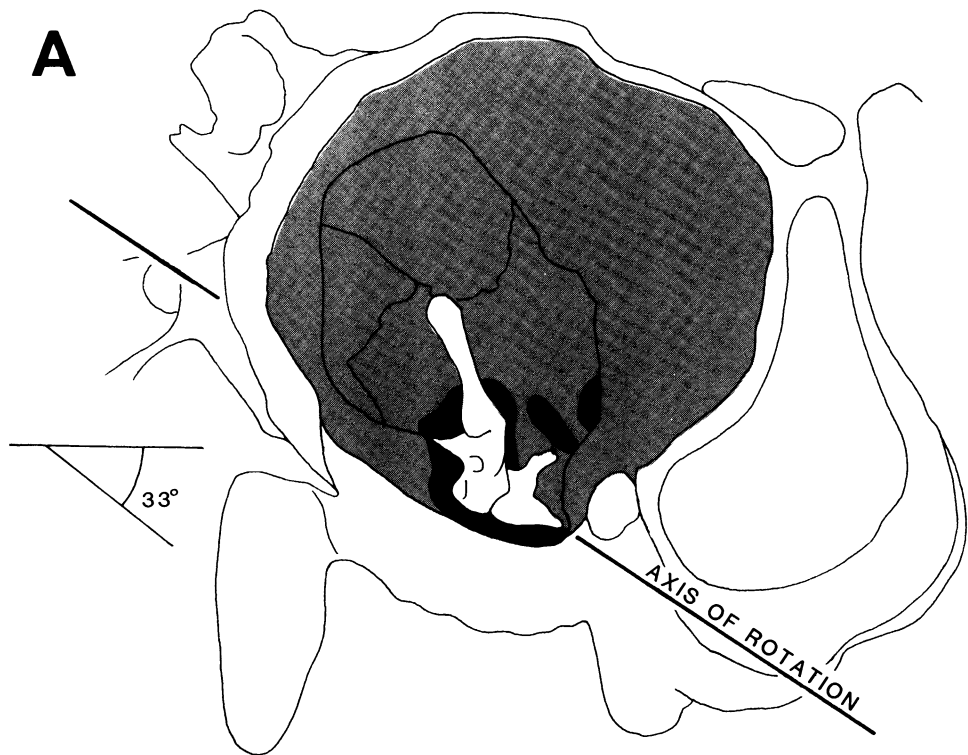
Hyaenids share aspects of both the viverrid-felid and herpestid end-members in terms of ossicular form and axial orientation. Hyaenids retain an alignment of the rotational axis similar to that of viverrids and felids, inclined approximately $33\text{--}37^\circ$ from the horizontal (fig. 11A). However, the attachment of malleus to ectotympanic is quite delicate (it is a thin osseous connection in

adults), the lamina is strongly reduced as in herpestids, and only a vestige of the pocketed lamina remains (figs. 12A, 13B). It is evident that hyaenids have not passed through a herpestid grade of ossicular orientation. The inclined rotational axis of hyaenids seems more plesiomorphic than the nearly horizontal axis of herpestids, but both groups have undergone significant reduction of the pocketed lamina of the malleus.

The fact that viverrids and felids share near-identity in their ossicular structure, whereas herpestids are much different and arguably more derived, does not necessarily substantiate the sister-group relationship that I have proposed for viverrids and felids on the basis of bulla ontogeny (Hunt, 1987). The orientation of the ossicular rotational axis and the form of the malleus in viverrids and felids are plesiomorphic (fig. 13), and could simply reflect the absence of significant change in these features over time. However, the fact that viverrids and felids share the enlarged petrosal promontorium and the concomitant tilting of the ectotympanic, correlated with the forward-growing caudal entotympanic element, constitutes more reliable grounds for the proposed sister relationship between these two families. Herpestids stand apart from this viverrid-felid dichotomy because of their derived bulla ontogeny and their ossicular orientation and morphology: they cannot be ancestral in their present form to any other group of living aeluroids. Living hyaenids are similarly derived in the form of their malleus, and so cannot be ancestral to viverrid and felid carnivorans in which the condition of the malleus is more plesiomorphic. However, the similarity of hyaenid and herpestid mallei is not necessarily evidence of close relationship, because it could represent parallel evolution, a result of the independent development of a more mobile ossicular chain in the two groups.

The close correlation between bulla morphology and ossicular geometry and orientation in living aeluroids suggests a plausible reconstruction of the ossicular chain in *Herpestides antiquus*. One can predict that this Aquitanian viverrid possessed a slightly inclined rotational axis; the incus will be small relative to the size of the malleus; the manubrium of the malleus will lie at a low angle

BASICRANIAL AXIS



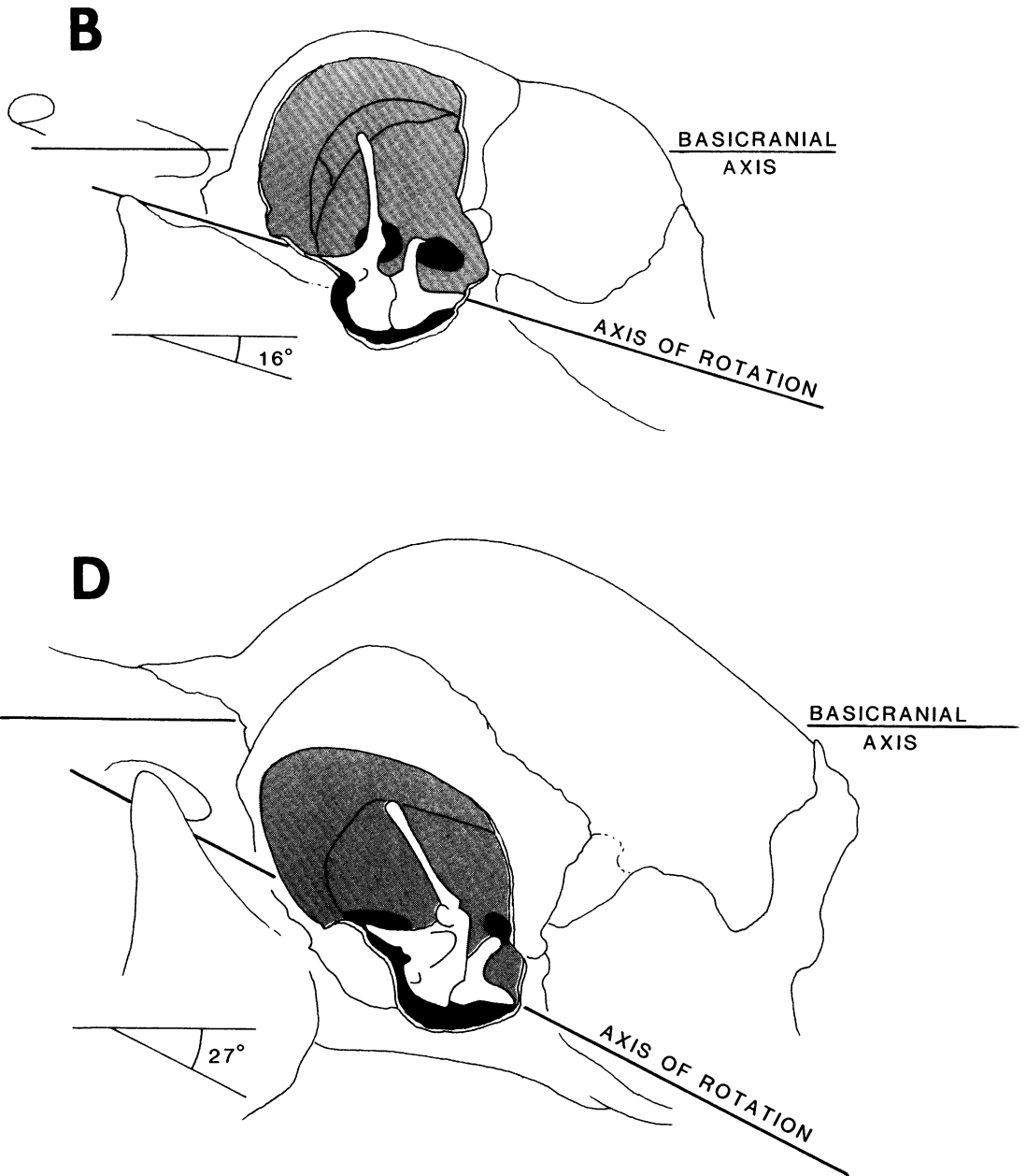


Fig. 11. Inclination of the ossicular rotational axis within the middle ear of aeluroid carnivorans, measured as the angle of intersection with the basicranial axis (an estimate of the horizontal). A, Hyaenid *Hyaena brunnea* (UNSM 16442); B, herpestid *Herpestes auropunctatus* (AMNH 232811); C, viverrid *Genetta* sp. (UNSM 14275); D, felid *Lynx rufus* (UNSM 14674). Lateral view, ventral to top, anterior to left (hyaenid in ventrolateral view).

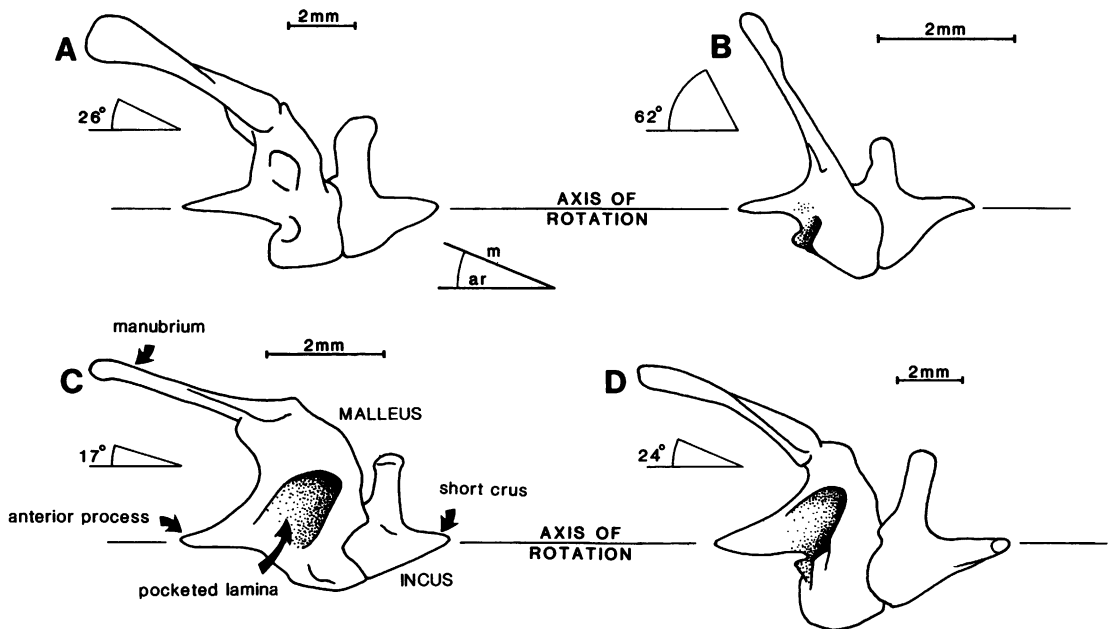


Fig. 12. Orientation of the manubrium relative to the ossicular rotational axis in aeluroid carnivorans (measured as the angle between the long axis of the manubrium [m] and the rotational axis [ar]). A, Hyaenid *Hyaena brunnea* (UNSM 16442); B, herpestid *Mungos mungo* (AMNH 118859); C, viverrid *Genetta* sp. (UNSM 14275); D, felid *Panthera tigris* (UNSM 15484). Lateral view, ventral to top, anterior to left. Viverrids and felids retain a plesiomorphic form of the malleus in which the pocketed lamina is retained as a vestige of the prominent transverse lamina of early therians. The lamina is reduced in hyaenids and nearly absent in herpestids.

to the axis of ossicular rotation; the malleus will retain a well-developed lamina, probably pocketed as in living viverrids; the connection between the malleus and ectotympanic will be osseous, not ligamentous. Viverrids, among living aeluroids, retain the most plesiomorphic ossicular chain, one which is markedly different from the derived ossicular morphology found in herpestids.

PHYLOGENETIC AFFINITIES OF *HERPESTIDES*

Basiscrania attributed to *Herpestides* in the Basel and Lyon collections, including several belonging to complete skulls with associated dentitions, all invariably possess a common morphology of the auditory region. Both intact and crushed skulls document the association of these basicrania (and auditory bullae) with dentitions undoubtedly referable to *Herpestides antiquus* (figs. 14, 15).

The basicranial morphology of *Herpestides*

is readily comparable to basicranial patterns found in living viverrids. Among the features common to *Herpestides* and viverrids are: (1) petrosal form and orientation; (2) configuration and ontogenetic growth pattern of the caudal entotympanic relative to other bulla elements and surrounding basicranial bones; (3) form, size, and structural relations of the three bulla elements (rostral and caudal entotympanics, ectotympanic); (4) path of the internal carotid artery in the auditory region. *Herpestides* has been considered a herpestid (Viret, 1929) or ancestral hyaenid (Beaumont, 1967; Beaumont and Mein, 1972; Hunt, 1989) in earlier studies. Petter (1974) believed that the auditory bulla was of the herpestid type. My opinion, initially based on illustrations in the European literature, changed when I was able to examine the fossils. The preceding review of herpestid and hyaenid auditory regions points to the absence of any distinguishing features in the Aquitanian aeluroid that would ally it with

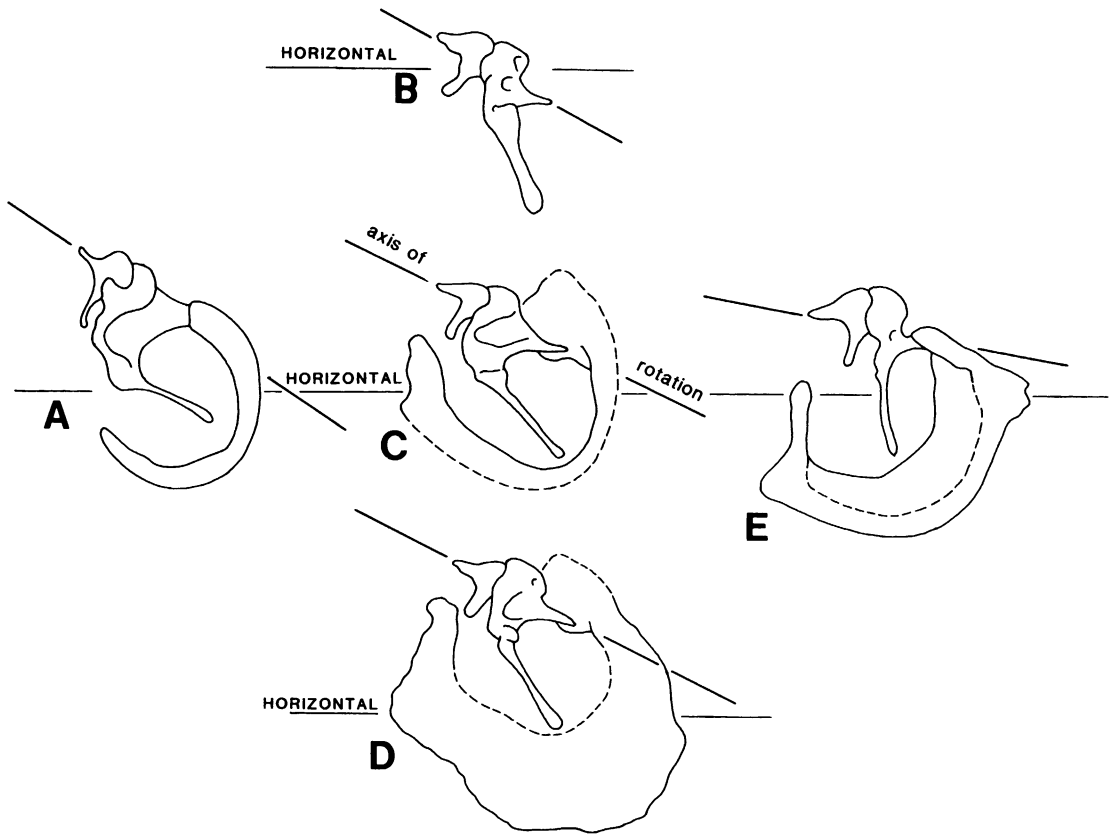


Fig. 13. Evolution of the ossicular complex in aeluroid Carnivora (B through E each presumed to be independently evolved from A). A, Early therian with marked axial inclination and plesiomorphic ossicle morphology (developed transverse lamina of malleus, small incus relative to malleus); B, hyaenid with moderate inclination and derived ossicle morphology (reduced lamina of malleus, incus enlarged relative to malleus); C, D, viverrid and felid with moderate inclination and plesiomorphic ossicle morphology (pocketed lamina of malleus, incus small); E, herpestid with low inclination and derived ossicle morphology (strongly reduced lamina, incus large relative to malleus). Lateral view of right middle ear, dorsal to top, anterior to right.

either of these families. Here I briefly summarize the important distinctions between *Herpestides* and herpestids/hyaenids.

Herpestids differ in their auditory structure from viverrids in having a differently shaped petrosal, characterized by a particularly prominent bony capsule anterior to the pars cochlearis that houses the tensor tympani muscle. The muscle is nearly encapsulated by bone in adults (a trait unknown in other aeluroids), and emerges through a restricted, laterally directed aperture about the same diameter as the round window (see Hunt, 1989: fig. 4B). This construction of the tensor tym-

pani fossa is unknown in living viverrids, felids, and hyaenids, and is considered a derived trait of herpestids on the basis of outgroup comparison with other carnivorans. An encapsulated tensor tympani fossa is not found in *Herpestides*.

The caudal entotympanic forms the posterior chamber of the auditory bulla in aeluroid carnivorans. In herpestids, the caudal entotympanic remains restricted to the posterior part of the auditory region during ontogenetic growth. In living herpestid species, inflation of the posterior (caudal entotympanic) chamber takes place during ontogeny



Fig. 14. Association of *Herpestides antiquus* dentitions with typical viverrid basicrania occurs in a number of skulls from the Aquitanian of the Allier basin, France (NMB 11407, Montaigu-le-Blin).

but is primarily directed ventrad and to the sides, never forward. However, in contrast to the orientation in herpestids, the caudal entotympanic chamber grows forward in viverrids and felids, penetrating into the anterointernal corner of the auditory region, often overgrowing the anterior chamber of the bulla. *Herpestides* shows a pattern of caudal entotympanic growth comparable to that of viverrids. No living or fossil herpestid has a bulla pattern even remotely similar to that seen in *Herpestides*.

The placement of the ectotympanic, and its relation to the petrosal, also distinguishes herpestids. Because the petrosal promontorium is relatively small and almost fully enclosed (more so in some species than in others) within the perimeter of the ectotympanic crescent in early developmental stages, the herpestid ectotympanic lies flat against the basicranium in the horizontal plane. However, in viverrids and felids the ectotympanic crescent fails to enclose the promontorium as completely as in herpestids, apparently because the promontorium is quite large and protrudes below the basicranial surface. As a

result the posterior limb of ectotympanic comes in contact with the apex of the enlarged promontorium (just anterior to the round window), causing the ectotympanic to tilt forward and outward so that it initiates its growth from a position much different than that found in herpestids. The orientation of the ectotympanic in both juvenile and adult *Herpestides* demonstrates a viverrid-like, rather than herpestid-like, ectotympanic-petrosal relationship. In *Herpestides* the ectotympanic has been tilted forward and outward by an enlarged promontorium, and the posterior limb of ectotympanic, unable to enclose the promontorium, is applied to the petrosal surface anterior to the round window.

A hallmark of the herpestid auditory region is an ectotympanic oriented nearly in a frontal plane in juveniles and even in adults (ectotympanic inflation causes slight outward rotation in some species). As a consequence the herpestid tympanum faces nearly directly ventrad, and were it to remain so in the adult, the anterior bulla chamber would be flooded by the eardrum. To avoid this, herpestids

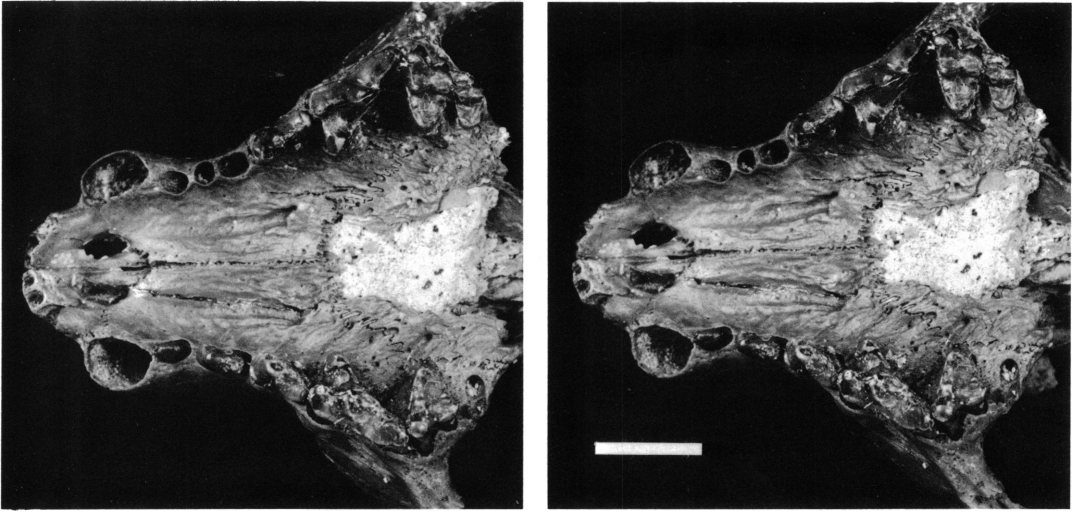


Fig. 15. The dentition of *Herpestides antiquus* has been attributed by Beaumont (1967) to a single, highly variable species. The upper teeth, although more plesiomorphic, show similarities in occlusal pattern to those of the African bush civet, *Civettictis civetta*, which may be a lineal descendant.

close the auditory meatus of the ectotympanic with bone, thereby creating an osseous floor beneath the eardrum. In viverrids and felids the more parasagittal orientation of the ectotympanic, both in early developmental stages and as a further result of ectotympanic inflation, does not result in closure of the auditory meatus by bone; rather, the meatus remains open as a prominent aperture into adult life (Hunt, 1989: fig. 2). In both juvenile and adult *Herpestides*, the bony external auditory meatus is open and shows the viverrid orientation; there is no evidence of the uniquely derived herpestid condition of the meatus.

It seems probable that the different orientation of the ectotympanic crescent relative to the promontorium in herpestids and viverrids/felids is the basis for the different configurations of the caudal entotympanic chamber in these two groups. The penetration of the caudal entotympanic into the anterointernal corner of the auditory region in viverrids and felids is correlated with outward and forward displacement of ectotympanic in early ontogeny. Because the ectotympanic is not displaced in herpestids, the caudal entotympanic cannot penetrate into the anterointernal auditory region and, as a result, it remains within the posterior part of the auditory re-

gion. *Herpestides* demonstrates the viverrid caudal entotympanic configuration, not the herpestid.

Enclosure of the internal carotid artery in the medial bulla wall (perbullar course) in all herpestids is a unique synapomorphy of the family not found in other aeluroids. The artery in *Herpestides* does not follow such a course but instead takes a transpromontorial path very similar to that of viverrids such as *Civettictis* (fig. 7). This transpromontorial course is probably plesiomorphic for Aeluroidae (Hunt, 1989).

The hyaenid auditory region differs fundamentally from that of *Herpestides* in the configuration of anterior and posterior bulla chambers. In living and fossil hyaenids (except *Proteles*) the bulla's anterior chamber, formed primarily by ectotympanic, extends backward to cover the posterior chamber. The posterior chamber formed by caudal entotympanic remains small in volume relative to the enormous anterior chamber. In fossil hyaenids there is no evidence that the posterior chamber of the hyaenid bulla was ever any larger than in living species, and the antiquity of this hyaenid bulla pattern extends to very primitive forms (*Tungurictis*, *Percrocuta*) in the mid-Miocene. This hyaenid pattern is the antithesis of the *Herpestides* pat-

tern, in which the caudal entotympanic grows forward and becomes the dominant chamber. Hyaenids plausibly originate from an aeluroid morphotype in which the caudal entotympanic was never enlarged and primarily confined to the posterior auditory region.

Because the dominant chamber of the hyaenid bulla corresponds to the subordinate chamber of the viverrid-felid bulla, and vice versa, it is evident that these ontogenetic growth patterns represent divergent solutions to the problem of middle ear enclosure. The hyaenid pattern and the pattern identified in juvenile and adult *Herpestides* lie on independent developmental trajectories. Thus a relationship of the Aquitanian aeluroid to hyaenids can be rejected on the basis of their distinguishing and contradictory bulla morphs.

THE PROBLEM OF HYAENID-HERPESTID RELATIONSHIP

The placement of the three auditory bulla elements in living hyaenids and herpestids suggested that the adult hyaenid bulla pattern might be derived from the configuration adopted by these elements in the neonatal herpestid bulla (Hunt, 1987, 1989: fig. 5). This remains a plausible hypothesis open to future testing, however, few other features of herpestid and hyaenid morphology lend support to this view. In my initial analysis of aeluroid carnivorans, some derived traits appeared to link hyaenids and herpestids (Hunt, 1987: fig. 19, node 4) but the nature of the evidence for a sister-group relationship was not compelling: (a) restriction of caudal entotympanic to the posterior auditory region; (b) blunt nonretractile claws; (c) an invaginated anal pouch with glands or sacs; (d) an absent or vestigial aural bursa; (e) external auditory meatus prolonged as a bony tube. As an additional complication, herpestids share a large number of autapomorphies that tend to obscure their relationships with other aeluroids. In this context, the morphological similarity of herpestid and hyaenid mallei merits comment. Both families have mallei with a reduced lamina and a short anterior process, contrary to felids and viverrids in which a well-developed pocketed lamina is present. Is this similarity inherited from a

common ancestry, or is this a case of parallel evolution?

If one accepts the morphocline polarity presented in figure 10 for the evolution of the auditory ossicular chain in eutherian mammals, then a malleus with a reduced lamina represents a derived character state. The hypothetical morphocline of figure 10 is supported by the taxonomic distribution of primitive and derived ossicular states among living mammals: the presence of a malleus with well-developed transverse lamina and gonial process occurs in all monotremes, nearly all metatherians, and in eutherians such as tenrecs, erinaceids, soricids, solenodontids, and bats; the configuration of the auditory ossicles (fig. 10A) with which such a malleus is associated is generally regarded as the plesiomorphic therian state (Fleischer, 1978). Mallei with reduced laminae (fig. 10B, C) are widely distributed across many orders of mammals, including both caniform and feliform Carnivora. Such a distribution is likely to result from repeated instances of parallel evolution, in each case directed toward the development of freely mobile ear ossicles having low mass, little stiffness, and reduced frictional resistance (Hunt and Korth, 1980).

Consequently, independent evolution of the mallei seen in living hyaenids and herpestids must be entertained as a hypothesis equally as plausible as derivation of these mallei from a common ancestor. Such mallei can be predicted as the frequent product of selective pressures directed toward a more mobile ossicular mechanism in various eutherian lineages. Hence, hyaenids and herpestids cannot be linked solely on the basis of the form of the malleus. Are there any other features of the auditory region that suggest affinity between the two groups?

The few species of hyaenids and herpestids that have been available for dissection of the auditory region show similar petrosal morphs. The promontorium appears to possess a characteristic shape, surmounted by a tall, bladelike ventral promontorial process. However, it has not been possible to survey petrosal shape in a large enough sample to determine the taxonomic distribution of this morph, and in the interim there remains a paucity of compelling synapomorphies to unite the two families. Thus, figure 16 depicts hyaenids and herpestids as independent ae-

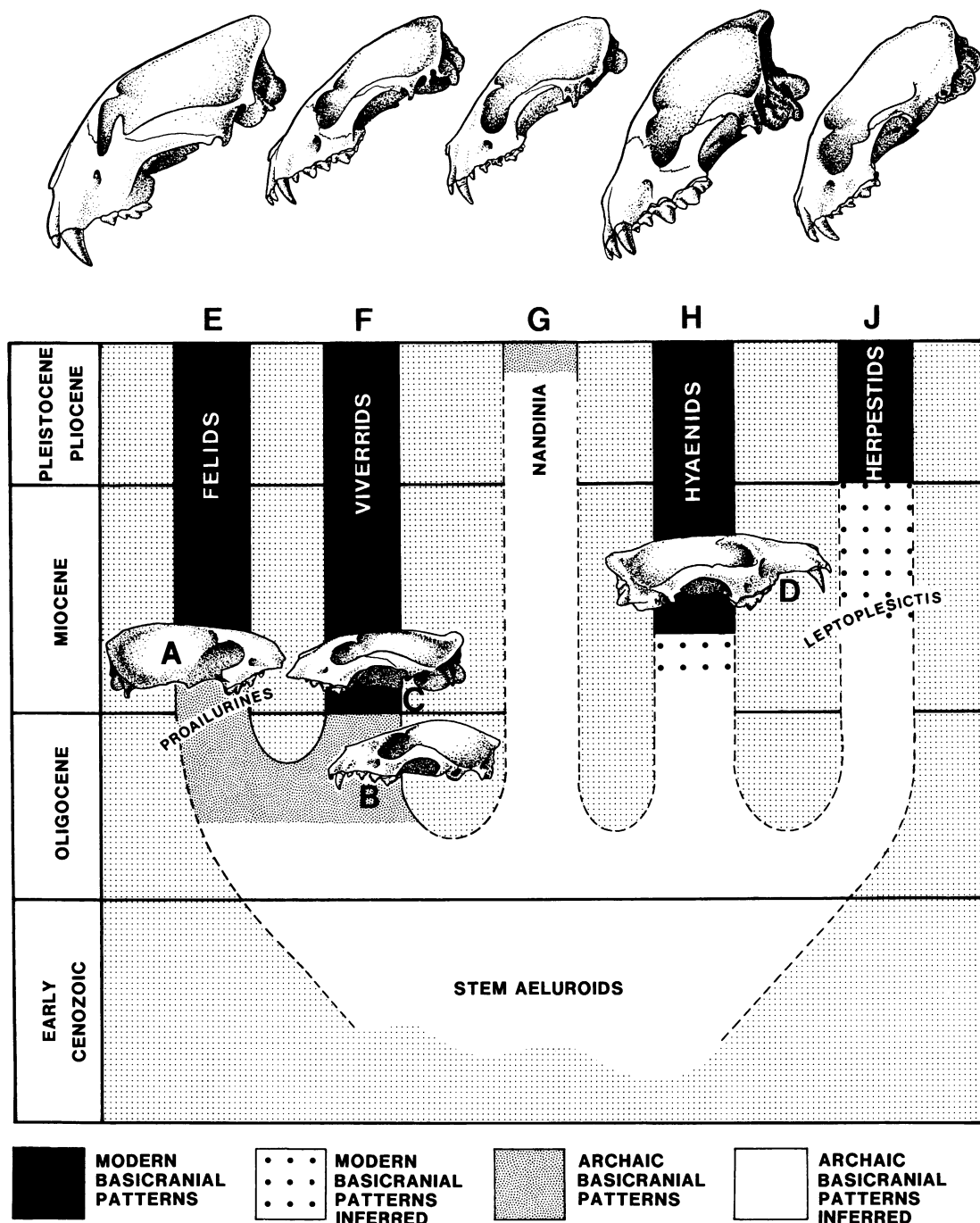


Fig. 16. Evolution of basicranial patterns within the aeluroid Carnivora (modified from Hunt, 1989). The modern basicranial patterns characteristic of the living families emerge during the late Oligocene to early Miocene interval in the Old World, and persist relatively unchanged for the remainder of the Neogene within each family. This revised chart incorporates new information on Eurasian aeluroids discovered since the publication of my initial hypothesis (Hunt, 1989: fig. 13): (a) transfer of early Miocene *Herpestides* to Viverridae, and (b) indication of a more ancient and independent derivation of hyaenids and herpestids from the stem aeluroid group. Early or mid-Miocene basicrania of modern grade are now known for all aeluroid families except Herpestidae. A, *Stenogale julieni*; B, *Palaeoprionodon lamandini*; C, *Herpestides antiquus*; D, *Tungurictis spocki*; E, *Panthera onca*; F, *Civettictis civetta*; G, *Nandinia binotata*; H, *Crocota crocota*; J, *Galidia elegans*.

luroid lineages that may in time prove to be derived from a common ancestry exclusive of that for felids/viverrids.

ANTIQUITY OF THE VIVERRID AUDITORY REGION

Prior to examination of the Aquitanian samples of *Herpestides*, my earlier research indicated that the oldest confirmed viverrid auditory regions belonged to Plio-Pleistocene fossils from the Siwaliks of southern Asia and the Langebaanweg locality in South Africa (Hunt, 1989). Other fossils that I was able to study in the British Museum (N.H.) from Oeningen in Europe and from the Miocene Siwaliks suggested that viverrid auditory regions of modern grade possibly extended to the mid-Miocene, but there was no confirming evidence. Now, however, because the basicranium of *Herpestides* is essentially that of a modern viverrid, the Lyon and Basel samples extend the record of viverrid basicrania to the early Miocene (European Neogene mammal zone MN2a). We may now anticipate that true viverrids were not only present but probably diverse in the Miocene of the Old World, and that the viverrid auditory pattern probably developed in Oligocene ancestors.

The oldest viverrid auditory region, however, appears to belong not to *Herpestides*, but to the small Quercy aeluroid *Palaeoprionodon lamandini*, whose skull was illustrated by Teilhard (1915: pl. 9, fig. 10). I have not examined the skulls figured by Teilhard in the collections of the Paris Museum, but his photograph indicates an auditory region with large petrosal promontorium, and an ectotympanic applied to the promontorium in the manner of viverrids and felids, whereby the posterior limb rests on the promontorium just anterior to the round window. Furthermore, although there is no caudal entotympanic preserved in *Palaeoprionodon*, it is clear from Teilhard's figure 10 that a small caudal entotympanic was probably present, occupying the posterior auditory region, and very likely extending forward a short distance along the medial side of the ectotympanic crescent. Comparison of Teilhard's photograph with the skull of the living *Prionodon* suggests that the Quercy aeluroid had not only a caudal entotympanic of similar size and

form, but that the auditory regions may have been nearly identical. An important aspect of the auditory region of *Palaeoprionodon* is that the mastoid and exoccipital bones surrounding the caudal entotympanic are quite thin and narrow in ventral view (Teilhard, 1915: pl. 9, fig. 10), and do not form a wide bony shelf as in the primitive aeluroid *Nandinia*. This configuration of mastoid and exoccipital reveals a posterior auditory region much like the modern viverrids *Prionodon* and *Poiana*.

In addition to *Palaeoprionodon*, there is another Old World Oligocene aeluroid carnivoran that often has been regarded as a viverrid: the Quercy *Stenoplesictis cayluxi*. The auditory region of *Stenoplesictis*, although undoubtedly aeluroid, is not certainly viverrid if an assessment is based on the superb skull described by Piveteau (1943) from the collection of the Faculté des Sciences, Marseilles. Here the ectotympanic is much more inflated than in *Palaeoprionodon*, and apparently encompasses the petrosal promontorium. This ectotympanic configuration would seem to preclude assignment to either viverrids or felids, and it appears to be too strongly inflated to belong to a herpestid. Moreover, the caudal entotympanic chamber must have been relatively small. This suggests that the Marseilles cranium referred to *Stenoplesictis* is either an early aeluroid lineage that terminates without living descendants, or possibly represents an ancestral hyaenid in which the bulla chambers presage the modern configuration.

CONCLUSIONS

1. The auditory region of the Aquitanian (early Miocene) aeluroid *Herpestides antiquus* is of the viverrid type, and cannot be referred to Herpestidae or Hyaenidae as previously believed.

2. Basicranial and auditory bulla patterns of viverrids and felids had evolved by the early Miocene in Europe. The auditory bullae of the viverrid *Herpestides antiquus* and the felid *Proailurus lemanensis*, both from the Aquitanian of the Allier basin, France, are essentially of modern grade, and demonstrate that the two families existed as independent lineages by that time.

3. Viverrids and felids exhibit parallels in the pattern of ontogenetic development of

their auditory structure that suggest they are sister groups, e.g., in the relationship of ectotympanic to petrosal promontorium, the geometry of the petrosal, and the pattern of bulla development.

4. Orientation and morphology of the auditory ossicles in aeluroids indicate that these carnivorans display transitional to derived states of the ossicular mechanism relative to a eutherian morphotype. Among aeluroids, viverrids and felids retain the most plesiomorphic patterns, whereas hyaenids and herpestids exhibit more derived states. Viverrids and herpestids are extremely different in ossicular morphology, one more item in a steadily accumulating body of evidence indicating the marked distinction between the two groups.

5. The hyaenid bulla pattern appears in the mid-Miocene fully developed in at least two distinct lineages of widely divergent adaptive type (*Percrocuta*, *Tungurictis*), indicating that the origin of the pattern predates the divergence of these lineages, and therefore is probably of early Miocene age or older.

6. Because aeluroids do not appear in the fossil record until mid- to late Oligocene, following the "Grande Coupure" event in Eurasia, and because basicranial patterns of modern grade first appear in viverrids, felids, and probably hyaenids in the early Miocene, the development of these patterns may take place over a relatively brief interval within the later part of the Oligocene. By inference, the herpestid pattern probably also originates during the late Oligocene to early Miocene interval.

7. Aeluroid basicranial types can be identified primarily from the structural relationships of auditory bulla, petrosal, and auditory ossicles. These patterns on present evidence must develop within the mid-Cenozoic Oligocene interval from about 34 to 24 Ma. Once established, they persist as stable morphs for the remainder of the Cenozoic history of these carnivoran groups. Stasis in patterns of auditory morphology characterizes the aeluroid Carnivora during the Neogene.

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