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Evolution of the Aeluroid Carnivora: Significance of the Ventral Promontorial Process of the Petrosal, and the Origin of Basicranial Patterns in the Living Families

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ABSTRACT

In studies of carnivoran phylogeny, the configuration and ontogenetic development of the auditory bulla enclosing the middle ear have been

useful in tracing modern lineages to their first appearances in the mid-Cenozoic. Pre-Oligocene carnivorans, however, lack preserved bullae and

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have been difficult to relate to later Cenozoic groups. The carnivoran petrosal bone, because of its durability both in intact skulls and as an isolated element, can be tracked through Cenozoic time, and can supply new information on lineage continuity through its geometry and spatial relationships.

Aeluroid carnivorans are united by a petrosal of characteristic shape, distinguished by a ventral promontorial process buttressing the lateral margin of the basioccipital. The configuration of the process is highly uniform in most living aeluroids (viverrids, herpestids, hyaenids) but has been suppressed in modern felids by encroachment of an inflated auditory bulla. Ancestral proailurine felids, however, retain the process.

Among living aeluroids, the African palm civet *Nandinia binotata* is distinguished by a somewhat differently configured ventral promontorial process, which is more posteriorly situated and robust. Comparison with fossil aeluroid basicrania

indicates that the form of *Nandinia*'s petrosal closely approximates the petrosals of Oligocene stenoplesictine aeluroids from the Quercy fissures of France. Stenoplesictines are the oldest generally acknowledged aeluroids represented by basicranial remains. The strong anatomical correspondence shared by the Quercy stenoplesictine basicrania with the basicranium of *Nandinia* reflects the plesiomorphic auditory structure of these groups. However, relative to stenoplesictines, *Nandinia*'s auditory region is more primitive in the structure of the auditory bulla and surrounding basicranium; its basicranium is arrested at a pre-Oligocene structural grade, and is representative of the projected ancestral aeluroid morphotype.

Survey of the aeluroid fossil record suggests that the modern aeluroid basicranial and bulla patterns developed in the mid- to late Miocene, and were well established by the Plio-Pleistocene. Prior to the mid-Miocene, an array of archaic basicranial patterns characterized the aeluroid Carnivora.

INTRODUCTION

An improved understanding of the evolution of the mammalian order Carnivora has resulted from detailed anatomical study of the auditory region in both living and extinct lineages (Flower, 1869; Hough, 1948; Tedford, 1976). Ontogenetic elements forming the auditory bulla join to create unique morphopatterns diagnostic of particular lineages (Hunt, 1974a). Such lineages are most commonly identified at the family level within the order, and can be traced in some cases into the Oligocene.

The auditory bulla has not been found in pre-Oligocene fossil carnivoran basicrania, and only rarely occurs in the extinct creodont carnivores (Mellett, 1977). This situation seems to result from (a) a record of very few well-preserved skulls of Paleocene and Eocene Carnivora in paleontological collections; (b) probable loose attachment of the bulla to the skull; (c) lack of ossification of some or all bulla elements.

Based on present knowledge of taxonomic distribution and morphology of the ontogenetic elements making up the auditory bulla in post-Eocene carnivorans, we might reasonably predict that Paleocene and Eocene carnivorans possessed a multipart bulla (formed by an ectotympanic and one or more entotympanics) as in living forms. However, such a bulla has yet to be discovered intact,

and details of its structure are only conjectural at the present time. The nature of auditory bullae in early Tertiary carnivorans may be eventually clarified by study of recently discovered fully articulated skeletons of Eocene carnivorans from Messel for which little postmortem disturbance is inferred (Springhorn, 1980, 1982, 1985).

However, in the interim, a useful insight comes from another quarter: identification of the small Holarctic Oligocene carnivoran *Palaeogale* as a relict lineage of the early Tertiary viverravids (Hunt, 1974b; see also Flynn and Galiano, 1982) demonstrates the structure of the auditory bulla in a member of one of the principal early Tertiary carnivoran families (Viverravidae). Although the dentition of *Palaeogale* exhibits aeluroid affinities (Flynn and Galiano, 1982), its unique single-chambered fully ossified bulla is not typically aeluroid, and suggests that early Tertiary viverravids probably did not possess the derived bulla configuration of the living aeluroid families. This conclusion raises several important questions concerning the living aeluroid groups: When did the modern bulla patterns develop? Can additional derived traits be identified that unite the aeluroid families in addition to bulla configuration?

Modern aeluroid bulla patterns appear in

the mid- to late Miocene, based on a review of aeluroid basicranial patterns in the fossil record, identified and summarized in this report. From this conclusion it follows that one should not expect to find aeluroid basicranial patterns typical of the living families in the early Tertiary.

Consequently, in the tracing of carnivoran lineages, it would be useful to identify other features of the skeleton that can be employed as reliable anatomical markers in lieu of the dentition and bulla. The basicranium of Carnivora has been a fertile source of data for phylogenetic studies in the past, so it is not surprising that a fresh examination of this part of the skull, particularly the auditory region, might provide new insights. My recent work indicates that the form of the petrosal bone has potential as a phyletic marker. In the Aeluroidea, a characteristic configuration of the petrosal promontorium can be identified (Hunt, 1987: 44). It is found in representative species of all the major aeluroid families: viverrids, herpestids, hyaenids, primitive felids, and in the living primitive aeluroid *Nandinia*. In addition, it appears that the petrosal configuration of aeluroids may be responsible for the unusual double-chambered arrangement of their auditory bulla, a structural peculiarity that has been difficult to explain.

To demonstrate this, I first illustrate and discuss petrosal form in representative members of the living aeluroid groups; then describe the structural parallels in petrosal and basicranium between the oldest generally acknowledged aeluroids (stenoplesictines) and the living African aeluroid *Nandinia*, with particular attention given to a recently identified stenoplesictine basicranium in the British Museum; and, finally, compare these results with basicranial structure in the remaining group of primitive fossil aeluroids, the proailurines. I conclude with a survey of aeluroid basicranial patterns in the fossil record, focusing on the time of origin of these patterns.

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ABBREVIATIONS

A	alisphenoid
AC	anterior carotid foramen
BO	basioccipital
BS	basisphenoid
Ca	anterior crus of ectotympanic
E	caudal entotympanic
EO	exoccipital
F	facet for ectotympanic on petrosal
FR	round window
G	gonial
H	hypoglossal (condyloid) foramen
ICA	internal carotid artery
L	middle lacerate foramen
M	mastoid
P	petrosal
PC	posterior carotid foramen
PLF	posterior lacerate foramen
PP	paroccipital process of exoccipital
R	rostral entotympanic
S	intrabullar septum of hyaenids
SQ	squamosal
T	ectotympanic
V	ventral process of the petrosal promontorium (VPP)
X	line of attachment of caudal entotympanic to ectotympanic
AMNH	Vertebrate Paleontology, American Museum of Natural History, New York
AMNH-M	Mammalogy, American Museum of Natural History, New York
BMNH	Palaeontology, British Museum (Natural History), London

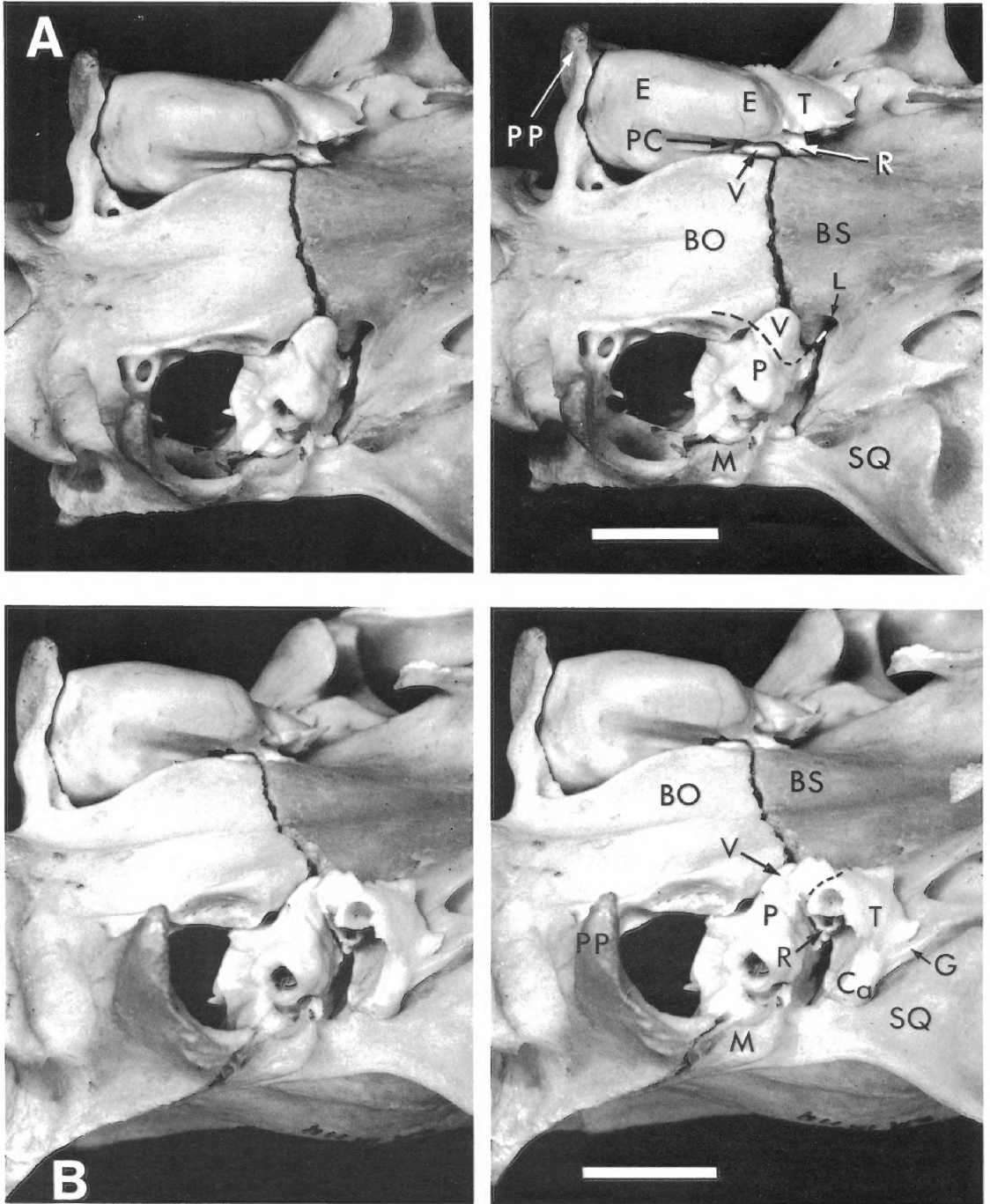


Fig. 1. **A**, Basicranium of the viverrid *Civettictis civetta* (UNSM-ZM 14114), young adult, Kibwezi, Kenya, oblique ventral view, showing auditory bulla in place in right auditory region, and bulla removed from the left auditory region, revealing the ventral petrosal process (V). Dashed line indicates path of internal carotid artery through left auditory region. White scale bar in this figure and all subsequent photographs is one cm in length. For all abbreviations not defined in figure captions, see p. 3. **B**, Basicranium of same individual as A, but with ectotympanic and rostral entotympanic elements of the auditory bulla in place, forming an anterior chamber of the bulla in front of the petrosal. This anterior chamber rests against the ventral petrosal process (V). Dashed line indicates zone of fusion between ectotympanic and the extreme anterior tip of caudal entotympanic; rostral entotympanic (R) is fused to

F:AM	Frick Collection, Vertebrate Paleontology, American Museum of Natural History, New York
SAM	South African Museum, Cape Town
UNSM-ZM	University of Nebraska State Museum, Zoology, Lincoln

PETROSAL FORM IN THE LIVING AELUROID FAMILIES

An aeluroid petrosal is characterized by a prominent ventral process or extension of the promontorium (fig. 1, V), forming the ventromedial edge of the petrosal. The process is best seen in ventral view with bulla removed. This ventral promontorial process (VPP) is applied to the lateral edge of the basioccipital, and often extends ventrad beyond the basicranial axis. The arctoid and cynoid Carnivora lack the process. Hence, the presence of VPP is an aeluroid synapomorphy, and the common ancestor of the living aeluroid groups must have had a petrosal with VPP present.

In living aeluroids, where a broad sample of representative species can be surveyed, the VPP takes one of two distinctive configurations:

(1) In living viverrids, herpestids, and hyaenids, VPP inclines forward from the promontorium, and is applied to the basioccipital immediately posterior to or at the basioccipital-basisphenoid suture. Thus in these animals, VPP is situated in proximity to the anterointernal corner of the auditory region;²

(2) In the primitive aeluroid *Nandinia binotata*, VPP is applied to the lateral edge of the basioccipital as in the other living aeluroids, but the process is not as anteriorly situated. It is placed closer to the midpoint of the basioccipital's lateral edge, well behind

² Living felids lack the VPP. However, in the ancestral stock of the felids (Proailurinae), VPP is present, but more posteriorly situated relative to the living aeluroid groups. In later Cenozoic and living felids, the inflation of the auditory bulla via relative growth of the enlarged caudal entotympanic results in suppression of VPP, so that loss of the process is a derivative trait of the younger Felidae.

the basioccipital-basisphenoid suture, and is not anteriorly inclined as in the first group, resulting in a more robust symmetrical promontorium.

Form of the *Nandinia* petrosal is strikingly similar to petrosal shape occurring in the oldest generally accepted aeluroid skulls yet identified in the fossil record, the stenoplesictines and proailurines from the Oligocene Quercy fissures of France (Teilhard, 1915; Piveteau, 1943; Lavocat, 1952). The similarity in form and basicranial relationships of *Nandinia*'s petrosal to those of stenoplesictines and proailurines is remarkable. It appears that this is not convergence but the result of retention of a primitive aeluroid petrosal structure in the living African palm civet. This trait accompanies numerous other plesiomorphic features which suggest that the structure of the auditory region of this animal closely approximates the primitive aeluroid morphotype (Hunt, 1987).

The evident correspondence among the living aeluroid groups in petrosal structure is demonstrated by the subsequent descriptions and stereophotographs of their auditory anatomy:

Viverridae. The viverrid petrosal (fig. 1A, B) is illustrated using the auditory region of the bush civet *Civettictis civetta*. The petrosal occupies the anterior auditory region, separating the middle ear from the cranial cavity. In primitive Carnivora, the posterior edge of the petrosal abuts against the exoccipital, but in viverrids like *Civettictis*, the petrosal is separated from the exoccipital by a wide space occupied by the caudal entotympanic. This separation is due to the enormous enlargement and posterior extension of the caudal entotympanic in living viverrids, relative to the primitive aeluroid condition in which no separation occurs.

Once the bulla has been removed from the skull (fig. 1A), the petrosal can be seen in ventral view. It is a compact rugose bone with a prominent ventral process, situated directly lateral to the basioccipital-basisphenoid suture. Anterior to the process is the middle

←

the ectotympanic (T) rim, producing the thictic bulla configuration of viverrids. The petrosal has been slightly displaced to the left in the photograph so that the registration mark upon its anterior promontorial surface for the rostral entotympanic can be seen (to right and slightly below letter P). Stereopairs.

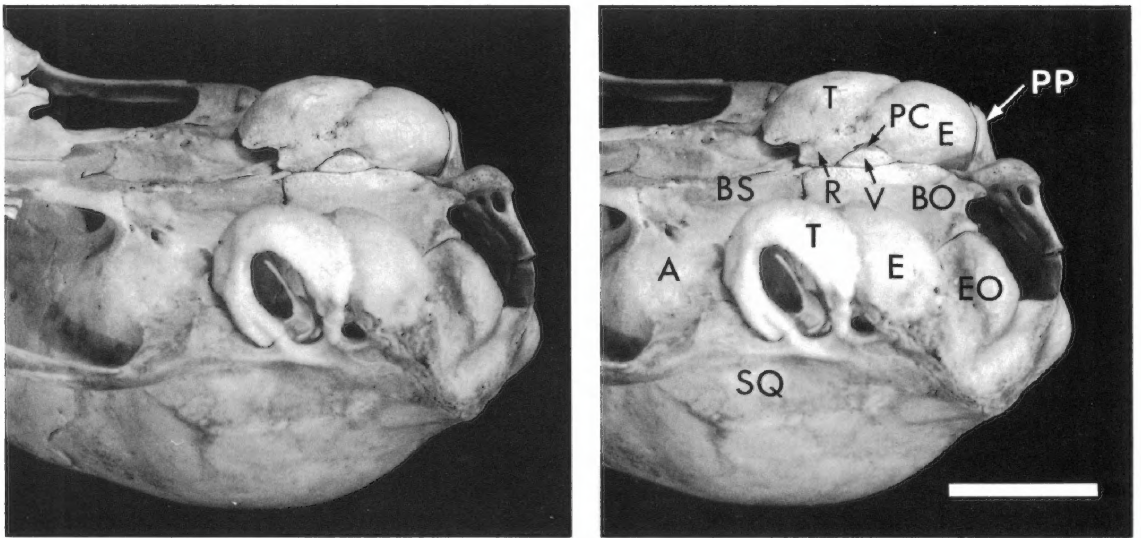


Fig. 2. Basicranium of the viverrid *Genetta genetta* (AMNH-M 169064), female neonate, Molepolole, Bechuanaland, South Africa, basilar length of skull 53.6 mm, dp3-4 nearly fully erupted, medial view of left auditory region to show relations of ventral petrosal process (V) to anterior chamber (T, R) and posterior (E) chamber of bulla in neonatal viverrid. Ventral petrosal process protrudes below the basicranial axis (BO) at this early ontogenetic stage. Note lines of recent fusion between ectotympanic (T), rostral (R), and caudal (E) entotympanics, the three bony elements making up the auditory bulla in the adult. Rostral entotympanic is situated on the anterior slope of the ventral petrosal process. Stereopair.

lacerate foramen for the entrance of the internal carotid artery into the cranial cavity. When the bulla is in place (fig. 1A), the ventral process is the only part of the petrosal that is exposed on the surface of the basicranium, its tip forming a tonguelike protrusion between bulla and basicranial axis.

The relationship of the bulla's ecto- and entotympanic components to the ventral petrosal process (VPP) is precise and of significance for the final adult form adopted by the bulla. In figure 1B, the caudal entotympanic and the posterior part of the ectotympanic have been removed from the auditory region to demonstrate the relationship of the rostral entotympanic to VPP. Rostral entotympanic fits against the anterior slope of VPP, and the ectotympanic is then fused to the edge of rostral entotympanic (this contact between rostral entotympanic and ectotympanic defines the thictic bulla of Viverridae—Hunt, 1987). Together these two elements form the anterior chamber of the viverrid auditory bulla. Note that the internal carotid artery enters the auditory region immediately posterior to VPP, travels along its lateral face, then enters a partial tube or groove in rostral entotym-

panic before turning medially to enter the cranial cavity at the middle lacerate foramen (fig. 1A).

This structural relationship of petrosal, VPP, rostral entotympanic, and ectotympanic is constant in the viverrids. Of special significance is the fact that the rostral entotympanic and ectotympanic ossifications are spatially segregated anterior to the petrosal promontorium by development of the ventrally extended process, resulting in development of a separate anterior bulla chamber. This suggests that the form of the petrosal, especially during its early ontogenetic history, could have been responsible for the division of the bulla into two chambers. Petrosal form seems to be a significant determining factor in the bulla configuration adopted by Viverridae.

In early ontogeny in viverrids (fig. 2), VPP is already developed, separating rostral from caudal entotympanic, and marking the entrance point of the internal carotid artery into the auditory region. So it is reasonable on developmental grounds that petrosal form plays a role in the creation of adult bulla pattern.

Herpestidae. The herpestid petrosal is situated much as in viverrids. In adult *Herpestes auro punctatus* (fig. 3A, B), VPP protrudes below the level of the basioccipital bone immediately posterior to the basioccipital-basisphenoid suture. As in viverrids, the process is well formed early in ontogeny (fig. 3A), maintaining its shape and relationships with bulla and basicranial bones into the adult stage.

The rostral entotympanic rests on the anterior slope of VPP in herpestids (figs. 3A, 4A) as in viverrids. Fused to the ventral edge of rostral entotympanic is the ectotympanic (thictic herpestid condition, Hunt, 1987), and along the line of contact between the two elements runs the internal carotid artery enclosed in the adult in a bony tube (figs. 3A, 4A, B). The petrosal acts as a transverse barrier within the auditory region, dividing an anterior chamber (formed by rostral entotympanic and ectotympanic, fig. 4A) from a posterior chamber (formed by caudal entotympanic, fig. 4B).

VPP in the neonatal herpestid (fig. 5) is a prominent tongue of bone tightly pressed against the basioccipital's lateral edge about at its midpoint. By contrast, in the adult herpestid (fig. 3B), the well-developed process is positioned closer to the anterior end of basioccipital. A considerable length of basioccipital occurs posterior to the process, indicating that relative growth during ontogeny posteriorly extended the basicranial axis and caudal entotympanic chamber of the bulla, paralleling the growth pattern of bulla and basicranial axis in viverrids (compare figs. 1 and 2 with figs. 3B and 5).

Hyaenidae. The hyaenid petrosal is developed as in viverrids and herpestids, having a prominent VPP extending ventrad to the level of, or slightly below, the basicranial axis in living *Crocuta* (fig. 6). In other hyaenids, VPP is present, but the process can be located deep within the auditory region hidden by the auditory bulla (e.g., *Hyaena brunnea*). VPP is situated slightly posterior to the basioccipital-basisphenoid suture in hyaenids, however the strong posterior growth of caudal entotympanic found in viverrids and herpestids is absent, and the distance posterior to the process is not great, remaining nearly constant during ontogeny. The strong pos-

terior growth of ectotympanic beneath the caudal entotympanic chamber has not been restricted in any way by the petrosal. In early ontogeny of *Crocuta* (Hunt, 1974a, fig. 35), VPP protrudes somewhat ventrad below the basioccipital as in the adult, and the overgrowth of the petrosal by ectotympanic seen in the adult has already occurred.

Felidae. In living felids, there is no evident VPP. Despite the apparent absence of the ventral process, felids parallel other living aeluroids in their dorsoventrally deep petrosal dividing the auditory region into anterior and posterior sections. In young lions, the petrosal promontorium is prolonged ventrad as an elongate arcuate crest. However, were it not for the fossil record, the fact that felids originally had a VPP would not be known. In the earliest true felids, assigned to *Proailurus* (figs. 11, 12), the petrosal retains a prominent VPP. As evolution progresses from *Proailurus* through *Pseudaelurus* to later felids, the developing bulla suppresses the ventral process of the promontorium, largely by means of caudal entotympanic growth and encroachment. Hence VPP is primitive for Felidae.

THE AUDITORY REGION IN THE OLDEST KNOWN AELUROID CARNIVORANS

The oldest generally acknowledged aeluroid carnivorans are represented by fossils from the Quercy fissures of France. The Quercy district has produced the world's largest and most diverse sample of early aeluroids from a single geographic area. The fossils can be placed for purposes of discussion into three groups, based on consensus common to the scientific literature: (a) the stenoplesictine aeluroids, *Stenoplesictis* and *Palaeoprionodon*, often considered viverrids (Teilhard, 1915; Piveteau, 1943, 1961; Bonis et al., 1973; Schmidt-Kittler, 1987) but placed by others within the Felidae (Beaumont, 1964; Ginsburg, 1979); (b) the proailurine felids, *Proailurus* and *Haplogale*, generally believed to include the ancestry of the modern felid radiation; (c) the nimravid cats (Ginsburg, 1979), *Nimravus*, *Quercylurus*, *Eofelis*, and *Dinailurictis*, first Old World representatives of a mid-Cenozoic radiation of catlike mam-

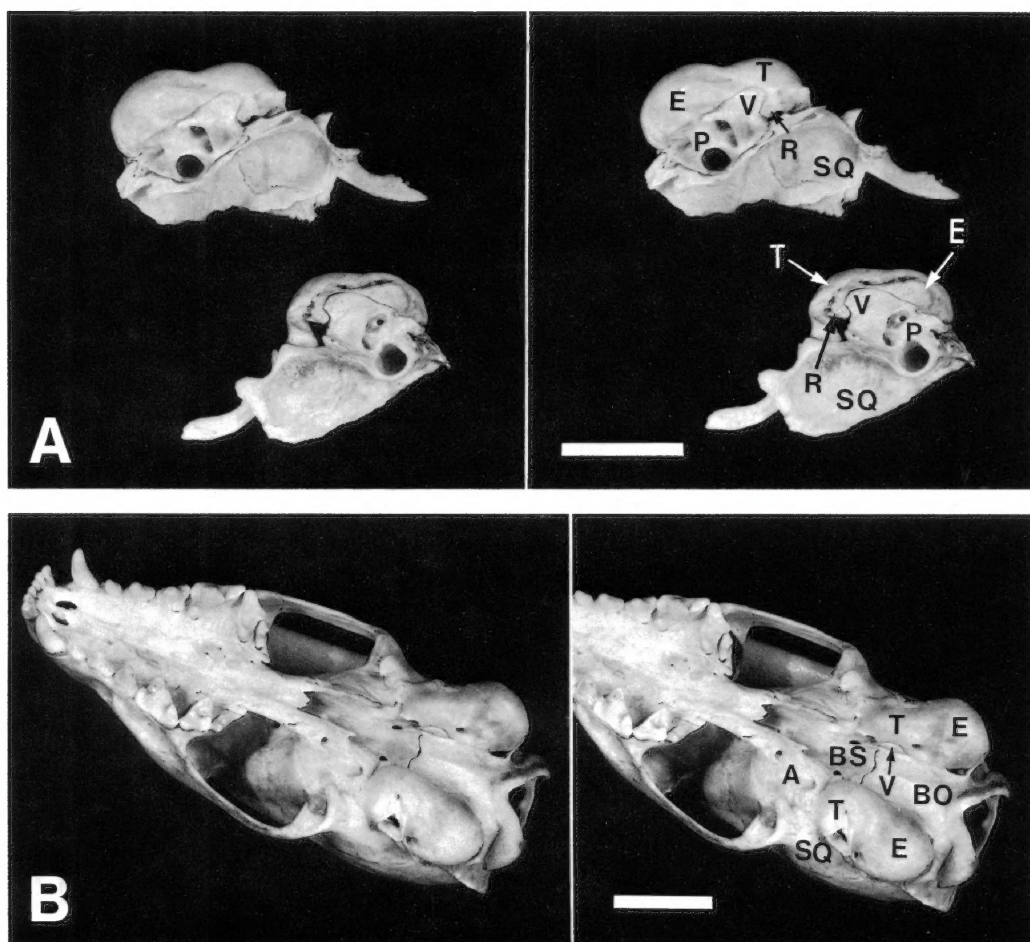


Fig. 3. Auditory region of the herpestid *Herpestes auropunctatus*: **A**, Internal (medial) view of petrosal-auditory bulla complex, removed from the skull, showing a developed ventral petrosal process (V) in both juvenile and adult; *top*, female adult (AMNH-M 189424), St. John, Virgin Islands, anterior to right; *bottom*, juvenile male (AMNH-M 59926), Nam Fong, Hainan, China, anterior to left. **B**, Basicranium of adult female in oblique ventral view, demonstrating the protrusion of the ventral petrosal process (V) below the bones (BO, BS) of the basicranial axis (AMNH-M 239641), St. Croix, Virgin Islands. Stereopairs.

mals on the northern continents, regarded by some workers as caniform Carnivora and not aeluroids. Also, even though its skull is not known, one should mention a problematical taxon, "*Viverra*" *simplicidens*, represented in the Quercy district by dental remains discussed by Teilhard (1915). It was later synonymized with *Proailurus* (Beaumont, 1964), but recently has been listed as a distinct early aeluroid genus, *Anictis* Kretzoi, present at the early Oligocene Quercy locality of Aubrelong 1 (Bonis et al., 1973; Bonis, 1974; Sigé et al., 1979: 44). *Anictis*, if in fact it is an aeluroid, and the nimravid *Eusmilus*, found at Aubre-

long 1 and Soumaillies, are the oldest European aeluroid carnivorans presently recorded in the paleontological literature.

Geographic distribution of these fossils reveals that all are exclusively Old World species with the exception of the nimravid cats. Nimravids occurred both in Eurasia and North America in the Oligocene, and extended into the Miocene of Europe, north Africa, and North America, becoming extinct worldwide in the late Miocene. Stenoplesictines occurred in the Oligocene of Europe (Teilhard, 1915; Sigé et al., 1979) and Asia (Hsanda Gol, Mongolia, Mellett, 1968), and have been

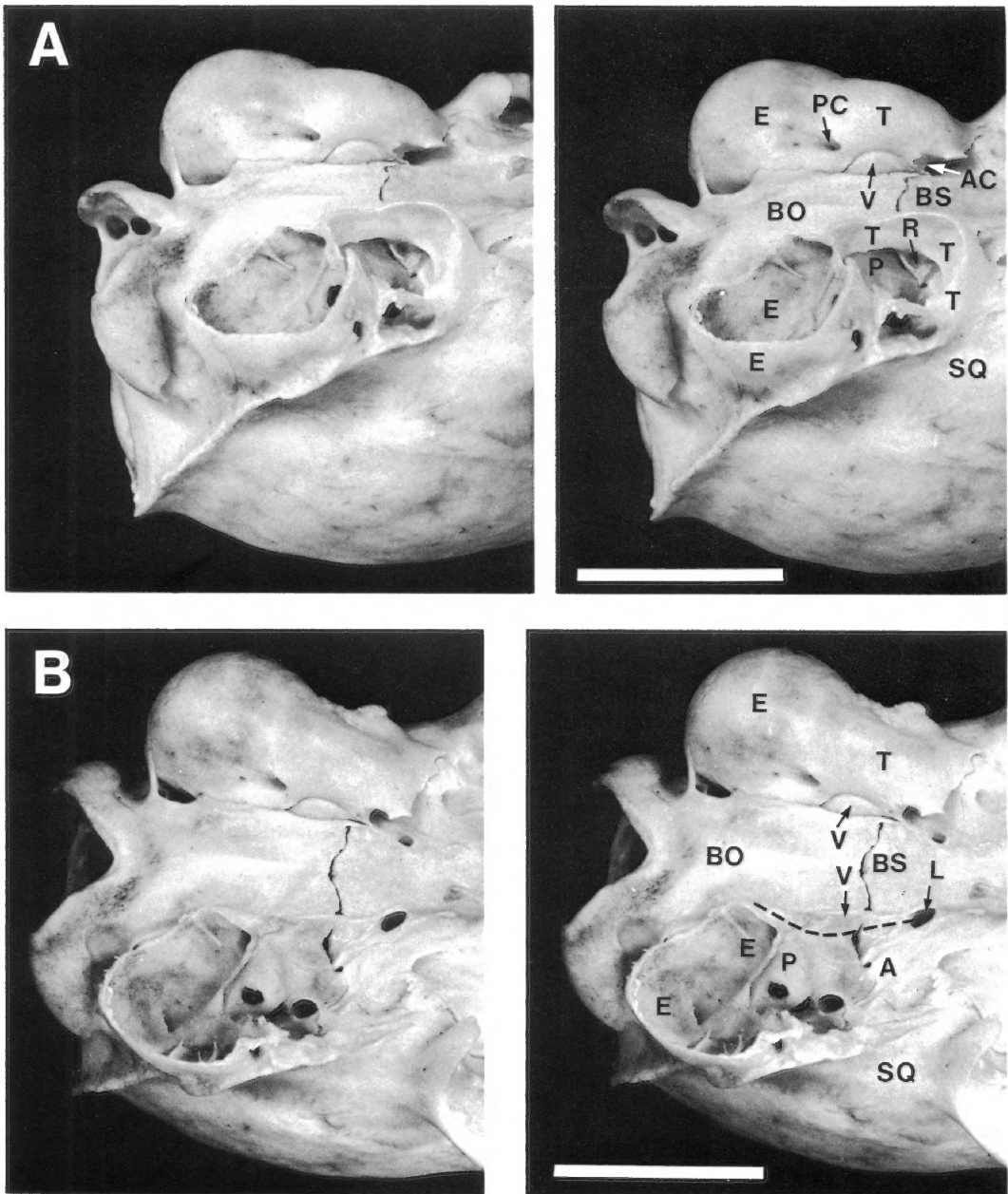


Fig. 4. Dissected auditory region of adult herpestid *Herpestes auro punctatus* (AMNH-M 239641), female, St. Croix, Virgin Islands, to show relationship of ventral petrosal process (V) to the auditory bulla: **A**, Basicranium in lateral view, bony floor removed from both anterior and posterior chambers of auditory bulla. Anterior chamber made up of ectotympanic (T) and rostral entotympanic (R) rests on petrosal, and displays contact between T and R (thicket herpestid state). A strongly inflated posterior chamber formed by caudal entotympanic (E) is situated behind the petrosal promontorium. Ventral petrosal process (V) is largely hidden by the bulla except where the process protrudes below the basioccipital; **B**, Basicranium in oblique ventral view, with the anterior chamber of the bulla (T, R) entirely removed, and only part of the caudal entotympanic remaining. Note the thin compressed ventral petrosal process (V) buttressing the lateral edge of basioccipital. Dashed line indicates path of internal carotid artery which runs within a bony tube formed by the medial wall of the bulla. Artery enters bulla at PC, exits bulla at AC, and enters cranium at middle lacerate foramen (L). Stereopairs.

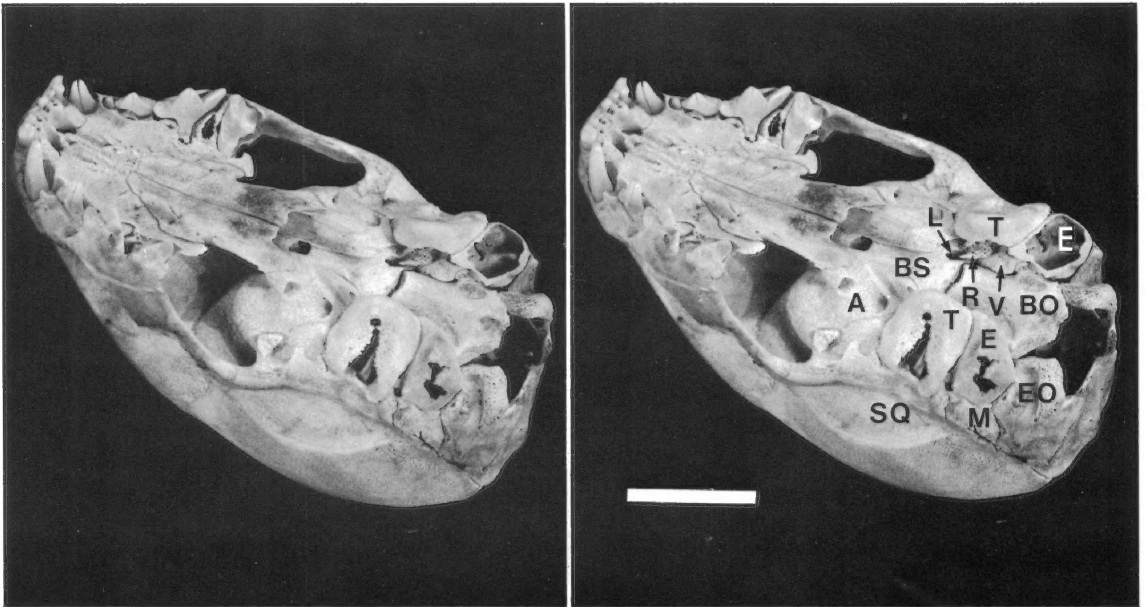


Fig. 5. Basicranium of the herpestid *Herpestes* (*Xenogale*) *naso* (AMNH-M 51089), male neonate, Medje, Zaire, basilar length 44.5 mm, showing developed ventral petrosal process (V) early in ontogeny, segregating rostral (R) from caudal (E) entotympanic bulla elements. Note junction of ectotympanic (T) and caudal entotympanic (E) to form incipient septum bullae. This spatial arrangement of bulla elements (T, E) is believed to have been present in the hypothetical herpestid-hyaenid ancestral stock whose bulla configuration transformed along two ontogenetic pathways, one leading to the modern herpestid, the other to the hyaenid condition. Stereopair.

recently reported from the early Miocene of Africa (Schmidt-Kittler, 1987). They are unknown from the New World. Proailurines in the strict sense are known only from the Old World Oligocene and early Miocene, and in fact are unknown outside Europe (Ginsburg, 1979).³

Identification of only two fundamental basicranial patterns among these early Old

³ A unique felid skull found in 1935 in mid-Hemingfordian rocks of North America (Ginn Quarry, Nebraska, FAM 61847) approaches the proailurine grade of European authors; P2 is present, reduced but still double-rooted. This cat is the oldest true felid known from the New World, and is much like *Pseudaelurus transitorius* from the Burdigalian of Wintershof-West (Dehm, 1950), the only Old World species of the genus in which P2 is still double-rooted. Dehm regarded this species as transitional between *Proailurus* and *Pseudaelurus*, hence such an animal might be considered a proailurine. The oldest known proailurines with unreduced double-rooted P2/p2 and P1/p1 present are not found outside Europe. Proailurines have not yet been reported in the recently excavated, stratigraphically controlled deposits in the Quercy district (Bonis et al., 1973; Crochet et al., 1981), although they are known from the older Quercy collections (Teilhard, 1915).

World aeluroids justifies their placement in two groups: (a) stenoplesictines and proailurines; (b) nimravids. Nimravids have been discussed in detail elsewhere (Hunt, 1987); they appear to represent an early aeluroid branch identified by a unique auditory bulla pattern in which a true septum bullae is absent, and the anterior wall of the bulla is formed by a nimravid autapomorphy: the overlap of an elaborate bony process of the ectotympanic and an anterior bony lamina of the caudal entotympanic. Although a developed VPP is not present, the nimravid promontorium is slightly elevated, forming in some individuals a medially situated bulge that may be a vestige of the process. Possibly the ancestral nimravid stock initially possessed a developed VPP as in other aeluroids, but in time it became reduced in size.

The auditory bulla of stenoplesictines and proailurines stands in contrast to the nimravid bulla. In stenoplesictines and proailurines, the bulla includes an anterior chamber largely formed by ectotympanic (with probable rostral entotympanic contribution), and a posterior chamber formed by a caudal en-

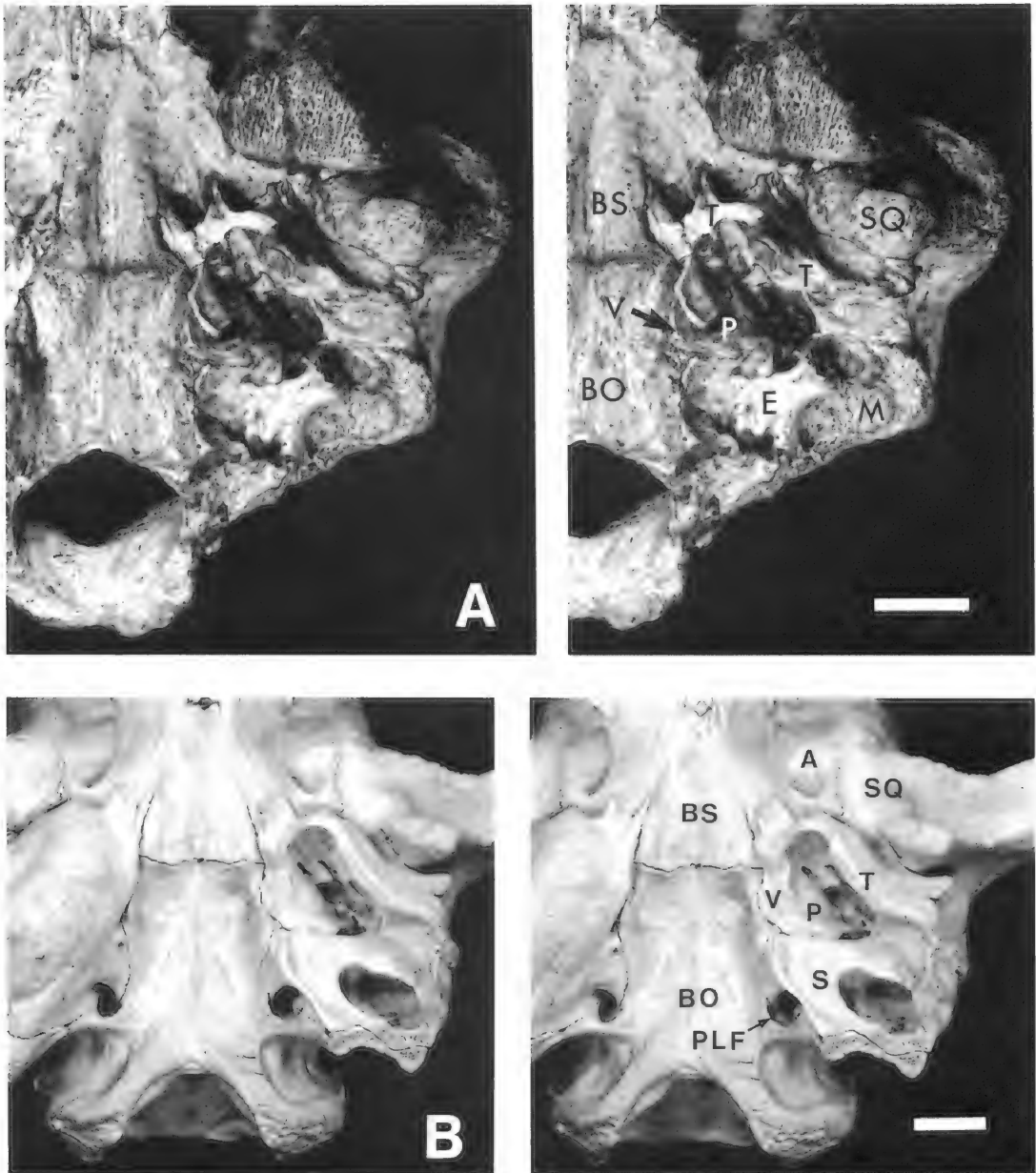


Fig. 6. Basicranium of the hyaenid *Crocuta crocuta*: **A**, Left auditory region of Pleistocene *Crocuta crocuta* (AMNH 18730), Wanhsien, China, ventral view. The ventral bony floor of the bulla has been removed (including the hyaenid internal septum) to reveal the ventral petrosal process (V) applied against lateral edge of basioccipital. Note caudal entotympanic fitted against the posterior slope of the promontorium, and rostral entotympanic resting on the anterior slope; **B**, Left auditory region of living *Crocuta crocuta* (UNSM-ZM 5012), Africa, ventral view. Ventral bony floor of bulla removed, showing ventral petrosal process applied to basioccipital. An opening has been cut in the hyaenid septum to reveal caudal entotympanic chamber dorsal to septum. Stereopairs.

totympanic. Ectotympanic in these carnivorans rests on the ventral promontorial surface of the petrosal where, in many specimens, a facet is developed at the contact between promontorium and ectotympanic rim (Lavocat,

1952). Behind the anterior chamber, a posterior chamber of very small size, enclosed by a caudal entotympanic element, was undoubtedly present in stenoplesictines and primitive proailurines. The caudal entotym-

panic has never been found in place in a skull, but its presence is documented by indentations registered upon the petrosal and surrounding bones of the auditory region. Earlier workers have suggested that the posterior chamber was formed by a cartilaginous [caudal] entotympanic, and this indeed may have been the case, or the entotympanic could as easily have been a loosely attached bony element. The double-chambered stenoplesictine-proailurine bulla is similar in configuration to the double-chambered bullae of living aeluroids, and is a principal reason why these groups have been considered aeluroids by earlier workers.

If, as bulla morphology indicates, stenoplesictines and proailurines are aeluroids, then other aspects of auditory anatomy should also reflect this ancestry. In fact, the petrosal in the two groups is characterized by a prominent ventral process of the promontorium (VPP) as in the living aeluroid families discussed earlier. There can be little doubt that these carnivorans are aeluroids as earlier studies have suggested. However, a close examination of the petrosal promontorium in stenoplesictines and proailurines demonstrates not only their near identity of form, but also their similarly developed VPP, which is more posteriorly situated in these Oligocene skulls than in the living aeluroids. VPP in these animals is a robust ventral continuation of the promontorium, not yet altered to the thinner bony lamina found in most living aeluroids, nor suppressed by bulla growth as in living felids. Furthermore, VPP is more centrally located along the lateral edge of the basioccipital bone, and is not displaced into the anterointernal corner of the auditory region as in many living aeluroids.

Because both stenoplesictines and proailurines are characterized by this type of petrosal with ventral promontorial process, it must be of considerable antiquity within the Aeluroidea.

THE STENOPLSICTINE CONCEPT

Although Stenoplesictinae was first used as a subfamily by Schlosser (1923), the concept of an allied group of genera including *Stenoplesictis* first appeared in Teilhard's classic monograph (1915) on the Quercy carnivorans.

Teilhard's stenoplesictoid concept united a group of small Quercy Carnivora on the basis of their similarly specialized shearing dentitions developed through parallel evolution: "I unite, under the name *Stenoplesictoides*, a very homogeneous, yet very confused grouping of forms, generally small, characterized by their common tendency to develop a dentition, at least in the lower jaw, approaching that of the Felidae: p3-4 triangular and denticulate [with accessory cusps]; m1 high and trenchant, with metaconid and talonid very reduced; m2 very small or absent; canine trenchant and grooved." Teilhard explained his concept further: "Because the *Stenoplesictoides* tend to develop a very simplified type of dentition, where convergences are inevitable, one must make a special attempt to understand, from certain [morphological] details, often very small, the [evolutionary] pathways they have followed. . . . Such research has a better chance of guiding us toward a natural classification of forms than simply grouping the fossils on the basis of the phases of reduction or of simplification of the teeth."

Teilhard never intended to designate stenoplesictoids as a formal taxonomic category. It was a convenient morphologic grouping of lower dentitions that reflected similar feeding specializations: the high shearing carnassial, reduction of the rear molars, and the development of multicusped tall, thin, catlike premolars. This morphologic trend, often seen among carnivorans, of convergence toward a shearing dentition is typical of dental patterns that Crusafont and Truyols (1956) defined under their concept of hypercarnivory. The original list of genera placed in the stenoplesictoid division by Teilhard included what today are understood to be primitive aeluroids (*Stenoplesictis*, *Palaeoprionodon*, *Stenogale*), primitive true felids (*Proailurus*), and a viverravid (*Palaeogale*). Hence Teilhard's stenoplesictoid division constitutes not only an adaptive dental grade, but one so broad that it would be meaningless in a formal taxonomic sense.

Shortly thereafter, Schlosser (1923) unfortunately created the subfamily Stenoplesictinae to encompass Teilhard's stenoplesictoid genera, a step at odds with Teilhard's original intent. Moreover, Schlosser failed to

clarify the phylogenetic relations of these small carnivorans. In fact, as Pilgrim (1931) later made clear, Schlosser gave no apparent reason for this grouping. Despite the fact that well-preserved basicrania of stenoplesictines were known, and also that basicranial anatomy had been emphasized as an important tool in decoding carnivoran phylogeny by English zoologists (Turner, 1848; Flower, 1869; Mivart, 1882a, 1882b), Schlosser placed his Stenoplesictinae as a subfamily of the Mustelidae, even though the majority of the genera considered by Teilhard and by Schlosser were, from the standpoint of basicranial anatomy, aeluroid carnivorans. This preoccupation with mustelid affinity was perpetuated by Helbing (1928) who called *Proailurus* a felinoid mustelid.

Pilgrim (1931) attempted to remedy the situation by removing some of the "stenoplesictoid" genera to living carnivoran families. Pilgrim (1931, 1932) recognized that Schlosser gave no valid phylogenetic criteria for uniting the various stenoplesictine genera into a subfamily, and argued that the similar features of these taxa, chiefly the teeth, "are no more than parallel adaptations or a modified retention of primitive features, in which case the various stenoplesictine genera should properly find a place among the primitive members of that modern family to which they most appropriately belong." He placed *Proailurus* and *Stenogale*⁴ in the Proailurinae, a subfamily of primitive felids, and regarded *Stenoplesictis* and *Palaeoprionodon* as primitive viverrids.

In 1943, following a thorough study of a complete skull of *Stenoplesictis*, Piveteau concluded, as had Pilgrim, that the stenoplesictoid group should be subdivided. Piveteau (1943: 71) thought the similarities between the auditory bulla of *Prionodon* and *Stenoplesictis* were sufficiently strong to place the latter as a viverrid. His description of the

auditory bulla of *Stenoplesictis* was detailed for its time, including the best photographic illustrations of its auditory region yet published. He (1943: 69) stressed the strong similarity, in fact to him near morphologic identity (except in teeth), between the skulls of *Stenoplesictis* and *Palaeoprionodon*. Later in 1961, he employed the subfamily Stenoplesictinae Schlosser 1923 for only *Stenoplesictis* and *Palaeoprionodon*, thus limiting Schlosser's subfamily to just these two genera, and explicitly stated that these two genera "ont atteint le stade structural viverrien et doivent constituer une sous-famille de Viverrides, les Stenoplesictines." Hence the studies by Teilhard, Pilgrim, and Piveteau are the basis for the current placement of stenoplesictines as Viverridae.

In grouping *Palaeogale* with early aeluroids such as *Stenoplesictis* and *Palaeoprionodon*, Teilhard necessarily relied on the dental evidence at his disposal. These carnivorans are simply convergent in their dentitions. Teilhard was aware that two distinctive basicranial types were included in the stenoplesictoid group: the type "viverrienne" of *Stenoplesictis* and *Palaeoprionodon*, and the "weasel-like" basicranium of *Palaeogale* figured earlier by Filhol [Teilhard had only lower jaws of *Palaeogale* from Quercy but was aware of the basicranial structure from a specimen of this genus figured by Filhol—at that time Teilhard (1915: 70) had knowledge of but had not seen the basicranium of *Stenogale*].

Today it is clear that, as Teilhard had supposed, stenoplesictoids comprise several diverse branches. Basicranial evidence confirms the wide separation of the viverravid *Palaeogale* from the early aeluroids *Stenoplesictis* and *Palaeoprionodon*; the affinities of *Stenogale* remain to be demonstrated on basicranial evidence, but if the holotype of "*Proailurus*" *julieni* is a *Stenogale* (Teilhard, 1915), then its basicranium indicates that it is an early aeluroid (see Lavocat, 1952). The creation of a subfamily by Schlosser from Teilhard's dentally based stenoplesictoid group was premature, since at that time the true affinities of the member genera were not clear. However, if *Palaeogale* is removed from Teilhard's initial grouping, then only primitive aeluroids sharing a close relationship re-

⁴ The phylogenetic position of *Stenogale* is not clearly resolved even in the more recent literature (compare Bonis, 1973; Sigé et al., 1979 with Beaumont, 1964; Ginsburg, 1979). In this report my concept of *Stenogale* is based upon the holotype skull and jaws of *S. julieni*, figured by Viret (1929, pl. 12, figs. 5, 8, 9), which preserves an aeluroid auditory region having a petrosal with the ventral promontorial process. Hence I regard this species as an early aeluroid.

main: *Stenoplesictis*, *Palaeoprionodon*, *Proailurus*, *Stenogale*. The basicrania of these four genera are morphologically very similar.

Beaumont (1964) placed all four genera in a felid subfamily Proailurinae, comprising the tribes Stenoplesictini (*Stenoplesictis*, *Palaeoprionodon*) and Proailurini (*Proailurus*, *Stenogale*). Ginsburg (1979) adopted a similar arrangement but used a slightly different taxonomy in which a felid subfamily Felinae includes a tribe Proailurini made up of two subtribes, one with *Stenoplesictis* and *Palaeoprionodon*, the other with *Proailurus*, *Stenogale*, and *Haplogale*.⁵ However, whether one employs the proailurine taxon at the level of subfamily or tribe, the category remains an aggregation of genera primarily based on plesiomorphic features, hence a paraphyletic group. Since it is not the intent of this study to establish the detailed cladistic relationships among these forms, I follow Beaumont and Ginsburg in recognizing a relationship between *Stenoplesictis* and *Palaeoprionodon* on the one hand, and among *Proailurus*, *Haplogale*, and *Stenogale* on the other. I shall call the first two genera "stenoplesictines," and the last three "proailurines," without formal taxonomic implications, emphasizing that placement of all five genera in the Felidae is inappropriate. It is sufficient to note that only *Proailurus* (including *Haplogale*) by current consensus seems to be involved in the ancestry of the true felids (Ginsburg, 1983), whereas the remaining genera (*Stenoplesictis*, *Palaeoprionodon*, *Stenogale*) appear to include species closely related to viverrids, as well as other early experiments in aeluroid evolution that left no known descendants. Therefore, retention of a subfamily (Stenoplesictinae) or tribe (Stenoplesictini) within Felidae for the primitive aeluroids *Stenoplesictis* and *Palaeoprionodon* is not supported by reliable synapomorphies: the hypercarnivorous dentitions of *Stenoplesictis* and *Palaeoprionodon* are only convergent on felids as Teilhard and others were well aware. The dental specializations that are present in these two genera

are aeluroid, not felid, specializations. If we turn to the stenoplesictine basicranium, it seems probable that the similarities shared with felids are primitive features, such as the shape of the petrosal. At present, only *Palaeoprionodon* among stenoplesictines appears to have a phyletic connection with living viverrids. However, both European stenoplesictine genera could eventually prove to be most closely related to Viverridae. Based on the present uncertain state of our knowledge, I conclude only that stenoplesictines are primitive aeluroids, not felids, and that while a relationship of certain stenoplesictines to viverrids is probable, it remains to be confirmed.

A NEW STENOPLESICTINE BASICRANIUM FROM QUERCY

Among the most plesiomorphic of the early aeluroids in terms of basicranial structure are the stenoplesictines *Stenoplesictis* and *Palaeoprionodon*. Basicranial structure of stenoplesictines is well preserved only in skulls from Quercy, all maintained in European museums (table 1). The skull, including the basicranium, of *Stenoplesictis* was described and figured by Piveteau (1943: 6–8), and the skull of *Palaeoprionodon* by Teilhard (1915: 77–78). These are small carnivorans with skull lengths of about 7 to 9 cm. Teilhard (1915: pl. IX, figs. 10, 14, text-fig. 13) illustrated two skulls of *Palaeoprionodon laman-dini*, both in the Paris Museum, one showing the basicranium and auditory bulla. Later, Piveteau (1943: pl. I, fig. 3, 3A, text-figs. 2, 3) illustrated a well-preserved skull, also with basicranium and bulla, of *Stenoplesictis cayluxi*, in the collection of the Faculty of Sciences, Marseille.

I am able to confirm Piveteau's description of the auditory region of *Stenoplesictis* through study of a partial skull (BMNH M1381) from Quercy in the British Museum, discovered during a research visit in 1987. Despite the absence of the teeth and palate, M1381 represents the skull of a small stenoplesictine, almost certainly *Stenoplesictis cayluxi*: it is nearly identical to the Marseille skull of *S. cayluxi* figured by Piveteau (1943). Although the auditory bullae are missing, the auditory region of M1381 is unquestionably that of a

⁵ *Haplogale* is considered a separate proailurine genus by Ginsburg (1983), and by Beaumont (1961) a synonym of *Proailurus*. The oldest proailurines are probably represented by the Quercy sample of *Haplogale media*.

TABLE 1
**Basicrania of Early Aeluroid Carnivorans
 Exclusive of Nimravids**

STENOPLESICTIS	
1.	Skull of <i>Stenoplesictis cayluxi</i> , Collection de Geologie, Faculte des Sciences de Marseille (Piveteau, 1943).
2.	Skull of <i>Stenoplesictis cayluxi</i> , collection of A. Muller, Leipzig, P2004 (Fischer, 1983).
3.	Skull of <i>Stenoplesictis</i> , not illustrated (Filhol, 1882: 66–67, listed in Fischer, 1983).
4.	Skull of <i>Stenoplesictis</i> , collection of the British Museum (M1381), not previously described.
PALAEOPRIONODON	
5–6.	Two skulls of <i>Palaeoprionodon lamandini</i> , collection of the Paris Museum (Teilhard, 1915: pl. 9, figs. 10, 14).
7.	Skull of <i>Palaeoprionodon</i> sp., collection of the British Museum (M1723) (Lydekker, 1885: 96–98, fig. 9).
8–9.	Two skulls of <i>Palaeoprionodon</i> , Munich Museum (Schlosser, 1889: 146).
Additional skull material of stenoplesictines is conserved at Montauban, Louvain, Lyon, and Basel (G. de Beaumont, personal commun., 1985).	
PROAILURUS	
10.	Skull of holotype of <i>Proailurus lemanensis</i> , Paris Museum (Filhol, 1879: pl. 26).
STENOGALE	
11.	Skull of holotype of " <i>Proailurus</i> " <i>julieni</i> , Paris Museum, Julien collection (Filhol, 1879: 192, pl. 27, figs. 5, 6, 8, 13; Viret, 1929: pl. 12, fig. 5; Lavocat, 1952: fig. 2).

stenoplesictine carnivoran. To demonstrate the close correspondence of petrosal structure between the British Museum stenoplesictine (M1381) and the skull of *Nandinia*, they are

compared in figures 7–10 and in the subsequent discussion.

A second stenoplesictine skull (M1723) in the paleontological collection of the British Museum, labeled as *Stenoplesictis cayluxi*, is also from Quercy, and was originally figured by Lydekker (1885: 97, fig. 9); the specimen includes an upper dentition in association with the anterior part of the basicranium, including the petrosal. Lydekker's skull, despite its attribution to *Stenoplesictis*, is much closer in size, skull form, and dentition to the stenoplesictine *Palaeoprionodon* figured by Teilhard (1915, figs. 10, 14), and it is referred here to this latter genus (table 1). Comparative measurements of skull and basicranium in representative stenoplesictines and proailurines are presented in table 2.

PETROSAL FORM IN THE LIVING AELUROID *NANDINIA BINOTATA*

In a previous discussion of the phylogenetic position of *Nandinia* (Hunt, 1987), I suggested that numerous plesiomorphic traits found in this small African arboreal civet indicate its retention of a primitive aeluroid morphology for much of Cenozoic time. The animal's auditory bulla, in fact its entire auditory region, is morphologically what one would predict in a stem aeluroid, a species that most probably existed in the early Cenozoic.

An important morphologic feature mentioned briefly in my earlier presentation (Hunt, 1987: 44) was the configuration of the petrosal in *Nandinia*. Here I wish to amplify that point. Unlike the majority of living ae-

TABLE 2
Comparative Dimensions (mm) of Stenoplesictine and Proailurine Skulls

Taxon	Basilar length	Greatest width of braincase	Width between condyloid foramina	Width between alisphenoid canals
<i>Stenoplesictis</i> (Marseille)	83.4	28.3	11.3	10.5
<i>Stenoplesictis</i> (M1381)	(80–85)	30.6	12.0	12.8
<i>Palaeoprionodon</i> (Paris Mus.)	73.2 (77.6)	28.6 28.6	10.3 —	10.2 —
<i>Palaeoprionodon</i> (M1723)	(70)	27.0	(10)	(9.5)
<i>Stenogale julieni</i>	(72–73)	25	10	(8.1)
<i>Proailurus lemanensis</i>	(130)	46	15.7	20.6

() = estimated.

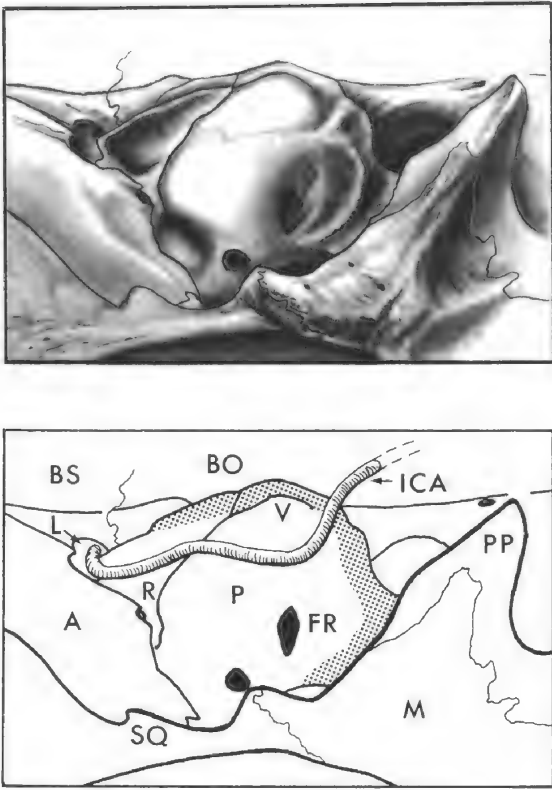


Fig. 7. Plesiomorphic features of the auditory region of the living aeluroid *Nandinia binotata* (shown in lateral view, anterior to left, bulla removed) are remarkably similar to equivalent features of the auditory region of Oligocene stenoplesictine aeluroids (see fig. 8), suggesting the antiquity of auditory pattern in *Nandinia*. *Nandinia*'s petrosal displays both the same general form and primitively configured ventral petrosal process as seen in stenoplesictines. The small size and rudimentary development of caudal entotympanic occur in both groups (attachment of caudal entotympanic to petrosal and rostral entotympanic indicated by stippled pattern). Transpromontorial path of the internal carotid artery in *Nandinia*, running in proximity to the medial wall of the bulla, is believed to be the primitive course of the artery for Aeluroidea.

luroids, *Nandinia* retains a petrosal shaped like that of Oligocene stenoplesictines. Petrosal form appears to have been arrested in *Nandinia* at a phylogenetic stage comparable to that found in primitive stenoplesictine basicrania from Quercy.

Nandinia's petrosal (fig. 7) was compared with the petrosal of the recently identified stenoplesictine basicranium (fig. 8) in the

British Museum (M1381), and with the petrosal retained in the British Museum skull (M1723) of *Palaeoprionodon* figured by Lydekker (1885). Comparisons also were made with descriptions and illustrations of stenoplesictines and proailurines in the literature (table 1).

Nandinia's petrosal promontorium retains the robust centrally situated VPP of these early aeluroids, buttressing the edge of the basioccipital. As in stenoplesictines, VPP is applied to the lateral edge of the basioccipital about midway along its length. Stereophotographs of the basicranium of *Nandinia* (figs. 9A, 10A) demonstrate that VPP extends ventrad beyond the plane of the basioccipital; VPP is similarly extended in the stenoplesictine skull (figs. 9B, 10B) but the extension is less obvious due to ventral downturn of the edge of the basioccipital, a condition of the basicranial axis found in stenoplesictines but not pronounced in *Nandinia*. Anterior to VPP, the surface of *Nandinia*'s promontorium forms a smooth, slightly concave slope. On the medial surface of this slope rests the rostral entotympanic (fig. 9A). This slope is similarly configured in the stenoplesictine; however in the extinct aeluroid, only fragments of bone are present at the location of rostral entotympanic.

Of particular interest is a facet on the promontorium just anterior to the round window in the stenoplesictine which has no counterpart in *Nandinia*. As indicated by Lavocat (1952), this facet receives the flanged edge of ectotympanic where it is seated upon the promontorium. This is a derived trait; the unfaceted state seen in *Nandinia* is regarded as more primitive. In *Nandinia* the posterior ectotympanic rim is very close to the promontorium but does not rest upon it or create a facet.

In living aeluroids, the ectotympanic usually contacts the promontorium adjacent to the round window where a similar facet often is developed (e.g., viverrid *Civettictis*, herpestid *Paracynictis*, felid *Lynx*). Because of the apposition of petrosal promontorium and ectotympanic rim in Aeluroidea, the promontorial facet is commonplace.

The development of a strong promontorial facet correlates with the slightly inflated condition of ectotympanic documented by Pive-

teau (1943) in *Stenoplesictis*. In stenoplesictines the ectotympanic is somewhat advanced in its slight to moderate degree of inflation or chambering, and has progressed beyond the primitive nearly planar form predicted in the hypothetical aeluroid ancestor, and closely approached by *Nandinia*. *Nandinia* remains the most primitive known aeluroid in this respect in that its ectotympanic is only slightly, if at all, modified from the plesiomorphic aeluroid state, and does not contact the promontorium (fig. 10A). However, *Nandinia*'s ectotympanic most closely approaches the petrosal promontorium at the point on that bone where the facet appears in stenoplesictines, and it is evident that inflation of the ectotympanic could lead to contact with petrosal and development of such a facet. Hence the morphology of ectotympanic rim and petrosal promontorium in *Nandinia* is arrested in a structural stage that immediately foreshadows the faceted condition seen in many living and extinct aeluroids.

In both *Nandinia* and the stenoplesictine (fig. 10A, B), the ventrally extended petrosal promontorium divides the auditory region into two parts, resulting in the segregation of bulla chambers common to the aeluroid group. In the stenoplesictines, this segregation is more complete, primarily due to the large dorsoventrally deep petrosals relative to the small skulls of these animals. The relative volumes of the bulla chambers also correspond in *Stenoplesictis* and *Nandinia*: the posterior chamber is small in volume, the plesiomorphic aeluroid condition.

Furthermore, the attachment of caudal entotympanic's posterior margin, whether cartilage or bone, produces in *Nandinia* and in stenoplesictines a diagnostic registration on the posterior margin of the petrosal, best described as a shallow trough or depression (this line of attachment is indicated by stipple in figs. 7, 8; see also fig. 9A, B, black triangles). In living *Nandinia*, we know from direct observation that this trough receives the only slightly inflected edge of the cartilaginous caudal entotympanic (Hunt, 1987, fig. 6). There is no doubt that this is its function in stenoplesictines as well, because the configuration of this trough in both *Nandinia* and the British Museum *Stenoplesictis* is nearly

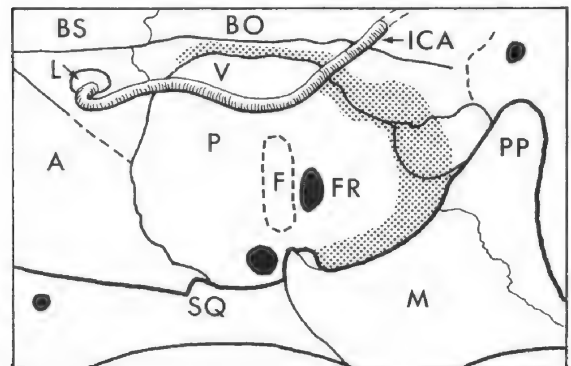
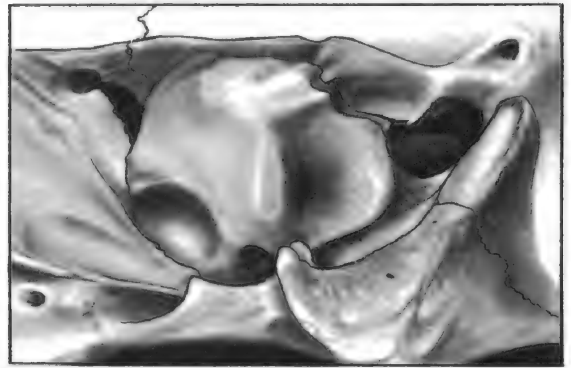


Fig. 8. Auditory region of the extinct Oligocene stenoplesictine aeluroid *Stenoplesictis cayluxi* (BMNH M1381, lateral view, anterior to left, bulla removed), from the Quercy district, France, for comparison with the auditory region of the living aeluroid *Nandinia* in figure 7. *Stenoplesictis* differs in having slightly greater inflation of ectotympanic, resulting in deeper registration marks for ectotympanic on squamosal and alisphenoid, and in a prominent facet on the petrosal (F) where the ectotympanic rim makes contact with the promontorium. Stipple pattern shows that line of attachment for rudimentary caudal entotympanic is developed as in *Nandinia*. Path of internal carotid artery restored in conformity to the path known in *Nandinia*.

identical, bordered by a flanged edge which marks the anterior limit of caudal entotympanic attachment (figs. 7–10). Lack of caudal entotympanic inflation in *Nandinia* and the stenoplesictine is demonstrated by the very small space available for the posterior chamber of the bulla, and is also indicated by the primitive posteroventrally directed paroccipital processes present in both animals (fig. 9A, B) which fail to contact the bullae. In living aeluroids with an enlarged caudal entotym-

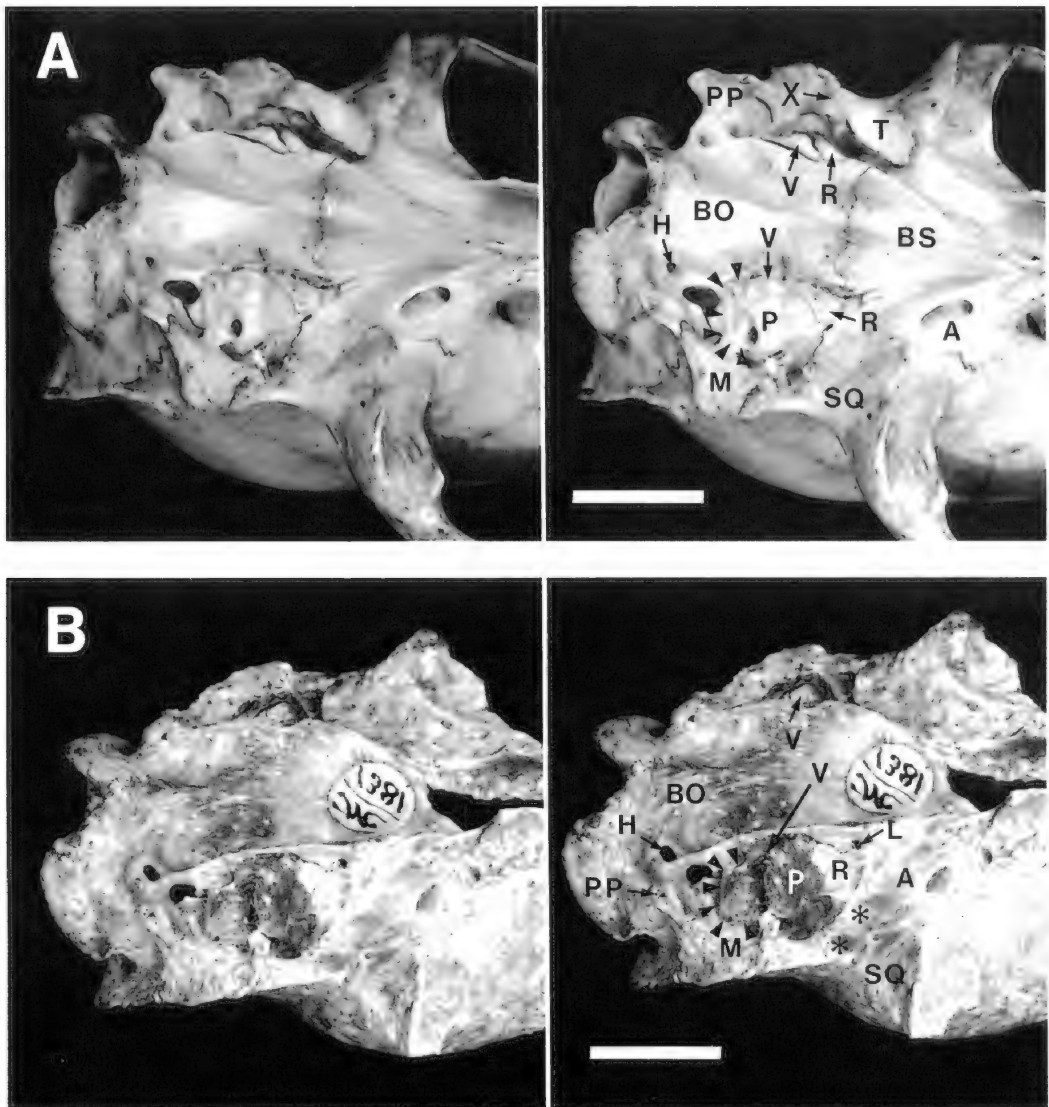


Fig. 9. **A**, Basicranium of the living aeluroid *Nandinia binotata* (AMNH-M 51492), young adult female, Niapu, Zaire, oblique ventral view, bulla removed from left auditory region, except for rostral entotympanic, and only cartilaginous caudal entotympanic removed from right auditory region. **B**, Basicranium of extinct stenoplesictine aeluroid *Stenoplesictis* (BMNH M1381), Quercy, France, oblique ventral view, showing bulla removed from auditory region, except for rostral entotympanic fragments. Note in both **A** and **B** the correspondence in form of petrosal, ventral petrosal process (V), and the small area posterior to petrosal for caudal entotympanic. A similar line of attachment (indicated by six black triangles in each photograph) of caudal entotympanic to the petrosal is found in both of these carnivorans. Asterisks mark registration of ectotympanic on squamosal and alisphenoid. Stereopairs (negatives printed in reverse for comparison with fig. 12).

panic (e.g., figs. 1, 4), the paroccipital process is contacted by and joined to the inflated bulla, and can become quite thin and expanded over the posterior surface of the caudal entotympanic.

Other details of petrosal form, including

the tensor tympani fossa, epitympanic recess, bony canal for the facial nerve, mastoid geometry, and the configuration of the surrounding basicranial bones, are very similar in *Nandinia* and *Stenoplesictis*.

The path of the internal carotid artery is

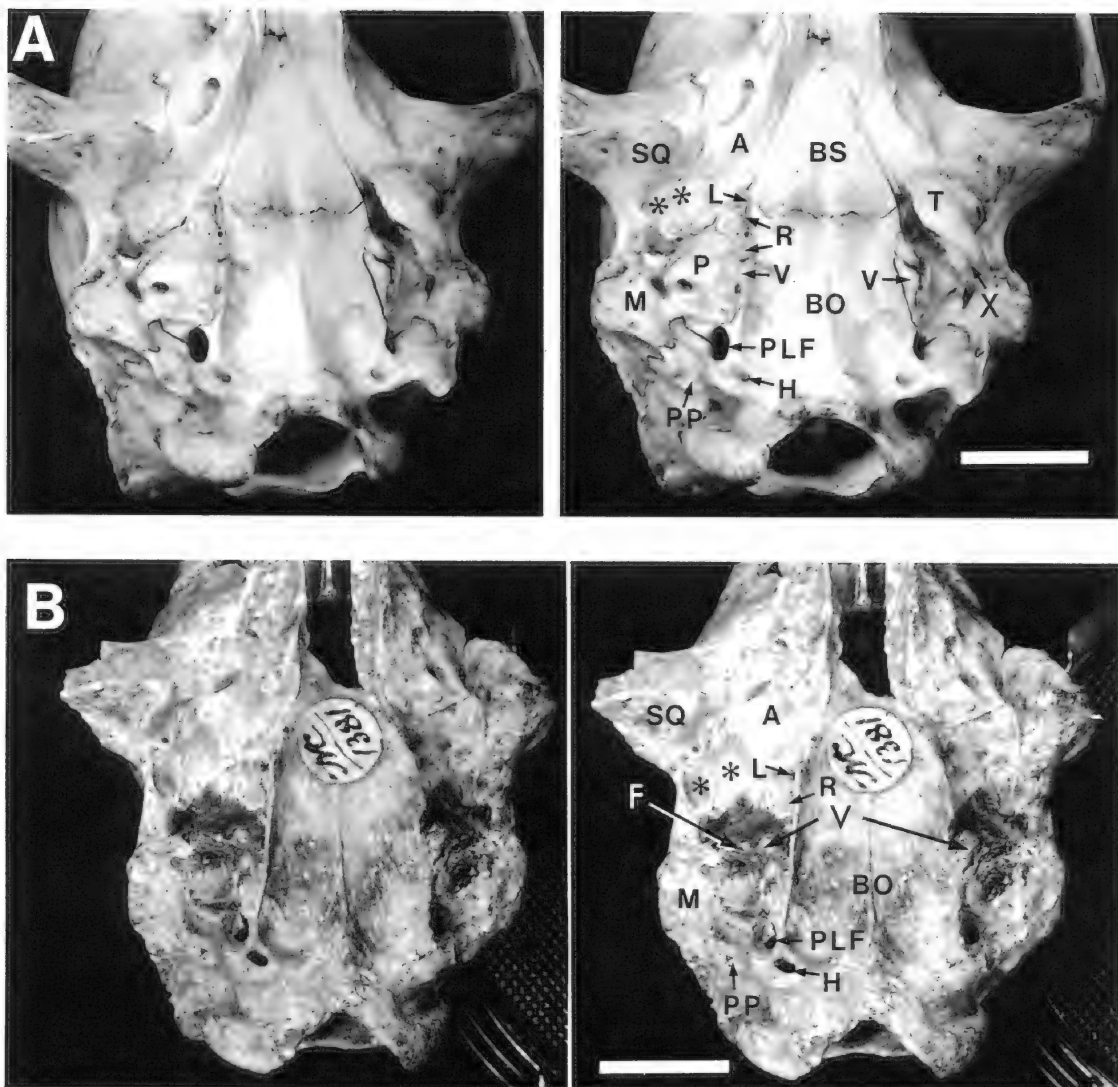


Fig. 10. **A**, Basicranium of *Nandinia binotata* (AMNH-M 51492), same individual as figure 9A, ventral view, bulla removed from right auditory region, except for rostral entotympanic, and only cartilaginous caudal entotympanic removed from left auditory region. **B**, Basicranium of *Stenoplesictis* (BMNH M1381), same individual as figure 9B, ventral view, bulla removed from right auditory region except for rostral entotympanic fragments. Note that the ventrally expanded petrosal tends to divide the auditory region into anterior and posterior parts. Asterisks mark registration of ectotympanic on squamosal and alisphenoid. Stereopairs.

confirmed in *Nandinia* by earlier work of Chapuis (1966) and Wible (personal commun., 1983). This path is restored in figure 7 wherein the artery travels lateral to VPP on the promontorium, then runs along the lateral face of rostral entotympanic, and turns mediad at the anterior end of rostral entotympanic to enter the cranial cavity at the middle lacerate foramen. A similar course is

inferred for the artery in stenoplesictines (fig. 8). In *Nandinia*, the artery traverses the middle ear cavity in proximity to (lateral to) the medial wall of the bulla; the path of the artery is not within the bulla wall, and in fact passes through it at only one point, just posterior to VPP, where it enters the middle ear cavity.

This route probably represents the primitive course of the internal carotid in the Ae-

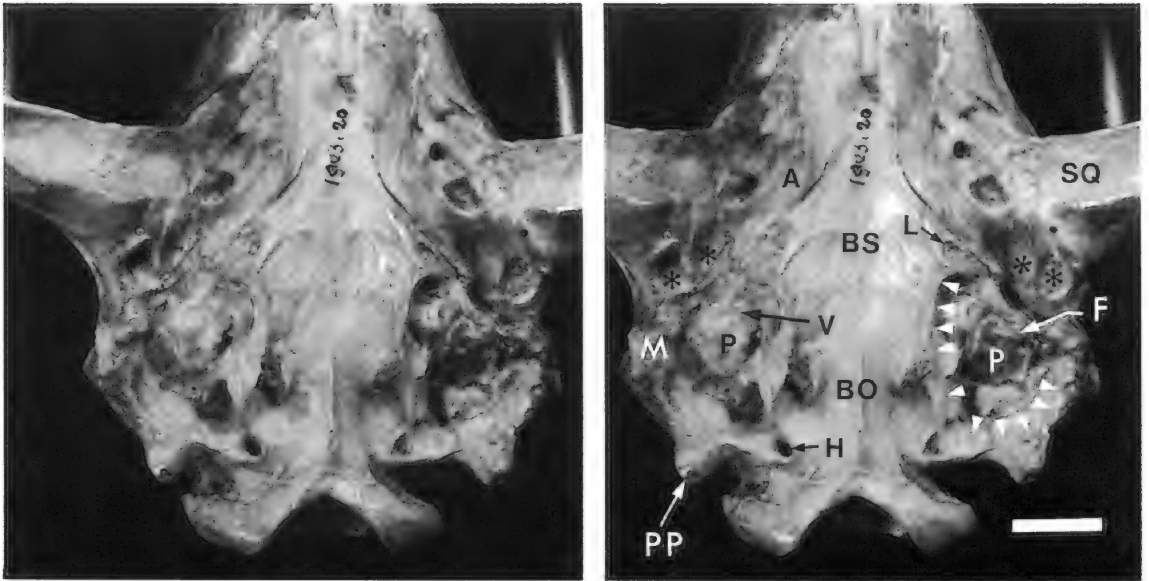


Fig. 11. Cast of basicranium of adult proailurine felid *Proailurus lemanensis* (Paris Museum 1903–20), St.-Gerand-le-Puy (Allier), France, Aquitanian, holotype, ventral view, bulla removed from auditory region. Petrosal form, including the ventral petrosal process (V), is similar to that of *Stenoplesictis* (compare fig. 9B) but in the proailurine the basicranial bones are emarginated by development of an enlarged caudal entotympanic (white arrows indicate extent of caudal entotympanic encroachment). Strong registration of ectotympanic on auditory region results in a petrosal facet (F) on promontorium and in cavities impressed in squamosal and alisphenoid (asterisks); these same features occur in *Stenoplesictis* (compare fig. 10B). Early felids (*Proailurus*) retain the ventral petrosal process of the Aeluroidea but it is lost in living felids due to apparent suppression by the enlarging bulla. Stereopair.

luroidea. All viverrids maintain this primitive course, modifying it in a few species in which the artery is enclosed for a short distance in a bony tube formed by rostral entotympanic. This tube forms by lateral extension of the rostral entotympanic around the artery as it passes the lateral face of the element, so that in fact the arterial path remains the same in all viverrids but enclosure of the artery by rostral entotympanic is variable (both among and within species). Hyainids and felids apparently both maintain the primitive course, but because the artery is reduced or vestigial in most living members of these families, this is not entirely resolved. In herpestids, on the other hand, the course of the artery is modified (perbullar carotid, Hunt, 1987: 45): the vessel runs in a bony tube between ectotympanic and rostral entotympanic, never entering the middle ear cavity. In herpestids the artery is situated on the ventral edge of rostral entotympanic, and does not seem to be diverted as far laterad as in viverrids. Application of ectotympanic

to the ventral edge of rostral entotympanic therefore results in complete enclosure of the artery within the medial wall of the bulla. Significantly, the observed courses of the artery found in the living aeluroid families, despite what at first appear to be rather different arterial paths through the auditory region, are in fact basically similar when studied closely, and can be derived from a common morphotypic pattern like that of *Nandinia*.

In aeluroids, the primitive course of the internal carotid artery was transpromontorial, but the path of the vessel lies close to the medial wall of the bulla within the middle ear, and was not diverted far laterad on the promontorium. The association of the artery with the bulla wall is so close that in herpestids it becomes incorporated in the bony wall. The artery's proximity to the bulla wall is in fact an expression of the close association of the internal carotid with the rostral entotympanic in all Carnivora (Hunt, 1974a).

Nandinia is thus confirmed as a primitive aeluroid based on the morphology of its au-

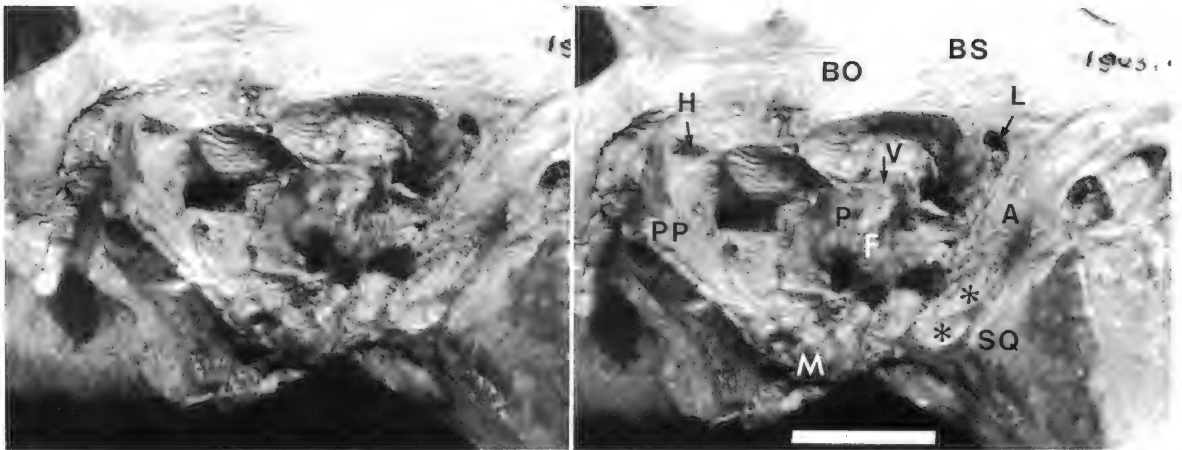


Fig. 12. Cast of left auditory region of *Proailurus lemanensis*, same individual as figure 11, lateral view, bulla removed. Note ventral petrosal process (V), deep emargination of basi- and exoccipital bones by the bulla, and elliptical promontorial facet (F) produced by the ectotympanic. Asterisks indicate registration of ectotympanic on squamosal and alisphenoid. *Proailurus* represents a transitional morphologic stage in the evolution of the felid auditory region between stenoplesictines and modern felids. Stereopair.

ditory region, both in terms of petrosal structure and relationships, auditory bulla pattern, and internal carotid relations. The degree of plesiomorphy of *Nandinia*'s auditory region is greater than that found in the oldest known confirmed aeluroids, the Oligocene stenoplesictines, suggesting that *Nandinia* is a living representative of the basal aeluroid stock whose origin must predate the Oligocene diversity of stenoplesictine and proailurine aeluroid carnivorans documented by the European fossil record.

THE PROAILURINE BASICRANIUM AND PETROSAL

Proailurine aeluroids share near identity of basicranial structure with the stenoplesictines, indicating that the two lineages are closely allied. However, early in their history the proailurines evolved a highly derived auditory bulla of felid type, in which an enlarging caudal entotympanic encroached upon and indented the basioccipital medial to VPP (fig. 11). By the Aquitanian (early Miocene), proailurines have markedly diverged from the primitive aeluroid auditory structure displayed by *Nandinia*.

I know of only two proailurine skulls in which the basicranium, including the petrosal, is well preserved (table 1): the first be-

longs to *Proailurus lemanensis*, a cat with basilar length of skull estimated at 13 cm, about the skull size of the living lynx; the second is the holotype skull of *Stenogale julieni*, a smaller cat with basilar length estimated at a little more than 7 cm, slightly smaller than a domestic cat skull. I have examined a cast (figs. 11, 12) of the basicranium of *Proailurus lemanensis* from the Aquitanian of St.-Gerand, France, originally described by Filhol (1879: pl. 26, figs. 2-4, 6-8); and have studied photographs of the skull of *Stenogale julieni* Filhol in Viret (1929: pl. 12), reported to come from the Aquitanian of Chaveroche-sur-Besbre. Neither of these skulls retains the auditory bulla.

As Lavocat (1952) pointed out, these basicrania are exceedingly similar, not only to each other but to the basicranium of *Stenoplesictis* (compare figs. 11 and 12 with figs. 9B and 10B). In fact, the basicrania of *Stenoplesictis* and *Stenogale julieni* are more alike than are those of *Proailurus lemanensis* and *S. julieni* because the auditory bullae in the first species pair have not developed the strong inflation and encroachment on the surrounding basicranial bones (basioccipital, exoccipital, mastoid) that occurs in the more advanced proailurine *Proailurus lemanensis* from St.-Gerand. *Proailurus lemanensis* differs primarily in the additional registration

marks impressed upon the basicranial bones surrounding the auditory region by the enlarged bulla (fig. 11, white triangles).

If a series of Miocene felid skulls is compared, beginning with the Aquitanian basicrania of the proailurines *Stenogale julieni* and *Proailurus lemanensis*, and continuing through Hemingfordian and Barstovian *Pseudaelurus* in North America, the gradual enlargement of the bulla and its encroachment on the bones of the basicranial axis, especially basioccipital, are clearly evident. The stenoplesictine basicranium could be placed as the first and most plesiomorphic stage in this series, since the basicranium lacks any significant encroachment of the bulla on surrounding basicranial bones. *Stenogale julieni* is very little evolved beyond the stenoplesictine condition, and shows no strong emargination of surrounding basicranial bones by the bulla (Lavocat, 1952); *P. lemanensis* (figs. 11, 12), however, is clearly evolved beyond the more plesiomorphic auditory region of *S. julieni*, and heralds the more advanced bulla and basicranium of *Pseudaelurus* and the later felids. A monophyletic felid clade can be identified using as a synapomorphy the medial encroachment of the bulla on the basioccipital (fig. 11); this clade would include *Proailurus lemanensis*, *Pseudaelurus*, and their extinct descendants, as well as the living felids.

The proailurine petrosal, including the configuration of the robust ventral promontorial process, is identical to that of stenoplesictines (compare figs. 9B and 12). Just as in stenoplesictines, VPP buttresses the basioccipital in primitive proailurines like *S. julieni*, but in the more advanced *P. lemanensis*, the emargination of the basioccipital bone by the bulla creates a space between VPP and the basicranial axis. In both proailurines and stenoplesictines, the promontorium of the petrosal is faceted to receive the ectotympanic (Lavocat, 1952).

Both stenoplesictines and proailurines possess a flanged ectotympanic. The flange is developed on the posteromedial rim of ectotympanic and makes contact with the petrosal promontorium. The fit between flange and petrosal is quite close, as demonstrated by the distinctive promontorial facet (F in figs. 8, 10B, 11, 12). In living felids such as the domestic cat, *Panthera tigris*, *P. pardus*, *Felis*

concolor, *F. tigrina*, and *Lynx rufus*, the ectotympanic rim or flange is directly applied to the promontorium, just anteroventral to the round window. In lions (*Panthera leo*) I have examined, the ectotympanic rim is raised a little distance above the petrosal, and there is no contact. As a result, in living felids, the expression of the promontorial facet ranges from moderately developed to absent.

However, it is apparent that most living felids maintain a tight registration between petrosal and ectotympanic rim, resulting in a faceted promontorium similar to the type found in proailurines and stenoplesictines. During evolution of later felids from a proailurine, this close ectotympanic-petrosal contact has been retained in many of the descendant species, despite modifications in petrosal shape.

The existence of the flanged and inflated ectotympanic in early aeluroids is of more than passing interest. The structural prerequisite in aeluroids for the formation of the diagnostic septum bullae is an ectotympanic resting on the promontorium (Hunt, 1987). An important shared derived character of living viverrids, herpestids, felids, and hyaenids is the application of the rim of ectotympanic to the promontorium, which closes off an anterior bulla chamber; the absence of this contact in lions and some hyaenas appears to be a secondary condition in which the ectotympanic has pulled away a short distance from the promontorial surface. Against the intrabullar partition formed by the posteromedial wall of this often inflated ectotympanic, an anterior surface of the caudal entotympanic is applied. The resulting double-layered internal septum is exclusive to aeluroids.⁶

⁶ A true septum bullae occurs only in aeluroids, but not all aeluroids (as recently defined, Hunt, 1987) possess one. Primitive aeluroids such as nimravids, *Nandinia*, and possibly stenoplesictines, lacked the septum. The aeluroid septum results from a unique juxtaposition of the surfaces of the caudal entotympanic and ectotympanic. In arctoid and cynoid carnivorans, the edges (not surfaces) of these two elements join to create an edge-to-edge contact so that the resulting bulla surface is a unilaminar subhemisphere. In aeluroids, the inturned posteromedial face of ectotympanic creates a surface that meets a second surface produced by the inflected anterior margin of caudal entotympanic; no edge-to-edge contact ever persists, but rather two surfaces are brought into contact to create a bilaminar septum of varying size.

Did proailurines and stenoplesictines possess the septum bullae? Piveteau (1943) and Beaumont (1964) believed that *Stenoplesictis* did not, interpreting the internal partition as unilaminar, formed by the ectotympanic only. In fact, we are ignorant of not only the type of connective tissue forming the caudal entotympanic of *Stenoplesictis*, but also do not know if it was applied as a lamina against the ectotympanic. Such application of caudal entotympanic might be very difficult to detect in the fossil, especially if cartilaginous. Here *Nandinia* can serve as a guide. In the African palm civet, the caudal entotympanic does not form a bilaminar septum with ectotympanic; rather its contact with the posteromedial face of ectotympanic is a linear feature, a line of attachment (X in figs. 9A, 10A) that potentially could evolve into a septum bullae upon the inflation of ectotympanic and inflection of caudal entotympanic. *Nandinia* is remarkable for its retention of this plesiomorphic pattern, which can be identified as a logical structural predecessor for all other aeluroids in terms of the ectotympanic-caudal entotympanic contact. *Stenoplesictis*, on the other hand, possesses a more derived (inflated) ectotympanic; yet the caudal entotympanic chamber of the bulla is about the same size as in *Nandinia*. There is no evidence of caudal entotympanic inflation in either animal; therefore the contact of caudal entotympanic and ectotympanic may not have been converted into a bilaminar septum bullae in *Stenoplesictis*.

I am in agreement with Piveteau and Beaumont that the weight of evidence argues against the presence in stenoplesictines of a typical septum bullae as seen in living felids, herpestids, or viverrids. This is supported by the illustrations of *Palaeoprionodon* supplied by Teilhard (1915: pl. 9, fig. 10) in which only a linear attachment of caudal entotympanic on ectotympanic is suggested, and in *Stenoplesictis* illustrated by Piveteau (1943: pl. 1, fig. 3A) where there is very little room adjacent to the flange for application of caudal entotympanic. This conclusion is also indicated by the distinctive trough on the posterior margin of the petrosal for registration of the caudal entotympanic in stenoplesictines (fig. 8, stipple pattern). This trough is developed as in *Nandinia*, where it receives

only a modestly inflected margin of caudal entotympanic, suggesting that the edges of caudal entotympanic have not begun to assume the strongly inflected configuration of the living aeluroid families. At best, in these two stenoplesictine genera, the caudal entotympanic contact with ectotympanic would range from the type found in *Nandinia* (rudimentary) to the incipient septum bullae seen in neonatal domestic cats (slightly inflected, as in Hunt, 1987: fig. 11).

The similarity of the proailurine basicranium, especially the petrosal, to that of stenoplesictines indicates that primitive proailurines such as *Stenogale julieni* very likely possessed a bulla in which ectotympanic-caudal entotympanic contact was rudimentary, so that a well-developed septum bullae probably did not evolve in felids until at least the stage represented by Aquitanian *P. lemanensis*. A virtually modern felid auditory bulla including a true septum bullae is present in North American mid-Miocene *Pseudaelurus*.

Consequently, we can conclude that primitive proailurines (*S. julieni*) and stenoplesictines possess certain plesiomorphic attributes of the auditory region that do not occur in any living aeluroid (except *Nandinia*), such as the small size of the caudal entotympanic chamber and the probable lack of, or only incipient development of, a septum bullae. However, in their development of a moderately inflated ectotympanic, deeply registered on alisphenoid and squamosal bones, that firmly contacts the petrosal by means of a prominent facet, stenoplesictines and primitive proailurines are advanced beyond the condition seen in *Nandinia*, having created a somewhat specialized enclosure for the anterior chamber of the bulla.

Basicranial evidence derived from these early aeluroids limits the range of possible hypotheses on the origin of the aeluroid families which we will next consider.

ORIGIN OF THE LIVING AELUROID FAMILIES

The modern felid radiation seems directly descended from a proailurine ancestry. There is an identifiable continuum of fossils beginning with *Proailurus*, leading to *Pseudaelurus*, and eventually to the later Cenozoic and

living felids (Ginsburg, 1983). Most importantly, the modification of the auditory region and bulla can be directly traced from the primitive proailurine state to living felids with their enormously inflated bullae.

Because of the scarcity of fossils, a similarly well-documented history of viverrids and herpestids is yet to be worked out. The later Cenozoic evolution of hyaenids is somewhat better known, whereas the early history of that group is only recently emerging.

True herpestids probably first appear as a discrete lineage in the earlier Miocene of Europe in the form of small mongooses (basilar skull lengths of about 6 cm) referred to *Leptoplesictis*. These fossils are similar in size to the living mongoose *Herpestes auropunctatus*. The earliest record of *Leptoplesictis* in Europe is mammal zone MN4 (Schmidt-Kittler, 1987) but to my knowledge no well-preserved basicrania are known. Because the basicranium of *Leptoplesictis* cannot be compared with stenoplesictine skulls, the relationship of these earliest herpestids to the stenoplesictines is not apparent.

Recent discoveries in east Africa (Schmidt-Kittler, 1987) show that the oldest known African herpestids found in early Miocene rocks of Rusinga Island are nearly the same age as the oldest European herpestids. The Rusinga faunas are radiometrically dated at about 17.8 Ma. The African herpestid fossils are dental remains that also can be referred to *Leptoplesictis* and, as in Europe, no basicrania are known.

Pleistocene herpestid basicrania from Africa are no different from those of living herpestids, and, based on the faunas from Olduvai, Omo, and from south Africa, as many as seven of the living herpestid genera (*Herpestes*, *Mungos*, *Ichneumia*, *Atilax*, *Helogale*, *Cynictis*, *Crossarchus*) were in existence by the early Pleistocene.

The modern herpestid radiation then must begin in the Pliocene or earlier, and may be of considerable antiquity, since the E Quarry fauna from Langebaanweg in south Africa dates from the early Pliocene (4–5 Ma) and preserves a diverse herpestid assemblage that may comprise up to five species (Hendey, 1976). A single Pliocene herpestid skull from Garussi in Tanzania preserves part of the auditory region (Dietrich, 1942); Petter (1963) was able to assign the skull to an extant sub-

genus (*Galerella*) of *Herpestes*, suggesting that the basicranium is essentially of modern type. Recently, two nearly complete herpestid skulls referable to *Herpestes* and *Helogale* have been reported in the Pliocene fauna from the upper unit of the Laetolil Beds (Tanzania), dated from 3.5 to 3.8 Ma (Petter, 1987). These two skulls are significant in possessing basicrania and auditory bullae of modern herpestid grade. Thus, in Africa, the evidence suggests that a herpestid fauna of modern aspect was in existence by the early Pliocene, and that the basicranial structure and auditory bulla pattern of the living Herpestidae probably evolved in the Miocene.

Herpestids are not recorded in Asia prior to the late Miocene. Recent work in the Siwaliks of northern Pakistan by Barry and co-workers (1980) produced herpestids at four localities in the Khaur region. These sites fall between about 7.1 and 9.5 Ma, hence late Miocene (MN11–12, Turolian). The fossils have not yet been described.

Pre-Pliocene herpestid basicrania with preserved auditory bullae are unknown to me. We are left primarily with a Miocene record of dentitions, referred either to *Herpestes* or to *Leptoplesictis*. These teeth are sufficiently similar to those of living herpestids to suggest that when good basicrania are found, they could have auditory regions similar to the modern species. This is significant because the auditory region of living herpestids manifests a clearly derivative morphologic pattern (Hunt, 1987); when this pattern first developed is important in judging the timing of the herpestid radiation. The herpestid basicranial pattern is distinguished by: anterior-posterior alignment of the two bulla chambers, resulting in transverse placement of the septum bullae; lack of pronounced overgrowth of either bulla chamber by the other; considerable distance between the anterior end of the bulla and the postglenoid process of the squamosal (except in genera with inflated ectotympanic); enclosure of the internal carotid artery in a bony tube between rostral entotympanic and ectotympanic (the artery never enters the middle ear cavity); and the anterior placement and complete enclosure within the basisphenoid of the middle lacerate foramen (including arterial anastomosis Y of Bugge, 1978).

The basicranial pattern of herpestids is so

similar among the extant genera that a late Cenozoic divergence would not be surprising: the herpestid radiation may be primarily a Plio-Pleistocene event (Hendey, 1974: 89, 337f.), geographically largely confined to Africa. Because of the uniformity of the basicrania of living herpestids, the radiation must stem from an ancestral herpestid already in possession of the modern basicranial pattern.

Hyaenids currently are thought to be derived from the European early Miocene aeluroid *Herpestides* (Beaumont and Mein, 1972). *Herpestides* already coexists as a separate lineage in the Aquitanian with primitive *Proailurus*, and must have diverged prior to this time in the Oligocene. It appears for the first time in European Neogene mammal zone MN2 (Schmidt-Kittler, 1987). The modern hyaenid bulla pattern had evolved at least by MN11–12, about 7 to 9 Ma (Turonian, late Miocene; see Hunt 1974a: fig. 42). Unpublished observations indicate that the hyaenid bulla type is recognizable somewhat earlier in east Asia in deposits of mid-Miocene age: (a) my examination of the auditory region of the holotype skull of *Tungurictis* (AMNH 26600) from Mongolia (Tung Gur Formation, Wolf Camp Quarry, zone MN8) convinces me that the bulla is of the hyaenid type; (b) hyaenids referable to *Percrocuta* from the Tongxin basin of north China, at least as old as zone MN8, are reported to have recognizable hyaenid auditory regions (Qiu Zhanxiang, personal commun., 1988). The existence in the later mid-Miocene in zone MN8 of two kinds of hyaenids as morphologically diverse as *Tungurictis* and *Percrocuta* that display hyaenid auditory regions is evidence for an even earlier evolution of this bulla type, hence development during or before the earlier mid-Miocene.

The auditory region of early Miocene Aquitanian *Herpestides* is preserved in several skulls, and has been described by Beaumont (1967) and Petter (1974). Beaumont initially thought that this carnivoran was closely related to living herpestids. However, the auditory region differs in several respects from those of known herpestids. Both authors restore the internal carotid artery in the primitive transpromontorial position. Hence, despite the herpestid-like fore-aft alignment of the anterior and posterior bulla chambers, and the apparent lack of overgrowth of either

chamber by the other, the auditory region does not possess the derived carotid path within the bulla wall typical of living herpestids. In addition, the isolation of the middle lacerate foramen within the basisphenoid that characterizes living herpestids does not seem to be developed in *Herpestides*. Herpestids also tend to fill in the ectotympanic crescent with bone, and may laterally extend the ectotympanic to form a short meatal tube, but this type of closure has not occurred in *Herpestides*.

Herpestides appears to be an early aeluroid that has not yet developed a basicranial pattern typical of one of the living families. The strong anteroventral overgrowth of ectotympanic by caudal entotympanic seen in viverrids and most felids is not present. Beaumont and Mein's (1972) suggestion that *Herpestides* is an early hyaenid is not contradicted by its auditory region. Its bulla structure could represent an early stage preceding the modern highly derived hyaenid condition (fig. 6), particularly since the carotid path in hyaenids, although vestigial, is apparently transpromontorial, just as in *Herpestides*. Posterior growth and enlargement of the ectotympanic in *Herpestides* could result in the hyaenid bulla configuration. Indeed, the comparison of *Herpestides* with herpestids is not unreasonable when one realizes that the bulla elements of a neonatal herpestid (fig. 5) are structured and positioned to evolve by allometric growth into the hyaenid state (fig. 6). Accordingly, it is possible that *Herpestides* is close to the ancestry of both hyaenids and herpestids.

The family Viverridae in the past has been indiscriminately employed as a taxon encompassing a variety of primitive and advanced aeluroids. With an awareness that true viverrids can be identified by a derived and distinctive basicranial anatomy, in particular, the pattern of ontogenetic growth of the bulla elements (Hunt, 1987), it is possible to separate groups such as herpestids and *Nandinia* from Viverridae. Despite the present diversity of true viverrids in the Old World, there are no described pre-Pliocene viverrid skulls with intact basicrania (excluding stenoplesictines) that can be certainly attributed to the family on the basis of auditory structure. The viverrid bulla pattern probably first appears in the Miocene, but reliable

paleontological evidence bearing on this issue has been difficult to identify, and is only now coming into focus.

The principal Old World Miocene viverrid genera from Europe (*Semigenetta*, *Jourdanictis*, *Viverrictis*, *Lophocyon*) are not represented by any well-preserved basicrania showing bulla structure. Fossils of these carnivorans are primarily teeth in jaw fragments and rare postcranial remains. Dentitions strongly indicate these are aeluroid carnivorans, and some may eventually prove to be viverrids on basicranial structure. At least two badly damaged basicrania of the dentally specialized *Lophocyon* are known (Fejfar and Schmidt-Kittler, 1987); sketches of the auditory region suggest it is an aeluroid, but the quality of preservation of the bulla is not sufficient to classify it as a true viverrid.

In Asia, the only described Miocene aeluroid skulls with basicrania that have been attributed to the Viverridae are the holotype of *Vishnuictis salmontanus* from the Dhok Pathan Siwaliks (Pilgrim, 1932), and the holotype of *Tungurictis spocki* from the mid-Miocene of Mongolia (Colbert, 1939). These are aeluroids with skull lengths of about 11 cm, the size of the living *Viverra*. The basicranium of *Vishnuictis* is too badly damaged to determine (Pilgrim, 1932), but that of *Tungurictis*, including the auditory bulla, is much better preserved.

Unfortunately, photographs of the only known skull and basicranium of *Tungurictis* have not been published, but I have been able to study the skull in the American Museum. The auditory region was originally described and figured by Colbert (1939) who reported that a large inflated entotympanic extended forward to cover the ectotympanic; this ontogenetic growth pattern of the bulla elements is typical of living members of the Viverridae, and suggested that Colbert was correct in classifying *Tungurictis* as a viverrid. However, upon firsthand examination of the skull, the anterior chamber of the bulla is not overgrown by caudal entotympanic; in fact, the anterior chamber is formed entirely by an inflated ectotympanic, as in hyaenids. In addition, the posterior chamber of the bulla preserves an internal floor that represents the nearly horizontal hyaenid septum. The form and proportions of the teeth are very much like, but smaller than, the early hyaenid *Tha-*

lassictis. Therefore, both auditory bulla structure and the dentition of *Tungurictis* better agree with placement in Hyaenidae, an alliance initially suggested by Beaumont (1967) and supported by Qiu et al. (1988).

By the beginning of the Pliocene, true viverrids with typical basicranial and bullar structure are known in Africa, and probably also were present in south Asia. The three known Pliocene basicrania with preserved auditory bullae belong to two very large true viverrids, the size of large coyotes or small wolves: *Vishnuictis durandi* (BMNH M1338, M37131) from the Pinjor Siwaliks (Pilgrim, 1932), and "*Viverra*" *leakeyi* (SAM L13097) from Langebaanweg in South Africa (Hendey, 1974). The intact well-preserved auditory bulla of *Vishnuictis durandi* is essentially that of a modern viverrid, very much like *Civettictis*, whereas the auditory region of the Langebaanweg viverrid has yet to be described in detail. Howell and Petter (1976) suggested that *V. durandi* and *leakeyi* are in fact the same species.

Recent discovery of a group of 8.2 Ma late Miocene Siwalik carnivoran skulls by Barry and others (personal commun., 1987) may include the first definite viverrid skulls of Miocene age with intact auditory regions. The structure of the auditory bullae of these Siwalik fossils will provide important constraints on the pattern of viverrid evolution when described, and may clarify the affinities of the Dhok Pathan *Vishnuictis salmontanus*.

Recently I was able to examine, through the courtesy of Dr. Alan Gentry, a complete fully articulated viverrid skeleton from the freshwater limestone of Oeningen (zone MN8) preserved in the British Museum, originally described as a canid. There were no canids in Eurasia at this time, and the teeth which can be seen in the lower jaw show viverrid dental traits: p4 with anterior accessory cusp; closed trigonid of m1; no m3. This is the most complete European fossil viverrid yet discovered, and includes skull and jaws in articulation. The basicranium and bulla are undoubtedly present, but the skull is crushed flat so that nothing of the basicranial structure can be seen without additional preparation. This is a large animal, with head-body length of about 65 cm (similar in body size to the living *Viverra*).

As a result of this situation, we cannot be

certain when in the mid-Cenozoic the modern viverrid bulla configuration materialized. If *Palaeoprionodon* from Quercy is in fact a true viverrid, then we can state that in the Oligocene its auditory structure was not yet of modern grade. However, it would require only slight structural changes, primarily a greater degree of development of the caudal entotympanic chamber, to evolve the bulla of living viverrids like *Prionodon* and *Poiana* from *Palaeoprionodon*. The living linsangs (*Prionodon*, *Poiana*), the former distributed in Asia from Nepal southward to Java, the latter in west Africa, are much like *Palaeoprionodon* in bulla structure, dentition, and general skull form (basilar skull lengths in the two genera are about 6 cm), and are plausibly directly descended from the Quercy genus (Gregory and Hellman, 1939). Dissection of a skull of *Poiana richardsoni* (AMNH-M 236487) from Cameroon shows that the petrosal possesses a VPP that is more vertical and robust than in other viverrids, hence closer to the plesiomorphic state found in *Palaeoprionodon*.

Conceivably, the ancestry of many of the living viverrid genera may be found in small aeluroids closely related to *Palaeoprionodon* that differentiated as distinct phyletic lineages during the Oligocene. For the moment, *Palaeoprionodon* seems to be the most reliable evidence of the first true viverrids documented by basicranial remains. The best estimate at present as to the time of origin of the modern viverrid auditory region is that, based on the skull of *Palaeoprionodon*, the modern grade of bulla structure was approached but not yet achieved in the mid- to late Oligocene and early Miocene, so that by mid-Miocene we might expect to encounter fossil viverrids with the modern bulla pattern. The Oeningen skeleton and the dentitions of *Viverrictis* and *Semigenetta* may well represent such animals. Future discoveries of cranial remains will be necessary to confirm or modify this prediction.

Nandinia remains as an isolated taxon among living Aeluroidea. It is the only living aeluroid that not only approximates the stenoplesictine grade of basicranial structure, but documents a stage of basicranial organization more plesiomorphic than the stenoplesictines. The existence of *Nandinia* implies that prior to and during the Oligocene

stenoplesictine presence in the Old World, there must have been somewhere in Eurasia or Africa a more basicranially primitive aeluroid stock that represents the ancestry of *Nandinia*. This ancient aeluroid lineage has persisted unchanged in basicranial structure, and probably in skull form and postcranial anatomy, for at least 35 to 40 million years. The only probable modification of this ancestral aeluroid necessary to arrive at modern *Nandinia* is the reduction of the dentition with development of a hypocarnivorous cusp pattern. It is remarkable that in the east African Songhor level, dated at about 19.6 Ma, there has recently been reported a rich diversity of small aeluroids including *Mioprionodon* and *Stenoplesictis*, both described as stenoplesictines (Schmidt-Kittler, 1987). *Mioprionodon* is known only from jaws and teeth but its dentition is rather similar to that of *Nandinia*. I think it probable that *Nandinia* has existed in Africa since at least the time of *Mioprionodon* in the early Miocene.

What then are stenoplesictines? Most current workers limit the group to *Stenoplesictis* and *Palaeoprionodon*, and ally them with the proailurine felids. Indeed, basicranial structure supports the inference that proailurines (*Proailurus*, *Stenogale*) and stenoplesictines (*Stenoplesictis*, *Palaeoprionodon*) are sister-groups, and that they are early derivative lineages of a more primitive aeluroid stock—whose existence we infer from basicranial structure—that survives in the living *Nandinia* (fig. 13). A phyletic connection of stenoplesictines and proailurines with living aeluroids is documented by the identification of *Palaeoprionodon* as the oldest probable viverrid lineage, and *Proailurus* as an early felid. The anatomical similarity of basicrania of the stenoplesictine *Palaeoprionodon* and the proailurine *Proailurus* indicates the close relationship between these lineages in the Oligocene, and this relationship is further reflected in the similar ontogenetic pattern of bulla growth in living viverrids and felids (Hunt, 1987). Thus a close tie between viverrids and felids is supported not only by the similar ontogeny of the auditory bulla of living forms but also by the paleontological evidence allying ancestral species from Quercy. Consequently, there is good evidence that at least some felids and some viverrids are products of an early aeluroid dichotomy, and

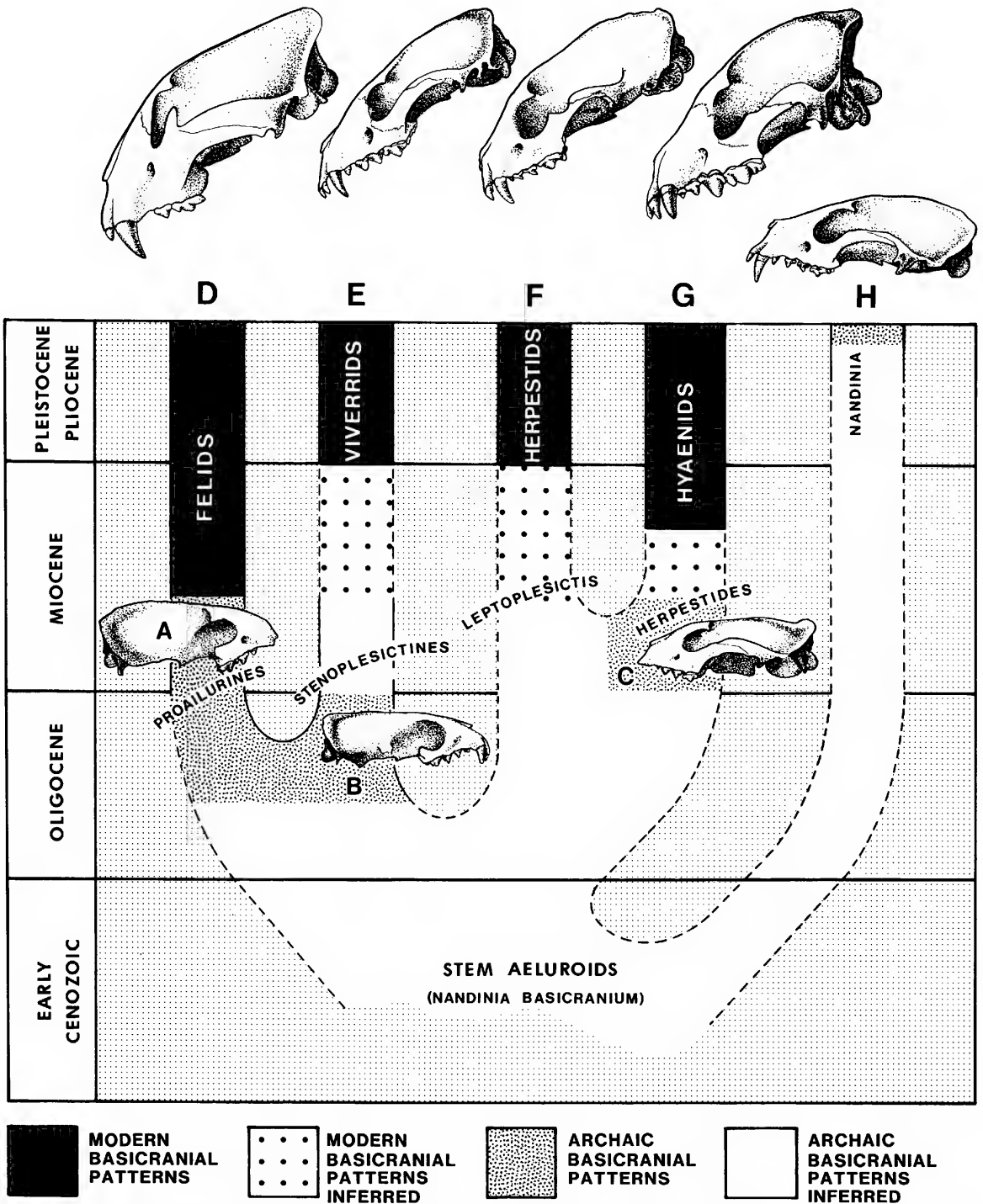


Fig. 13. Diagram of the evolution of aeluroid basicranial patterns during the Cenozoic. The patterns typical of the modern families first appear in the fossil record in the mid-Miocene to Pliocene: all probably originate, however, during the mid- to late Miocene. Prior to the mid-Miocene, archaic basicranial patterns characterize the aeluroid lineages. A close relationship between felids and viverrids is supported by the pattern of bulla ontogeny in the two families, and by the strong anatomical correspondences in the basicrania of proailurine and stenoplesictine aeluroids. Less certain is the suggested dichotomy of herpestids and hyaeuids: at present, lack of knowledge of the basicranium of the oldest

this conclusion can be reasonably extended to unite the two families as sister taxa.

In both Europe and Africa, other aeluroids developed into what can tentatively be described as protohyaenids (*Herpestides*) and protoherpestids (*Leptoplesictis*) by the early Miocene. However, neither of these two genera can be clearly confirmed as ancestors of their respective families based on basicranial evidence. Nor are they demonstrably derived from a common hyaenid-herpestid stem group, although no evidence prevents such an interpretation. We must await new fossil discoveries to better determine hyaenid and herpestid origins. In the interim, we may consider these two genera as hypothetical ancestral stocks for hyaenids and herpestids. However, when additional fossil skulls of early aeluroids are eventually discovered, an important criterion needs to be satisfied before they can be reliably attributed to the protohyaenid or protoherpestid groups: we should be able to show that the bulla and basicranium of the fossil taxon have developed along an ontogenetic trajectory in evidence in the living members of these two families.

The coexistence of profelids, -viverrids, -hyaenids, and somewhat later, protoherpestids in Europe in the late Oligocene and earlier Miocene indicates that separation of these lineages had already taken place by Aquitanian time in the Old World (fig. 13). Nevertheless, the modern grades of basicranial and bulla structure that identify members of the living families were only incipiently developed in these four ancestral lineages, and this nascent condition of the auditory region has contributed to the problem of their recognition in the fossil record. More importantly, the more plesiomorphic structure of the auditory region of *Nandinia* relative to these Aquitanian species implies that it also must have been in existence at that time as an even more primitively configured lineage, at least in terms of its basicranium. Thus the aeluroid differentiation must have occurred in pre-

Aquitanian time, probably during the Oligocene, with the origin of the aeluroids within the Carnivora plausibly dating to the early Cenozoic.

CONCLUSIONS

A ventral promontorial process of the petrosal characterizes the aeluroid Carnivora, living and fossil. This process is applied against the lateral edge of the basioccipital, and often protrudes below (ventral to) the basicranial axis. Living aeluroids have a forwardly inclined petrosal process situated near the basioccipital-basisphenoid suture, but the oldest known generally acknowledged aeluroids, the stenoplesictines and proailurines, have a more robust and vertically aligned petrosal process which is applied to basioccipital about midway along its lateral margin. The living African aeluroid *Nandinia* still retains a petrosal process configured as in these ancient Oligocene aeluroids. In fact, its auditory region in its entirety is more plesiomorphic than the auditory regions of these oldest fossil aeluroids. *Nandinia* is a "living fossil," representative of the earliest stage of aeluroid evolution in terms of its basicranial and auditory anatomy.

The time of origin of the living aeluroid families, based on auditory anatomy, is difficult to determine because well-preserved basicrania are scarce in the fossil record, but the known paleontological evidence suggests that the modern basicranial and bullar patterns of most lineages developed during the Miocene. In the Oligocene and early Miocene, ancestral stocks of the modern families can be cautiously recognized on the basis of basicranial structure likely to precede the distinctive basicranial patterns identifying the living families. In the mid- to late Miocene, basicranial patterns typical of the living felids and hyaenids were fully developed. Because of the paucity of fossil basicrania, modern herpestid and viverrid basicranial patterns

←
herpestids (*Leptoplesictis*) prevents determination of their relationship to proposed oldest hyaenids (*Herpestides*). The living palm civet *Nandinia* maintains a basicranial pattern plesiomorphic for all these fossil and living aeluroid groups. A, *Stenogale julieni*; B, *Stenoplesictis cayluxi*; C, *Herpestides antiquus*; D, *Panthera onca*; E, *Civettictis civetta*; F, *Galidia elegans*; G, *Crocuta crocuta*; H, *Nandinia binotata*.

are not certainly recognized until the Pliocene, but almost surely were in existence by the late Miocene.

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Note Added in Proof: A primitive mongoose with a head-body length of 50 cm has recently been reported from complete skeletons found at Fort Ternan, Kenya, by R. J. G. Savage (R. J. G. Savage and M. R. Long, 1986, *Mammal Evolution*, British Museum (Nat. Hist.), London, p. 80). This sample apparently includes at least one skull of a juvenile with a complete or nearly complete auditory bulla (J. Barry, written commun., 1988). The mid-Miocene age of Fort Ternan (about 14 Ma) falls in a critical interval in the course of herpestid basicranial evolution, thus when these specimens are described, they will shed considerable light on the pattern of aeluroid basicranial change.

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