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Evolution of the Aeluroid Carnivora: Diversity of the Earliest Aeluroids from Eurasia (Quercy, Hsanda-Gol) and the Origin of Felids

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ABSTRACT

The oldest known fossil aeluroids are from Lower Oligocene sediments in France (Quercy) and Upper Eocene–Lower Oligocene sediments in Mongolia. These small (< 5 kg) carnivorans are primarily represented by mandibles, with hypercarnivorous dentitions in almost all lineages. The six aeluroid genera from France and those from Mongolia share a common dental pattern despite their geographic separation near the extremes of the Eurasian landmass. This similarity is not surprising, however, because faunal exchange across Eurasia at this time is documented not only by populations of small aeluroids but also by small arctoid carnivorans.

Basicrania of Oligocene aeluroids are preserved only in the Quercy deposits. The auditory regions of two genera from Quercy (*Palaeoprionodon*, *Stenoplesictis*), and of two additional aeluroid genera (*Stenogale*, *Proailurus*) known only from mandibles at Quercy (but matched with congeneric mandibles with associated basicrania from early Miocene sediments at St.-Gérard), reveal a common basicranial morphotype. The living African palm civet *Nandinia binotata* retains a basicranial and auditory anatomy closely approaching the ancestral aeluroid morphotype.

European paleontologists working with the Quercy faunas have regarded several of these aeluroids as early members of the Viverridae and Felidae. However, basicrania of the Quercy and St.-Gérard aeluroids share a common petrosal morphology overprinted by anatomically distinctive and evolutionarily divergent auditory bulla types that differ from those of living felids and viverrids. These basicranial patterns suggest their recent common ancestry more strongly than they support any potential affinity with living viverrids and felids. Among the Quercy crania, only *Palaeoprionodon* shares significant similarities with a living viverrid, the Asian linsang *Prionodon*. No early felid crania are known from Quercy deposits.

The oldest known basicrania with derived features indicative of felid affinity are those of *Proailurus lemanensis* and *Stenogale julieni*, from

St.-Gérard, France. They share a derived petrosal morphology that incorporates a uniquely configured bony flange on the medial border of the promontorium. *Proailurus lemanensis*, long considered to be an ancestral felid, has a particularly distinctive, dorsally depressed petrosal flange produced by auditory bulla hypertrophy. This *Proailurus* pattern may be derived from the more plesiomorphic basicranium of *Stenogale julieni*, and together the two genera could be included in a felid subfamily Proailurinae, or, alternatively, the proailurines could be limited to *Proailurus* and its descendant taxa.

Living felids share a morphologically uniform petrosal morphology that lacks the medial flange of the promontorium present in *Proailurus* and *Stenogale*. In the living felids the flange is either suppressed and/or reoriented so that it bears no resemblance to the archaic petrosal type. However, the oldest known early and mid-Miocene New World felids (Ginn Quarry, Echo Quarry) described in this study retain archaic petrosals more similar to the petrosal of *Proailurus* than those of living felids. The origin of the derived petrosal of living felids has yet to be identified among the fossil felids of the later Neogene.

The auditory region of the oldest known New World felid (latest early Miocene) from Ginn Quarry, Nebraska, retains a more plesiomorphic petrosal than known in St.-Gérard *Proailurus*, yet the Ginn Quarry cat is geologically younger. The existence of these two archaic petrosal morphs in early Miocene felids suggests that at least one other felid lineage was present in the early Miocene in addition to *Proailurus lemanensis*.

The subfamily Stenoplesictinae (including *Stenoplesictis* and *Palaeoprionodon*) is a paraphyletic taxon lacking reliable derived traits to unite its genera, and the name is no longer employed.

The origins of the Herpestidae and Hyaenidae are not illuminated in any way by fossils from Quercy or from Mongolia, and the oldest members of these families are not recorded in the Oligocene.

INTRODUCTION

The oldest known occurrences of aeluroid carnivorans in the fossil record are from western Europe and Mongolia (fig. 1). By far the richest samples come from the karst terrain of the Quercy district in southwestern France where fissure fills mined for phos-

phate yielded hundreds of specimens from 1871 onward. These abundant remains were first described by Gervais (1872–1876) and by Filhol (1872–1894) in numerous publications. During the same period Schlosser (1887–1890), working in Germany, also



Fig. 1. The oldest aeluroid carnivoran assemblages are found in Oligocene sediments of France (Quercy) and Mongolia (Hsanda-Gol).

studied the steadily accumulating carnivoran material from Quercy. This early work culminated in a monographic review of the small Quercy carnivores by Teilhard (1915) who established the remarkably broad diversity of dental types found in the fissures. Following the initial discovery and publication of the small carnivores from Quercy (1871–1915), the American Museum's Central Asiatic Expedition in 1922 discovered a rich Oligocene mammalian fauna in the Hsanda Gol Formation within the Tsagan-Nor basin of Mongolia. Among the carnivorans were rare but singularly important remains of small aeluroids, subsequently described by Matthew and Granger (1924).

The Quercy and Hsanda-Gol fossils currently provide the best glimpse of the nature and diversity of the basal aeluroids. Review of the abundant Quercy aeluroids in the collections at the Muséum National d'Histoire Naturelle in Paris and the more fragmentary and rarer Hsanda-Gol material at the American Museum of Natural History, New York,

demonstrates the presence of closely related aeluroid lineages at these geographic extremes in the vicinity of 45°N latitude, and hence suggests that a similar aeluroid assemblage was broadly distributed across Eurasia during the later Oligocene. This Oligocene aeluroid radiation appears to have been confined to Eurasia, because no aeluroid fossils are yet known from Africa or the New World at this time.

Because aeluroid families are most reliably defined and identified from cranial anatomy, particularly basicranial structure (Flowery, 1869; Hunt, 1974, 1987, 1989; Hunt and Tedford, 1993), the existence of well-preserved skulls of the earliest known aeluroids is of considerable interest, providing the opportunity for comparison with living aeluroids and other carnivorans. Although no skulls of aeluroids have yet been described from Mongolia, the early collections from the Quercy district have produced a small number of relatively complete crania (Teilhard, 1915; Piveteau, 1943). These rare

skulls are particularly important because they demonstrate a common type of basicranial structure: a plesiomorphic auditory region that predates the appearance of the more derived basicranial patterns that characterize the modern (post-Oligocene) aeluroid families.

The analysis presented here is based on earlier work demonstrating the value of basicranial patterns in the study of carnivoran evolution (Flower, 1869; Hunt, 1974, 1987). The anatomy of the petrosal and the ontogenetic growth trajectories of the elements making up the auditory bulla are particularly useful in defining aeluroid lineages. Aeluroid carnivorans have auditory bullae assembled from three components: ectotympanic, rostral entotympanic, and caudal entotympanic (Hunt, 1974). These bulla elements fuse in ontogeny to form the floor of the middle ear cavity. During this process, differential growth of the bulla elements results in a distinctive adult bulla pattern in each of the living aeluroid families (Viverridae, Felidae, Herpestidae, Hyaenidae, Nandiniidae). The ontogenetic growth pattern of the bulla components (ectotympanic, entotympanics) in each family is as important in identification of these lineages as is the final anatomical configuration of the adult bulla (Hunt, 1987). Despite a wide range of dental and skeletal adaptations in aeluroids, basicranial patterns at the family level are conservative and can be traced to the Miocene and, in some cases, Oligocene.

My earlier studies established polarities for basicranial and auditory characters defining the aeluroid groups, and identified plesiomorphic basicranial traits in living and extinct aeluroids (Hunt, 1987, 1991). The living African palm civet, *Nandinia binotata*, was identified as an extremely primitive living aeluroid, essentially a living fossil, preserving plesiomorphic aeluroid petrosal and bullar anatomy (Hunt, 1987, 1989, Hunt and Tedford, 1993). Comparison of *Nandinia* with early aeluroids such as *Stenoplesictis* from the Oligocene of Quercy demonstrated a remarkably similar petrosal and bulla structure (Hunt, 1989), indicating the antiquity of the nandiniid pattern. From these studies I developed a hypothesis of aeluroid evolution relying on basicranial structure, in particular

the identification of a progressive transformation of the petrosal and bulla from a state like that of *Nandinia* to the configurations found in each of the modern families. This report continues this theme, describing the oldest known aeluroid basicrania, all from Quercy, to develop a concept of pattern in these earliest members of the group. Unfortunately, the skulls of these Quercy aeluroids are rarely associated with mandibles, which serve as the type specimens for all Quercy aeluroid species. Thus, the first part of the study establishes the dental hypodigms of small Quercy aeluroids to which the basicrania can be referred, and also reviews the rare Mongolian aeluroids of similar age. No attempt is made to assess the relationships among these aeluroid species, which, of necessity, must be based on the dentitions. At present such an assessment would be difficult because of the scarcity of Paleogene Mongolian aeluroids and uncertainty as to the nature of the few recently discovered Asian specimens.

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I am grateful to Prof. L. de Bonis, Université de Poitiers, who kindly prepared a cast of the cranium and mandibles of the Marseille *Stenoplesictis* essential to the study. Dr. M. C. McKenna generously provided a mandible of *Asiavorator gracilis* (American Museum field number 86), collected at Tatal Gol during his expedition to Mongolia in August 1991; this specimen supplied critical information defining this aeluroid and clarified fragmentary material collected in Mongolia by the American Museum in 1922.

For useful reviews of the manuscript, I am particularly appreciative of the efforts of Drs.

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ABBREVIATIONS

Anatomical

A	alisphenoid
ac	alisphenoid canal
a	"apron" of the petrosal
b ₁	anterior basioccipital emargination produced by caudal entotympanic
b ₂	posterior basioccipital emargination produced by caudal entotympanic
BO	basioccipital
BS	basisphenoid
ca	pit for anterior crus of ectotympanic
ce	anterior limit of forward-migrating caudal entotympanic in <i>Proailurus</i>
d	alisphenoid depression for anterior face of ectotympanic
E	caudal entotympanic
eo	exoccipital
er	epitympanic recess
F	facet on petrosal promontorium for ectotympanic
fc	facial canal
fo	foramen ovale
fp	medial flange of the promontorium
fr	fenestra rotundum
gf	postglenoid foramen
h	hypoglossal (condyloid) foramen
ICA	internal carotid artery
L	middle lacerate foramen
m	mastoid
P	petrosal
plf	posterior lacerate foramen
pp	paroccipital process
R	rostral entotympanic
R _s	space for rostral entotympanic
s	styiform process of ectotympanic
sb	posterior wall of ectotympanic where caudal entotympanic is applied to form <i>septum bullae</i>
SQ	squamosal
T	ectotympanic
tr	trough on petrosal's medial margin for attachment of caudal entotympanic
tt	tensor tympani fossa
V	ventral process of the promontorium
x	line of caudal entotympanic attachment to ectotympanic
Z	contact of ectotympanic flange with petrosal promontorium

Institutional

AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History), London
FM	National Museum of Natural History, Sofia, Bulgaria
MGL	Musée Guimet d'Histoire Naturelle, Lyon
MNHN	Muséum National d'Histoire Naturelle, Paris
UPM	Faculté des Sciences, Université de Provence, Marseille

DIVERSITY OF AELUROID CARNIVORA AT QUERCY

Examination of the Paris Museum collection of Quercy aeluroids, including material originally studied by Filhol and Teilhard in their initial investigations, reveals a remarkable diversity of small aeluroid carnivorans (< 5 kg) from the fissures (fig. 2). No less than seven species (*Stenoplesictis cayluxi*, *S. minor*, *Palaeoprionodon lamandini*, *Anictis simplicidens*, *Stenogale gracilis/intermedia*, *Haplogale media*, *Proailurus lemanensis*) can be recognized, in keeping with the diversity first monographed by Teilhard (1915). The fact that the Quercy samples came from many different fissures that filled over different time intervals, and plausibly at variable rates, requires that both geographic and temporal variation must be considered in sample evaluation.

The type specimens of most small Quercy carnivorans are isolated mandibles with diagnostic teeth (fig. 2). Thus, most species and genera are based on dental characteristics. In some cases the scarcer maxillae, rostra, and partial to complete crania are either associated with, or can be referred to, these lower dentitions. When reliable associations can be made, the basicranial traits of these early aeluroids can be established (Teilhard, 1915; Piveteau, 1943).

Compared to the variation in body size among living aeluroid Carnivora, which ranges from the small dwarf mongoose *Helogale* (0.25 to 0.65 kg) to the Asian tiger of Siberia, *Panthera tigris* (to 300 kg), the extinct Quercy aeluroids are all small. *Stenoplesictis minor* was approximately the size of the living dwarf mongoose *Helogale* (< 1

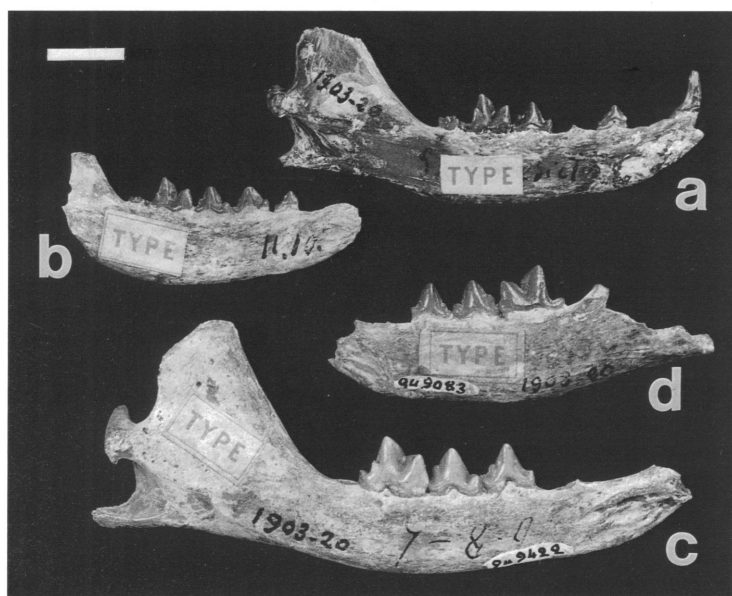
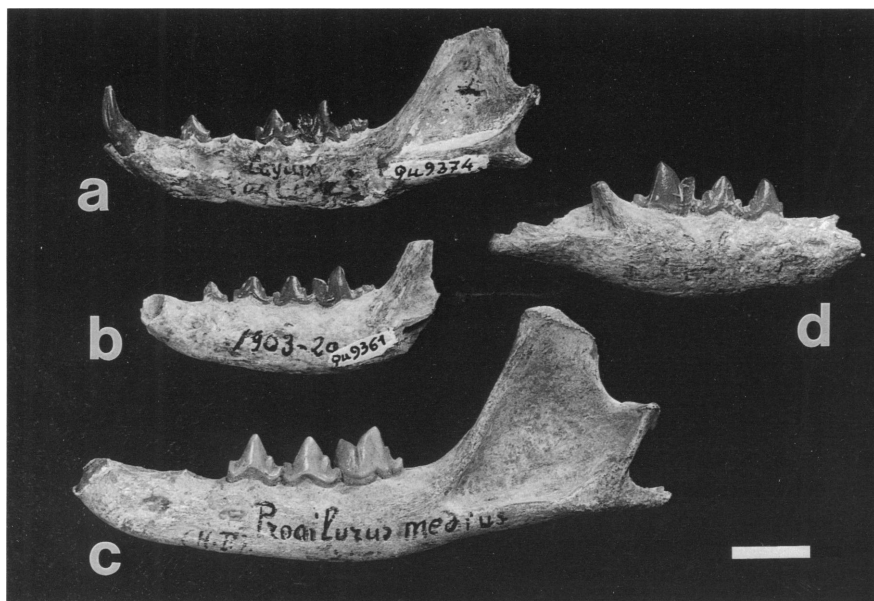


Fig. 2. The diversity of small aeluroid carnivorans from the Quercy district, France (mandibles in labial [above] and lingual [below] view): **a**, *Stenoplesictis cayluxi*, holotype, Qu 9374, Teilhard, 1915: pl. 8, fig. 14; **b**, *Palaeoprionodon lamandini*, Qu 9361, Teilhard, 1915: pl. 9, fig. 9; **c**, *Haplogale media*, holotype, Qu 9422, Filhol, 1882: pl. 4, figs. 6–8; **d**, *Stenogale intermedia*, holotype, Qu 9083, Teilhard, 1915: pl. 9, fig. 4.

Scale bar in this and all subsequent figures is 1 cm unless otherwise noted.

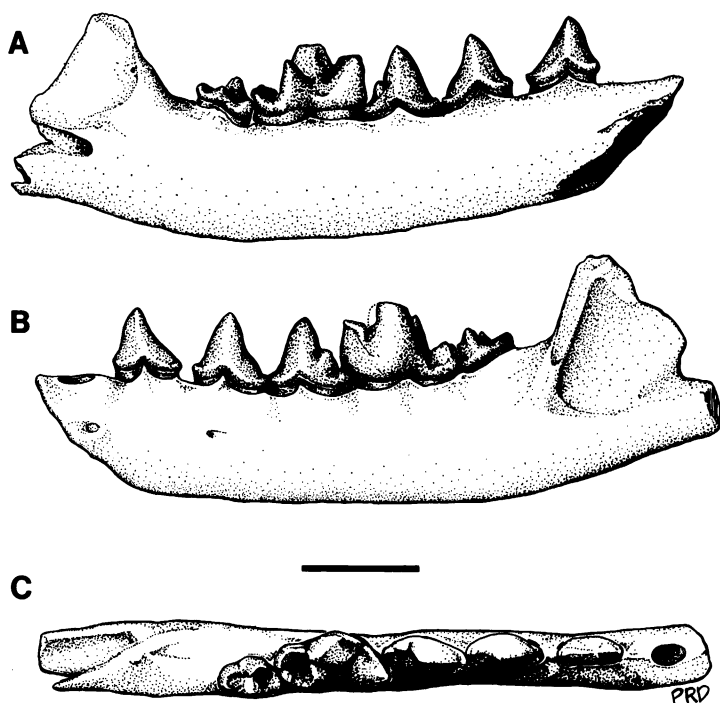


Fig. 3. Mandible with p2-m2 of the dentally plesiomorphic aeluroid *Anictis simplicidens* (Schlosser) from Quercy (MGL PQ567). A, lingual; B, labial; C, occlusal views.

kg); the largest was the rare *Proailurus lemanensis*, a catlike aeluroid about the size of a living North American lynx (5–20 kg). None of the Quercy species exceeded 20 kg in life, and most would have weighed < 4 kg.

An interesting aspect of the Quercy aeluroid fauna is the tendency of most taxa to develop a hypercarnivorous dentition. Hypercarnivory has evolved in parallel in numerous carnivoran lineages from the Oligocene to Recent: the shearing function of the carnassial teeth becomes predominant while crushing occlusion of tribosphenic molars is greatly diminished or lost. Hypercarnivory is recognized both by the shape of the teeth and by the reduction or loss of particular teeth in the dental battery—it involves (1) progressive reduction of the posterior molars (thus loss of crushing occlusion) until in the final stage only bladelike carnassials remain as the principal shearing locus of the dentition; (2) reduction of the anterior premolars, especially p1–2/P1–2; (3) maintenance of functional canines and incisors; (4) transformation of the carnassial pair (P4/ml) into shearing

blades (this occurs through the loss of the ml talonid and metaconid, and by reduction or loss of the P4 protocone). The living felids all have well developed hypercarnivorous dentitions.

Because hypercarnivorous dentitions evolved from a plesiomorphic (tribosphenic) eutherian dentition, hypercarnivorous species of Carnivora must have descended from ancestors having a full complement of premolars and 2–3 tribosphenic molars in each jaw (with the principal shear locus centered at the carnassial pair). Only the genus *Anictis* Kretzoi 1945 (fig. 3) from Quercy retains a moderately plesiomorphic dentition of this type. All other Quercy aeluroids exhibit a greater degree of hypercarnivory than seen in *Anictis*. Based on the morphology of the mandibles and teeth, *Anictis* is similar in dental characteristics to living viverrids and was about the size of a smaller species of *Viverra*.

The more common and smaller Quercy aeluroids were referred by Teilhard (1915) to *Stenoplesictis* Filhol 1880 and *Palaeoprionodon* Filhol 1880. Two dentally similar species of *Stenoplesictis* are usually recognized



Fig. 4. Crania and mandibles of the small hypercarnivorous aeluroids *Palaeoprionodon lamandini* (A) and *Stenoplesictis cayluxi* (B). The *Palaeoprionodon* cranium (MNHN Qu 9348) is not associated with its mandible (Qu 9323) whereas the *Stenoplesictis* cranium and mandible (a cast of UPM PQ305) are associated.

(Filhol, 1882): *S. cayluxi* and *S. minor*. Teilhard mentioned only the larger and more common species, *S. cayluxi*, in detail and discussed the smaller *S. minor* only in a footnote, considering it a “simple variété” of the larger species; a lectotype for *S. minor* has been recently designated by Bonis and Cirot (1995). *Palaeoprionodon* was first distinguished as a single species, *P. lamandini*, by Filhol based on material he had earlier referred to *Plesiogale mutabilis*. Teilhard (1915) considered *Palaeoprionodon* to be slightly more hypercarnivorous in comparison with *Stenoplesictis*. Differences in the teeth of the two genera are subtle and not easily recognized without the abundant samples available to Teilhard. *Stenoplesictis* and *Palaeoprionodon* are among the most well-represented Oligocene aeluroids and more-

over, they are also known from complete skulls (fig. 4).

The remaining aeluroids from Quercy fall into two distinct groups (fig. 5): (1) short-snouted, small to medium-sized catlike hypercarnivores placed in the genera *Stenogale* and *Proailurus*; (2) a long-snouted viverrid-like aeluroid (*Haplogale*) with normally spaced premolars (but with reduced p1–2) set in long slender mandibles, and with its carnassials and molars also modified for hypercarnivory.

The genus *Stenogale* is problematic due to uncertainty surrounding the identity of the holotype species (Teilhard, 1915). The name *Stenogale* was created by Schlosser (1888) for the *S. gracilis*-*S. intermedia* group from Quercy (as well as two additional species from the Miocene Sables d’Orléanais,

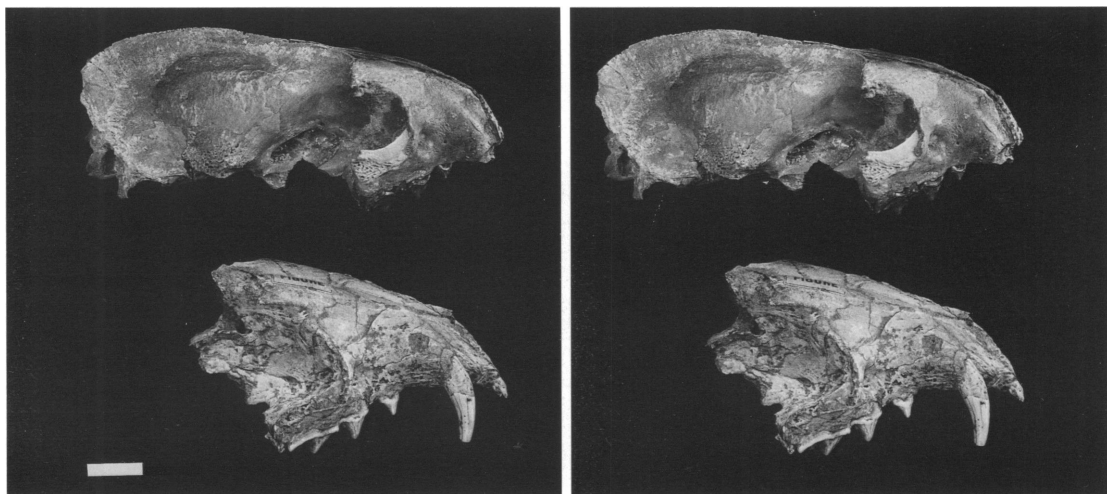


Fig. 5. The short-snouted aeluroid *Stenogale julieni* (above, Aquitanian, St.-Gérand-le-Puy, holotype cranium, Viret, 1929: pl. XII, fig. 5) compared with the long-snouted aeluroid *Haplogale media* (below, Quercy, a referred rostrum, Teilhard, 1915: pl. IX, fig. 12, Qu 9436). Note difference in size of orbit and rostral length in these two small aeluroids.

France, and the Aquitanian of Haslach near Ulm, Germany) and has been used, for example by Teilhard (1915: 70–71), for small, robust, rather short mandibles in which hypercarnivory is well advanced, i.e., the m1 is dominated by a blade-like paraconid-protoconid with a much reduced metaconid and trenchant talonid (not basined). The m2 is very small, with a distinctive trigonid. A significant aspect of Schlosser's diagnosis of *Stenogale* concerns the premolars: p1–p2 are markedly reduced relative to p3–4, thus creating, when taken together with the modified m1–2, a miniature catlike dentition. Specimens that Teilhard (1915, pl. IX, figs. 1–3) attributed to *S. gracilis* that I have examined show this size reduction of p1–p2. Teilhard discusses two species, the tiny *S. gracilis* and the somewhat larger *S. intermedia*. Here I employ the genus *Stenogale* for a suite of three species that represents this lineage of small (< 2 kg) catlike hypercarnivores: *S. gracilis* (Filhol, 1877); *S. intermedia* (Filhol, 1876); *S. julieni* (Filhol, 1879), this last species not from Quercy but from the Aquitanian of St.-Gérand.

A few mandibles of larger catlike carnivorans also occur at Quercy (Teilhard, 1915: 75–76; Ginsburg, personal commun. 1992). These animals, the size of a living lynx, are the largest aeluroids known in the Quercy de-

posits. They have been assigned to *Proailurus lemanensis* by Teilhard (1915), the type species of *Proailurus* later selected by Viret (1929: 159). The holotype of *P. lemanensis* is not from Quercy but was described by Filhol (1879) from St.-Gérand. However, the rare Quercy mandibles preserved at the Paris Museum are identical to the holotype mandible of *P. lemanensis* (MNHN S.G. 3509) from St.-Gérand. As Teilhard noted, there is no doubt that *P. lemanensis* is present in certain Quercy fissures.

An additional long-snouted aeluroid (fig. 5) about the size of a species of the viverrid *Genetta* is included in the collections of the Paris Museum. A rostrum and mandible of this carnivore were illustrated by Teilhard (1915: pl. IX, figs. 12, 17). The elongate rostrum and mandible preclude a catlike facial structure and alternatively suggest a skull form like *Genetta*. Although the associated rostrum and mandible are not type specimens, they compare very well with the holotype mandible of "*Proailurus*" *medius* Filhol 1882; the rostrum and associated mandible can be confidently assigned to the same species. "*P.*" *medius* was later removed from *Proailurus* and made the holotypic species of a new genus *Haplogale* by Schlosser (1888); I employ the taxon *Haplogale media*.

for this long-snouted genetlike aeluroid from Quercy.

ANALYSIS OF DENTITIONS AT QUERCY

ANICTIS KRETZOI: This large aeluroid was initially described by Schlosser (1890) as *Viverra simplicidens* using Quercy fossils, and later briefly reviewed by Teilhard (1915: 24–25, 48–49, 80, tabl. VII) who was able to study only four mandibles. Schlosser (1890: 391) originally described *Viverra simplicidens* from Escamps based on a sample consisting of four complete lower jaws, several jaw fragments including one with milk teeth, and a partial maxilla with P4, M1 and the M2 alveoli. No type was specifically designated; however, only one of the complete lower jaws was illustrated (Schlosser, 1888: pl. IX, fig. 54), although it clearly shows the characteristic features of the lower dentition in this species, and it is the most reasonable choice as holotype, if it can be located in the Munich collections. Later Kretzoi (1945) without discussion placed the species within his monotypic genus *Anictis*. A single species, *A. simplicidens* (Schlosser), is usually recognized (fig. 3). Teilhard was uncertain of its placement: in discussing this species, he considered an affinity to *Cynodictis*, regarded here as an amphi-cyonid, but rejected this based on the tall, simple, slender premolars, which were not at all like those of *Cynodictis* species. He also considered possible relationships to amphi-cynodont arc-toids and to the Quercy aeluroids via *Stenoplesictis* (Teilhard, 1915: tabl. VII). Despite his uncertainty, Teilhard (1915: 48) was able to provide a list of the diagnostic dental features of the species: “*Viverra simplicidens* se reconnaissent facilement . . . à leurs P [= premolars] grêles, hautes, à peine denticulées, à l’aplatissement de leur m1, et surtout au talonide de cette dernière dent, qui est très réduit, creux, mais armé d’un fort hypoconide coupant.” From alveoli in a few mandibles, he also recognized that m2 was long and not as reduced as it is in *Stenoplesictis* and *Palaeoprionodon*.

Despite the scarcity of remains *Anictis* is easily identified at Quercy, primarily because of the plesiomorphic quality of its lower

teeth (no certainly referred upper dentitions are known to me). The species can be contrasted dentally with the more common *Stenoplesictis* and *Palaeoprionodon*. *A. simplicidens* is recognized by its tall, acuminate slender premolars, particularly p2–p3, which lack (or have much reduced) posterior accessory cusps. The height of p2–p3 is at least equal to that of p4 and is reminiscent of the tall premolars of some living viverrids (*Viverricula indica*, Szechuan province, China, AMNH 58373, 58374; see also *Cynogale*, *Osbornictis*). However, *Anictis* mandibles represent a larger species than *Viverricula indica* and compare well in size with mandibles of the living *Viverra tangalunga* (Borneo and Sulawesi, basilar length of skull, 10.8–11.0 cm). *Anictis simplicidens* was much smaller than the living *Viverra megaspila* (Thailand, basilar length, ~14.2 cm), and somewhat smaller than *Viverra zibetha* (China, basilar length, 13.0–13.2 cm).

The lower teeth of *Anictis* are larger and more robust than equivalent teeth of *Stenoplesictis* and *Palaeoprionodon*, despite the nearly equivalent depth of the mandibles below the carnassial. In *Anictis* the m1 metaconid is less reduced and the m1 talonid more developed (with a more prominent hypoconid) than in the latter two genera, yet the paraconid-protoconid blade of m1 is advanced to about the same degree in all three genera. The anterior cingulum cusps of p3–4 tend to be reduced in *Anictis* but are prominent in the other two genera.

As Teilhard was aware, the m2 of *Anictis* is the most fully developed and hence plesiomorphic of any Quercy aeluroid (fig. 6), with its three trigonid cusps positioned at the points of an equilateral triangle, and the talonid fully developed, in contrast to a diminutive m2 with reduced talonid seen in the other two genera. Because the trend toward hypercarnivory results in reduction and eventual loss of the m2, the Quercy aeluroids other than *Anictis* generally display a variety of m2 morphs, all diminished in size, and showing varying degrees of talonid reduction (fig. 6).

Thus, *Anictis simplicidens* is distinctive among Quercy aeluroids because of its plesiomorphic dental and mandibular features (size and form of molars, retention of a full

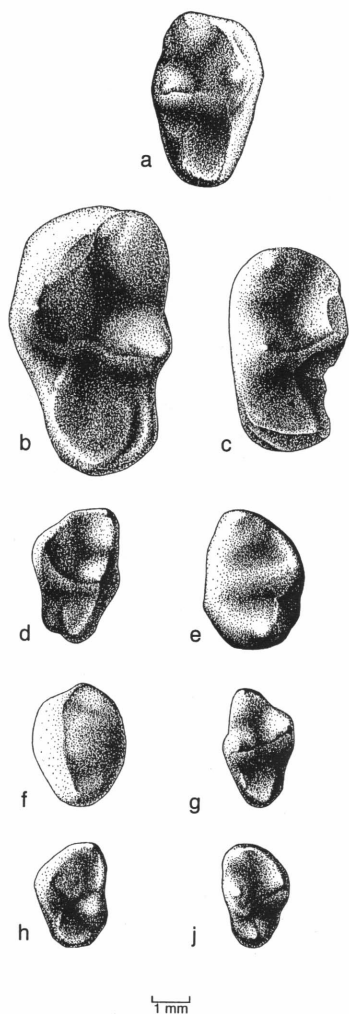


Fig. 6. Comparison of m2 in early aeluroids from Quercy and Hsanda-Gol (in occlusal view). The form of this molar in Quercy aeluroids was considered diagnostic by Teilhard (1915). **a**, *Asiavorator gracilis* (AMNH field no. 86); **b**, *Anictis simplicidens* (MGL PQ567); **c**, *Asiavorator gracilis* (AMNH 19123); **d**, *Stenoplesictis cayluxi* (MNHN Qu9374); **e**, *Haplogale media* (MNHN Qu9435); **f**, *Proailurus lemanensis* (MNHN Qu9438); **g**, *Stenoplesictis minor* (MNHN Qu9399); **h**, *Palaeoprionodon lamandini* (AMNH 10095); **j**, *Stenogale gracilis* (AMNH 10112).

complement of premolars, “normal” mandibular dimensions), yet its tall, slender, acuspate p2–p3 appears to be a derived trait important in its identification. The teeth of *A. simplicidens* are similar to those of living vi-

verrids with plesiomorphic dentitions. Unfortunately, the basicranium and skull of *Anictis* are unknown.

STENOPLSICTIS FILHOL AND *PALAEOPRIONODON* FILHOL: My study of the small Quercy aeluroids in the Paris Museum, which included Teilhard’s (1915) specimens, convinced me of the validity of Filhol’s two dentally similar genera, *Palaeoprionodon* and *Stenoplesictis* (figs. 7, 8). The former averages smaller than the latter, has a more reduced and posteriorly retracted (“reculée”) m1 metaconid, commonly shows a sharp size break between p2 and p3 (p1–2 are much reduced), and usually lacks a pronounced basining of the m2 trigonid. *Stenoplesictis cayluxi* is on the average a somewhat larger animal, has a developed m1 metaconid (hence a wide m1 measured at the posterior trigonid margin), may or may not show a sharp size break between p2 and p3, and commonly displays a distinct basin in the center of the m2 trigonid. I observed no reliable distinctions between the two genera with regard to the m2 talonid, but the m1 talonid tends to retain a hypoconid in *Stenoplesictis* and not in *Palaeoprionodon*. Also, five of eight mandibles of *Palaeoprionodon* either lack or have only a weak posterior accessory cusp on p3, whereas this cusp is always present in *Stenoplesictis*. Tables 1–4 present these observations based on the Paris Museum samples, using mandibles that include an intact m2.

Teilhard (1915: 76) placed considerable emphasis on the form of m2 in his analysis of the two genera (fig. 6). Because of this, I examined all mandibles of these genera in the Paris Museum that retained m2. I found nine mandibles corresponding to the holotype of *S. cayluxi* (the genoholotypic species) that had an intact m2. These could be discriminated from the m2 of *Palaeoprionodon* as follows:

(1) The *Stenoplesictis* m2 has a basined trigonid, that is, a shallow, flat-bottomed concavity surrounded by the three trigonid cusps—this feature is better developed than in *Palaeoprionodon* because of the wider molars (both m1 and m2) of *Stenoplesictis*. The relatively narrow molars in *Palaeo-*

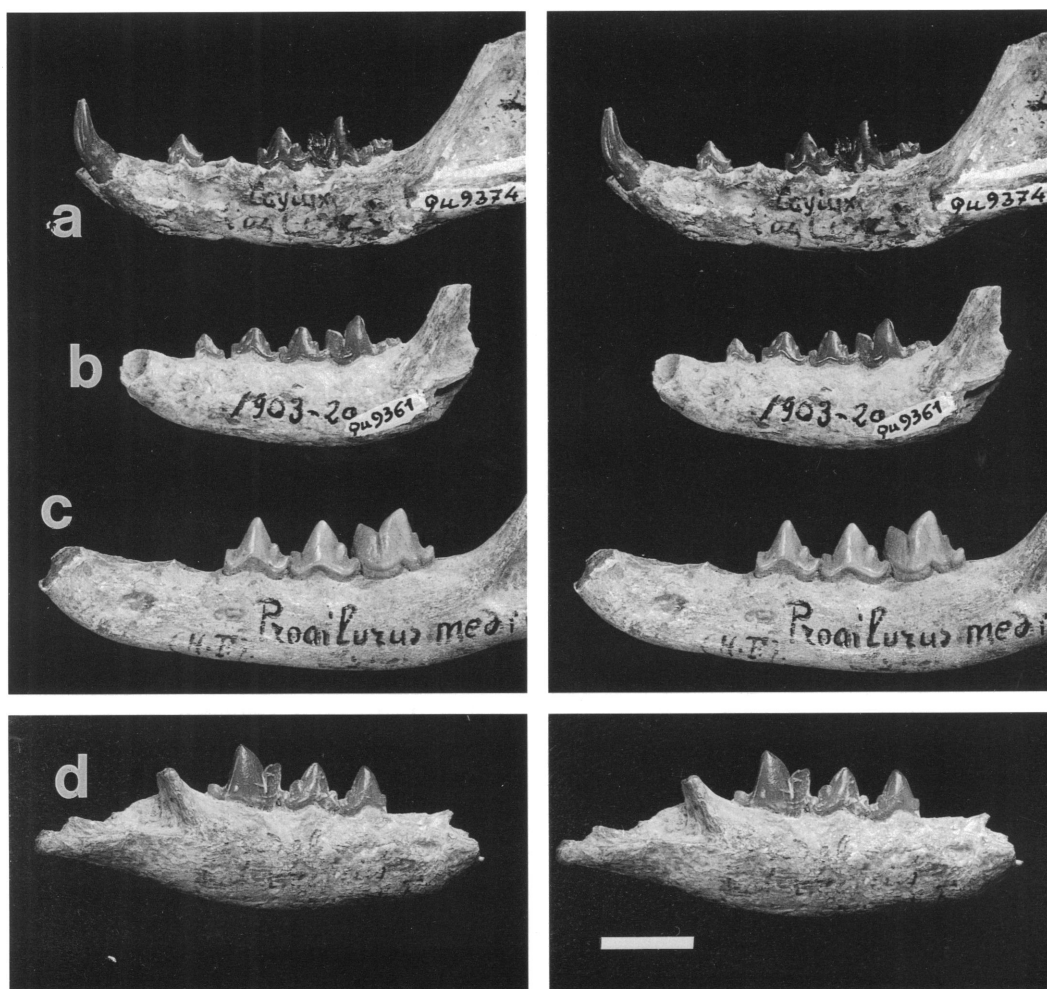


Fig. 7. Stereophotographs comparing the mandibular dentition (labial view) of the Quercy aeluroids **a**, *Stenoplesictis cayluxi*, Qu 9374, holotype; **b**, *Palaeoprionodon lamandini*, Qu 9361; **c**, *Haplogale media*, Qu 9422, holotype; **d**, *Stenogale intermedia*, Qu 9083, holotype.

prionodon preclude adequate space for an m2 trigonid basin (table 1).

(2) A ridge connects the protoconid with the metaconid of m2 in all but one specimen of *Stenoplesictis*, and a notch occurs midway along the ridge joining the two cusps. There is no ridge in *Palaeoprionodon*.

(3) Based on the Paris Museum samples, the degree of basining of the trigonid is probably the only feature of m2 that consistently differs between the two genera. The nature of the m2 talonid is much the same in both genera.

Only one species of *Palaeoprionodon* is

apparent in the Quercy sample in the Paris Museum. Teilhard (1915) followed Filhol in using the name *P. lamandini* for this small aeluroid. On the other hand, *Stenoplesictis* is probably represented by three species: *S. minor* Filhol (the smallest Quercy aeluroid), *S. cayluxi* Filhol (the best-known form, intermediate in size between the other two species), and *S. n. sp.* (the largest form, known from very few specimens: MNHN Qu 9400–9402, 9373, table 6).

The study of samples of sufficient size in the Paris Museum corroborates Teilhard's analysis and reaffirms the validity of these

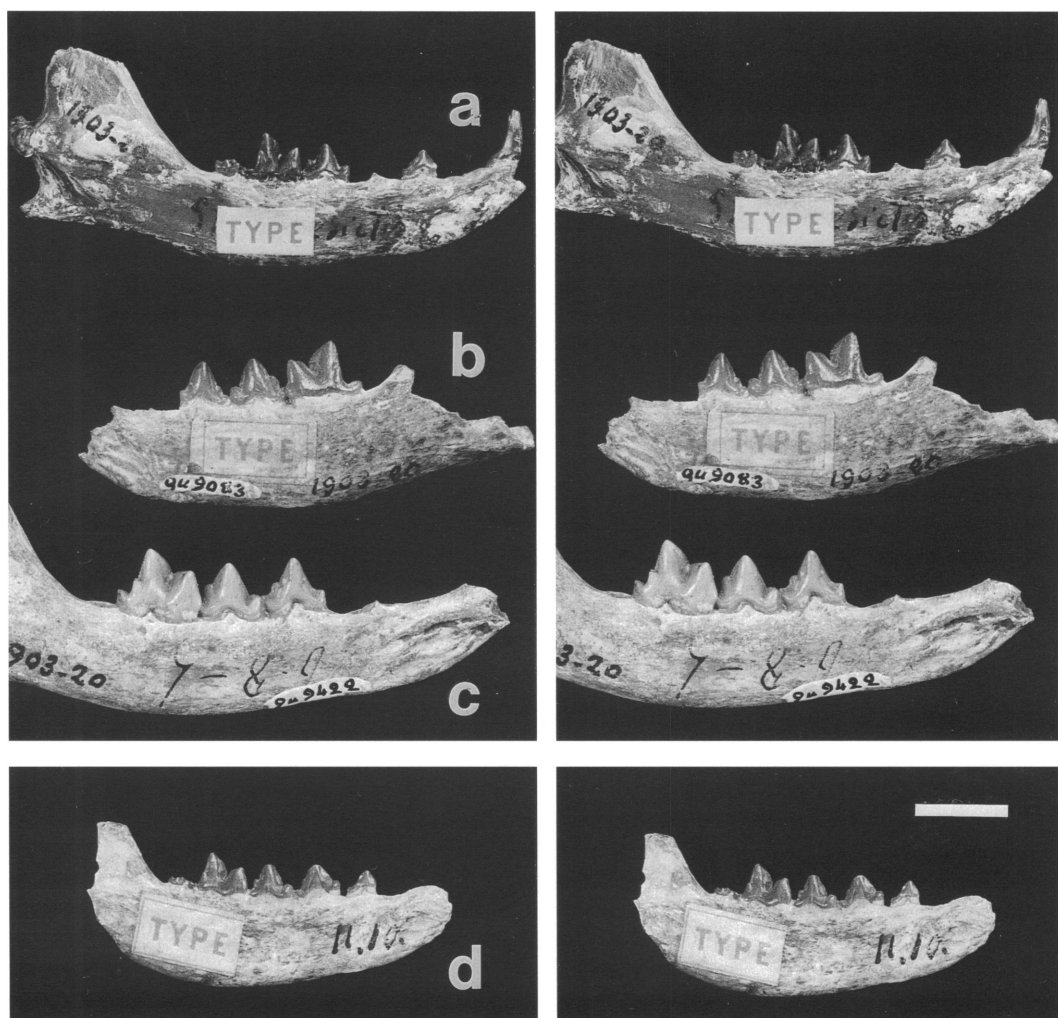


Fig. 8. Stereophotographs comparing the mandibular dentition (lingual view) of the Quercy aeluroids **a**, *Stenoplesictis cayluxi*, Qu 9374, holotype; **b**, *Stenogale intermedia*, Qu 9083, holotype; **c**, *Haplogale media*, Qu 9422, holotype; **d**, *Palaeoprionodon lamandini*, Qu 9361.

two genera at Quercy. However, included among the samples are individual mandibles that retain, omit, and combine dental traits in a manner that makes some of these jaws very difficult to allocate to either genus. Thus, sufficiently large samples are necessary to establish the identity of these species at a particular locality. This requirement is underscored by the possibility of a high degree of parallel dental evolution in early aeluroids where multiple lineages may be independently trending toward hypercarnivory.

HAPLOGALE SCHLOSSER: A long-snouted aeluroid "*Proailurus*" *medius* was first recog-

nized at Quercy by Filhol (1882: 75, pl. 4, figs. 6–8). Later, this unusual carnivore was described as a distinct genus by Schlosser (1888: 372) who called it *Haplogale*. Schlosser's generic designation is useful in discriminating this long-snouted animal at Quercy from the short-snouted catlike forms (fig. 5). The genus *Proailurus* had previously been created by Filhol (1879) for the early felid *Proailurus lemanensis* from St. Gérard; however, *P. lemanensis* was a short-faced catlike carnivore, the size of a lynx, very different from the smaller, long-snouted *Haplogale*. The long-jawed nature of *Haplogale*

TABLE 1
Measurements (in mm) and Other Characters of
the Lower Carnassial of Quercy *Stenoplesictis*
and *Palaeoprionodon* (MNHN, Paris)

MNHN no.	m1 L × W ^a	Basined m1 talonid ^b	m1 metaconid ^c
<i>Stenoplesictis</i>			
Qu 9374 ^d	6.8 × 3.12	yes, hp	pr, nr
Qu 9392	7.3 × 3.27	yes, hp	pr, nr
Qu 9104	7.4 × 3.26	yes, hp	pr, nr
Qu 9103	7.6 × 3.56	yes, hp	pr, nr
Qu 9398	7.1 × 2.70	yes, hp	pr, re
Qu 10880	8.0 × 3.35	yes, hp	pr, nr
Qu 10881	7.7 × 3.19	yes, hp	pr, re
Qu 10889	8.1 × 3.45	yes, hp	pr, nr
<i>Palaeoprionodon</i>			
Qu 9361 ^d	6.8 × 2.57	yes, ha	sr
Qu 9319	6.8 × 2.62	yes, ha	sr
Qu 9321	6.5 × 2.54	yes, ha	sr
Qu 9322	6.5 × 2.58	yes, ha	sr
Qu 9323	6.8 × 2.56	yes (reduced), hp	mr
Qu 9324	6.9 × 2.78	yes, ha	mr
Qu 9325	6.4 × 2.37	yes, ha	sr
Qu 9327	6.5 × 2.52	yes, ha	sr
Qu 9330	7.4 × 2.78	yes, ha	sr
Qu 9331	6.6 × 2.46	yes, ha	sr
Qu 9343	6.2 × 2.33	yes, ha	sr
Qu 9344	6.3 × 2.50	yes, ha	sr
Qu 9346	6.7 × 2.55	yes, ha	sr
Qu 9356	6.3 × 2.52	yes (reduced), hp	mr
Qu 9336	5.7 × 2.14	—	—
Qu 9339	5.9 × 2.65	yes, ha	mr
Qu 9367	5.9 × 2.30	yes, ha	sr

^a L × W = length × width. Width measured at level of posterior trigonid.

^b hp = hypoconid prominent; ha = hypoconid not prominent.

^c pr = prominent; nr = not retracted; re = retracted (reculée); sr = strongly retracted; mr = slightly retracted.

^d Holotype.

was emphasized by Schlosser in his initial description.

In this report I regard *Haplogale* as a small long-snouted aeluroid with a viverridlike rostrum and mandible, similar to the living genets, but with a more hypercarnivorous m1. On present evidence it is not in the direct ancestry of later neofelids (*Proailurus lemanensis*, *Pseudaelurus*, and descendants). The basicranium and postcranial skeleton of *Haplogale media* are unknown. Based on the dimensions of the mandible and rostrum, the

TABLE 2
State of Reduction of the Anterior Premolars in
Quercy *Stenoplesictis* and *Palaeoprionodon*
(MNHN, Paris)

<i>Palaeoprionodon</i>	
Mandibles with marked size decrease between p3 and p2 (reduced p1-2):	
Qu 9361 ^a , 9319, 9321, 9322, 9323, 9327, 9337, 9344, 9356, 9339, 9367	
Mandible with less evident size decrease between p3 and p2:	
Qu 9325	
<i>Stenoplesictis</i>	
Mandibles vary in degree of reduction of anterior premolars:	
Qu 9374 ^a	p3 absent but alveoli suggest possible size decrease
Qu 9398	size decrease between p2 and p3
Qu 9103	p2 absent: small p2 alveoli suggest possible decrease
Qu 9104	p2 absent: small p2 alveoli suggest possible decrease
Qu 10880	p2-4 present: size decrease but not pronounced
Qu 10881	p2 broken but small size decrease
Qu 10889	p3 broken: possible small but no marked size decrease

^a Holotype.

TABLE 3
Diagnostic Characters of m2 in Quercy
Stenoplesictis and *Palaeoprionodon*
(MNHN, Paris)

<i>Stenoplesictis</i>	
m2 trigonid <i>basined</i> , with 3 cusps equidistant from center, and with small talonid; ridge joins metaconid to protoconid; protoconid joined by ridge to low or vestigial paraconid:	
Qu 9374 (holotype), 9398, 9392, 9103, 9104, 10880, 10881, 10889	
<i>Palaeoprionodon</i>	
m2 trigonid lacking basin or with only weakly developed basin; prominent protoconid joined by continuous ridge to low paraconid; low metaconid occurs posteromedial to protoconid and is always separated from it by valley; a small reduced talonid with a single major cusp (hypoconid):	
Qu 9361 (holotype), 9319, 9321 (damaged), 9322, 9323, 9324, 9325, 9327, 9331, 9339, 9343, 9344, 9346, 9367	
m2 as above, but atypical in lacking talonid:	
Qu 9356	
m2 as above, but with exaggerated metaconid retraction:	
Qu 9330	

TABLE 4
Presence of Accessory and Cingulum Cusps on
Premolars of Quercy *Stenoplesictis* and
Palaeoprionodon (MNHN, Paris)^a

	p3			p4		
	pcs	pac	acc	pcs	pac	acc
<i>Stenoplesictis</i>						
Qu 9374 (h)	p3 lost in holotype			+	+	+
Qu 9398	+	+	+	+	+	+
Qu 9392	+c	+	+	+c	+	+
Qu 9104	+c	+	+	+c	+	+
Qu 9103	+	+	+	+	+	+
Qu 10880	+	+	+	+	+	+
Qu 10881	+	+	+	+	+	+
Qu 10889	+	+	+	+c	+	+
<i>Palaeoprionodon</i>						
Qu 9361 (h)	+c	+	+	+	+	+
Qu 9323	+	+	+	+	+	+
Qu 9322	+	a	+	+	w	+
Qu 9319	+	w	+	+	+	+
Qu 9331	+	w	+	+	+	+
Qu 9324	+	w	+	+	+	+
Qu 9344	+	a	+	+	w	+
Qu 9343	+	+	+	+	+	+
Qu 9330	+	w	+	+	+	+
Qu 9325	+	+	+	+	+	+
Qu 9327	+	w	+	+	+	+
Qu 9321	+	a	+	+	a	+
Qu 9339	+	w	+	+	+	+
Qu 9367	+	+	+	+	+	+
Qu 9346	+	+	+	+	+	+
Qu 9356	+c	+	+	+c	+	+
Qu 9336	+	a	+	+	w	+

^a All specimens of *Stenoplesictis* and *Palaeoprionodon* in table 4 retain the m2 in the mandible. Abbreviations: (h), holotype; +, cusp present; w, cusp weak; a, cusp absent; acc, anterior cingulum cusp; pac, posterior accessory cusp; pcs, posterior cingulum shelf (c = cusp on shelf).

skull of the animal had an estimated basilar length of ~10.5 cm, making it one of the larger Quercy aeluroids.

The genus *Haplogale* must be based on Filhol's holotype mandible of "*P.*" *medius* (MNHN Qu 9422, figs. 7C, 8C). Schlosser emphasized the slender elongated nature of this jaw. There are even small diastemata between C and p1, p1 and p2, and p2 and p3. Because only p3, p4, and m1 are present in the holotype (C, p1–2, m2 are represented by alveoli), the dental diagnosis rests on the size and form of these teeth. The p3 and p4 each

have an anterior cingulum cusp, a posterior accessory cusp, and a posterior cingulum shelf produced into a low posterior cingulum cusp. This animal is typical of early aeluroids with the full complement of accessory cusps on p3–p4.

The closest match in the Paris Museum collection to Filhol's holotype (Qu 9422) is a mandible (Qu 9435, Teilhard, 1915: pl. IX, fig. 17) in association with a rostrum (Qu 9436, Teilhard 1915, pl. IX, fig. 12) of a long-snouted aeluroid (fig. 9). This association (documented by Teilhard, 1915: 75 and in pl. IX) is critical because it demonstrates that this carnivore was not short-faced, but more similar to a small viverrid. The teeth that can be compared (p3–m1) between the holotype and Qu 9435 are nearly identical (the anterior cingulum cusp of p3 in Qu 9435 has been broken off): the m1 talonid of both is very small and more of a flat platform than a basin, although a weak concavity is present. However, Qu 9435 alone supplies information on p1–2: p1 is a single-rooted simple tooth (although broken, it was quite small, low); p2 is double-rooted, much smaller than p3, yet rather tall and without accessory cusps. The m2 is also present on Qu 9435 (fig. 6): Teilhard emphasized the importance of this tooth. He stated that m2 was without a talonid and this is clearly the case. What at first appears to be an m2 talonid is in fact a prominent posteriorly displaced metaconid: this trait distinguishes the m2 from those of *Stenoplesictis* and *Palaeoprionodon* where a small talonid occurs, and from *Anictis* in which a talonid is well developed. The associated rostrum (Qu 9436) has the right I1–2, C, P1 alveolus, P2–4, M1. There seems to be no M2, although it may have occurred as a very small vestigial tooth. I can see no definite alveoli for M2 on the posterior margin of the maxilla. The left upper dentition includes I1–3, the base of C, P1 alveolus, P2–3 and anterior part of P4; the remainder of the maxilla has been broken and lost. The anterior rostrum is quite narrow and elongate from P2 forward, and is not the shortened rostrum of a catlike carnivoran. The canines are long, slender, and oval in cross-section but not bladelike or strongly laterally compressed.

There are additional mandibles from Quer-

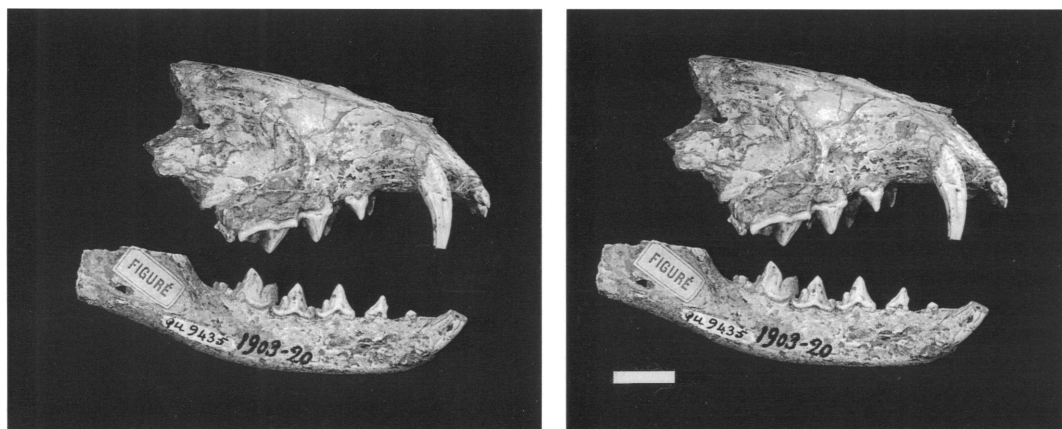


Fig. 9. Stereophotographs of associated rostrum and mandible of the long-snouted aeluroid *Haplogale media* from Quercy (MNHN Qu 9435, Qu 9436), showing a profile similar to the living viverrid *Genetta*.

cy in the Paris Museum collection that can be referred to *Haplogale media* (Qu 9427, Qu 9428, Qu 9429, Qu 9431, Qu 9432, see table 5), and two mandibles in the Museum of Comparative Zoology, Harvard University (MCZ 8936, 8937 also from Quercy). This hypodigm shares dental similarities with *Palaeoprionodon*, but the teeth of *H. media* are larger (table 6) and its m1 metaconid is less reduced.

STENOGALE SCHLOSSER: The type species of this genus remains in doubt. A type species and specimen were not formally designated by Schlosser (1888) when he created the genus. However, a practical solution to the problem can be developed through review of the European literature and of fossils preserved in the National Museum (Paris). Schlosser clearly implied that the Quercy species *S. gracilis* and *S. intermedia* were important to his concept of the genus by their placement in his text: *S. gracilis* has page priority as the first of the species included by him in *Stenogale*, and *S. intermedia* directly follows it in his text. The two remaining species placed in *Stenogale* by Schlosser were not from Quercy and are each represented only by a single mandible, whereas *S. gracilis* was known from numerous mandibles and *S. intermedia* from a sample of four. Thus, the Quercy fossils composed most of

the material placed in the new genus and were its nucleus.²

Schlosser was justified in including both *Stenogale gracilis* and *S. intermedia* in a single genus, based upon the mandibles and dentitions from Quercy. Teilhard (1915) fol-

² It would seem to be a simple matter to designate *S. gracilis* as the holotype species of *Stenogale* Schlosser, if for no other reason than its page priority. Teilhard (1915), however, explained the difficulty in taking this step: the species *gracilis* was created earlier by Filhol (1877) for two mandibles previously illustrated and briefly described by Gervais (1876; pl. XIII, figs. 8, 9) who had preferred not to name a species in 1876; both Gervais and Filhol had placed the two specimens in the genus "*Plesiogale*," but Filhol had noted that the mandibles did not conform to other species in that genus. Furthermore, Filhol did not select one of the two mandibles as a holotype, nor did he refigure the material, leaving the illustrations of Gervais as the only means to visually identify the species. Unfortunately, the two mandibles of Gervais from which a type could be selected are lost or misplaced (Bonis and Cirot 1995).

Aware of the difficulties surrounding the initial descriptions of Gervais and Filhol, Teilhard (1915) attempted to resolve the problem of the identity of *Stenogale* by assembling a small sample of mandibles in the National Museum (Paris) that conformed to Filhol's (1877) verbal description of *S. gracilis*. Teilhard described and provided illustrations of several of these mandibles that he believed were representative of the hypodigm of *S. gracilis*. A number of additional mandibles in the National Museum (Paris) can be combined with Teilhard's figured specimens (1915, pl. IX, figs. 1-3; pl. VIII, fig. 19) to create a small hypodigm. From this hypodigm a lectotype mandible (MNHN Qu 9111) has recently been selected by Bonis and Cirot (1995).

TABLE 5
Measurements (in mm) of Lower Teeth of Quercy
Haplogale media and *Proailurus lemanensis*

	ml L × W ^a	p3-ml L ^a
<i>Haplogale media</i>		
Qu 9422 ^b	9.2 × 3.5	22.3
Qu 9435	9.2 × 3.4	22.0
Qu 9432	8.3 × 3.3	20.7
Qu 9431	7.3 × 3.0	18.5
Qu 9429	8.0 × 3.2	19.8
Qu 9428	8.9 × 3.5	(22) ^c
Qu 9427	9.3 × 4.3	—
MCZ 8936	8.8 × 3.4	21.7
MCZ 8937	9.2 × 3.4	(22.3)
<i>Proailurus lemanensis</i>		
Qu 9437	12.8 × 5.8	30.3
Qu 9438	13.0 × 5.5	30.3
Qu 9439	12.5 × 5.5	29.4
Qu 9440	12.4 × 5.1	28.7

^a L = length; W = width.
^b Holotype.
^c Estimated measurements in parentheses.

lowed Schlosser, including both *S. intermedia* and *S. gracilis* in his concept of the genus. A holotype mandible of *S. intermedia* had been designated earlier by Filhol (1876: figs. 108, 109), and was refigured by Teilhard (1915: pl. IX, fig. 4). This fossil (figs. 7D, 8B) differs only in its larger size from the specimens of the *S. gracilis* hypodigm. Consequently, it is uncertain whether the two species represent (1) a single evolving line-

age, (2) sexual dimorphism within a single species, or (3) two contemporaneous species. Some mandibles that I examined in the Paris Museum (MNHN Qu 9109, 9110) bridge the size gap between the *S. gracilis* sample and the holotype of *S. intermedia* (the holotype is the largest Quercy *Stenogale* mandible that I observed), and a recently described mandible of *S. intermedia* from Rigal Jouet (Bonis and Cirot, 1995) also falls in this interval (table 6). The likelihood that the *S. gracilis*-*S. intermedia* hypodigm samples a temporally and geographically variable species (with possible sexual dimorphism) appears plausible.

Thus, my concept of *Stenogale* Schlosser is based upon a small hypodigm of Quercy fossil mandibles, attributed to the species *gracilis* and *intermedia*. These specimens are numbered in the National Museum (Paris) as Qu 9111 (lectotype of *gracilis*), 9113, 9114, 9115, 9109, 9110, 9083 (holotype of *intermedia*).

The specimens of these two species figured by Teilhard (1915: pl. IX, figs. 1–4) are small, short-jawed, robust little mandibles, catlike in their general form. They are extremely similar to mandibles from the Aquitanian deposits of St.-Gérard that were placed in *Stenogale julieni* by Teilhard (1915: 70) and Viret (1929: pl. XII, figs. 8–9), and are associated with a remarkably well-preserved skull with basicranium [the skull and associated mandibles were initially figured and described by Filhol (1879: pl. 27,

TABLE 6
Measurements (in mm) of the Lower Carnassial of Quercy Aeluroid Carnivorans

	ml length	ml width
<i>Stenoplesictis minor</i>	5.9–7.0 (N = 9)	2.40–3.0 (N = 9)
<i>Stenoplesictis cayluxi</i>	6.8–8.1 (N = 8)	2.70–3.56 (N = 8)
<i>Palaeoprionodon lamandini</i>	5.7–7.4 (N = 17)	2.14–2.78 (N = 17)
<i>Haplogale media</i>	7.3–9.3 (N = 9)	3.0–4.3 (N = 9)
<i>Stenoplesictis</i> n. sp.	9.5–10.3 (N = 4)	(3.7) ^a –4.9 (N = 4)
<i>Stenogale gracilis</i>	6.6–8.1 (N = 5)	3.2–3.7 (N = 5)
<i>Stenogale intermedia</i>	8.4 (N = 1) ^b	4.2 (N = 1) ^b
<i>Stenogale intermedia</i>	8.3 (N = 1) ^c	3.9 (N = 1) ^c
<i>Proailurus lemanensis</i>	12.4–13.0 (N = 4)	5.1–5.8 (N = 4)

^a Estimated measurement.
^b Holotype.
^c Referred (Bonis and Cirot, 1995).

figs. 5–6, 8–10) as *Proailurus julieni*]. The skull is short-snouted, very different from the longer snouted *Haplogale* (fig. 5). It is this particular skull that provides a detailed anatomy of the *Stenogale* basicranium. The basicranium shares a number of similarities with the basicranium of *Proailurus lemanensis*, also from the Aquitanian of St.-Gérard (see below).

GEOLOGIC OCCURRENCE AND AGE

The Quercy deposits (southern France) fill karstic fissures formed in Jurassic limestones. The limestone plateaux form karst highlands situated between the Massif Central to the east and the Aquitaine Basin to the west. The ages of the majority of the fissure faunas range from ~38–40 Ma (Le Bretou) to ~25–26 Ma (Pech Desse, Pech du Fraysse), hence late Eocene to late Oligocene in age (Legendre and Bachelet, 1993; Lévêque, 1993). More recently, the temporal range of the fissures has been extended by the discovery of lower and middle Eocene faunas (Legendre et al., 1992; Sudre et al., 1990) and an early Miocene assemblage (Sigé et al., 1991) within the Quercy district. The phosphate-rich sediments that filled the fissures were mined extensively from 1865 to 1900: initially, fossils were crushed together with the phosphate nodules to produce commercial phosphate for shipment to England through Bordeaux (Bonis et al., 1977). In 1872 Gervais, Filhol, and Delfortrie published the first descriptions of Quercy mammals (Vianey-Liaud and Legendre, 1986). Subsequent studies in the later 19th and early 20th century made known the rich “faune quercinoise” but, regrettably, due to the nature of the phosphate mining process, neither stratigraphic nor precise locality data on the occurrence of the fossils were recorded.

Since 1965 an organized effort has been carried on by French paleontologists to systematically survey, excavate, and document the fauna of the remaining fissure deposits. These excavations have identified over 70 productive fissures with mammalian assemblages. The resulting biochronology, organized as a series of reference levels (Remy et al., 1987; Crochet et al., 1981; Bonis et al., 1973; Bonis, 1974), continues to be re-

finied, and has been correlated to the Paleogene standard levels (MP zones) proposed at Mainz in February 1987 (Schmidt-Kittler, ed., 1987). A Paleogene biochronological reference scale, based on representative and species-rich mammalian faunas from single localities, has been developed in part from the detailed faunal sequence of late Eocene and Oligocene mammals now available in the Quercy district.

The recently established sequence of fissure faunas from Quercy has allowed the placement of the earliest aeluroid carnivorans in an improved temporal reference scale (Remy et al., 1987; Legendre et al., 1991). Aeluroids are unknown in the fissures of Eocene age predating the Grand Coupure of Stehlin (1910) that marks the Eocene-Oligocene boundary, currently placed at ~33.7 Ma (Montanari et al., 1988; Lévêque, 1993). The first aeluroid to appear in western Europe is the dentally plesiomorphic *Anictis simplicidens* from Aubrelong 1, a fissure placed in reference level 6 (MP zone 21) of Remy et al. (1987), with an estimated age of about 33 Ma (Legendre and Bachelet, 1993; Lévêque, 1993). The first nimravid (*Eusmilus*) is found at Soumaillies at about the same time. The next nimravid appearances (*Nimravus*, *Eusmilus*, *Quercylurus*) occur in reference level 8 (MP zone 23), dated to ~31–32 Ma, and *Nimravus* occurs together with the tiny aeluroid *Stenoplesictis minor* in three of the level 8 fissure faunas (Itardies, Pech Crabit 1, Mounayne). *Stenogale gracilis* is also found in level 8 at Itardies. In reference level 10 (MP zone 25), estimated at ~29–30 Ma, a considerable diversity emerges that includes three nimravid cats (*Nimravus*, *Quercylurus*, *Dinailurictis*), both species of *Stenoplesictis* (*S. minor*, *S. cayluxi*), and the small *Stenogale intermedia* (Bonis and Cirot, 1995). Both *Stenoplesictis cayluxi* and *Stenogale intermedia* continue to level 13 (MP zone 28), hence range in time from ~30 Ma to perhaps 25–26 Ma. Remy et al. (1987) do not report *Haplogale*, *Palaeoprionodon*, or *Proailurus* from the more recent excavations where newly obtained aeluroid material makes plain its general scarcity and often fragmentary condition (Bonis and Cirot, 1995).

Absence of aeluroids prior to the Eocene-

Oligocene boundary in Europe appears to be a reality, and not merely an artifact of the incompleteness of the geologic record. Nimravid cats and smaller aeluroids appear following the Grande Coupure as early as reference level 6 (MP 21), and continue to the highest reference levels dated at ~25 Ma; thus, their range in these fissures spans the Oligocene. The aeluroids *Haplogale*, *Proailurus*, and *Palaeoprionodon* also probably occur for the first time in the Oligocene fissures of reference levels 6 to 13 (MP 21 to 28), but establishing the exact time of their appearance depends on new discoveries in the Quercy district, or the placement of earlier-discovered fossils of these genera in fissures of known age.

Carnivorans are poorly represented relative to creodonts in the Quercy fissures prior to the Grand Coupure, but after that event carnivorans greatly exceed creodonts in number of species during the Oligocene (Legendre et al., 1991: fig. 8). The transition from lower to upper Oligocene faunas is marked by low diversity in MP zone 26, an interval yielding few fossil Carnivora. This zone is believed to correspond to a time of environmental change in western Europe, namely an arid interval accompanied by climatic cooling (Legendre et al., 1991).

AELUROID BASICRANIA FROM QUERCY AND ST.-GÉRAND

Basicrania of Quercy aeluroids in association with dentitions are uncommon, but a number of well-preserved skulls with intact basicrania are known (Teilhard, 1915; Piveteau, 1943; Hunt, 1989). Of the six aeluroid genera (*Stenoplesictis*, *Palaeoprionodon*, *Stenogale*, *Haplogale*, *Proailurus*, *Anictis*) known from the Quercy fissures, only *Palaeoprionodon* and *Stenoplesictis* are represented by complete skulls in which teeth are associated with the auditory region. However, the dentitions of *Stenogale* and *Proailurus* from Quercy can be matched with nearly identical dentitions from the Aquitanian of St.-Gérard-le-Puy that are associated with superbly preserved skulls. The Aquitanian skulls of *Stenogale* and *Proailurus* establish the basicranial anatomy of these two genera. The following descriptions and analysis em-

phasize the commonality of basicranial structure shared by these four early aeluroid genera.

AUDITORY REGION OF *PALAEOPRIONODON*

Teilhard (1915: pl. IX, figs. 10, 14) figured and briefly described two skulls of this genus from Quercy in the Paris Museum. I examined and photographed them in 1992 (figs. 10, 11). One of the skulls (MNHN Qu 9348) is somewhat smaller and better preserved than its sister skull (MNHN Qu 9370). Both skulls show little crushing or distortion.

Qu 9348 retains a superb basicranium with both ectotympanics ossified and in place (fig. 11A). Qu 9370 also preserves the basicranium, but the left ectotympanic has been lost, allowing an unobstructed view of the petrosal and middle ear (fig. 11B). Dimensions of the skulls are given in table 7.

The dental formula of Qu 9348 is 3-1-4-1: there is no indication of a second upper molar. However, alveoli for a vestigial M2 are present in Qu 9370.

The general morphology of the auditory region of Qu 9348 is similar to the auditory region of the basicranially plesiomorphic living aeluroid *Nandinia binotata*, and frequent comparisons between the two animals will be made in the following discussion.

ECTOTYMPANIC-PETROSAL RELATIONS: The ectotympanic is fully ossified in both right and left auditory regions of Qu 9348 (fig. 12). It is similar in shape and orientation to that of *Nandinia*, differing only in a somewhat more inflected medial margin. In *Palaeoprionodon* the posterior limb of the ectotympanic rests against the petrosal promontorium, making contact with the promontorium just anterior to the round window: the elliptical facet developed at the point of contact is conspicuous and easily observed in fossils where the ectotympanic has been removed (Qu 9370, fig. 13, F). The promontorial facet is better defined and somewhat less vertical than the facet in *Stenoplesictis* (BMNH M1381, Hunt, 1989). In the living *Nandinia* the posterior limb of the ectotympanic closely approaches the promontorium, perhaps making a delicate contact with it in life, since the posterior limb is thickened on its inner face adjacent to the promontorium.

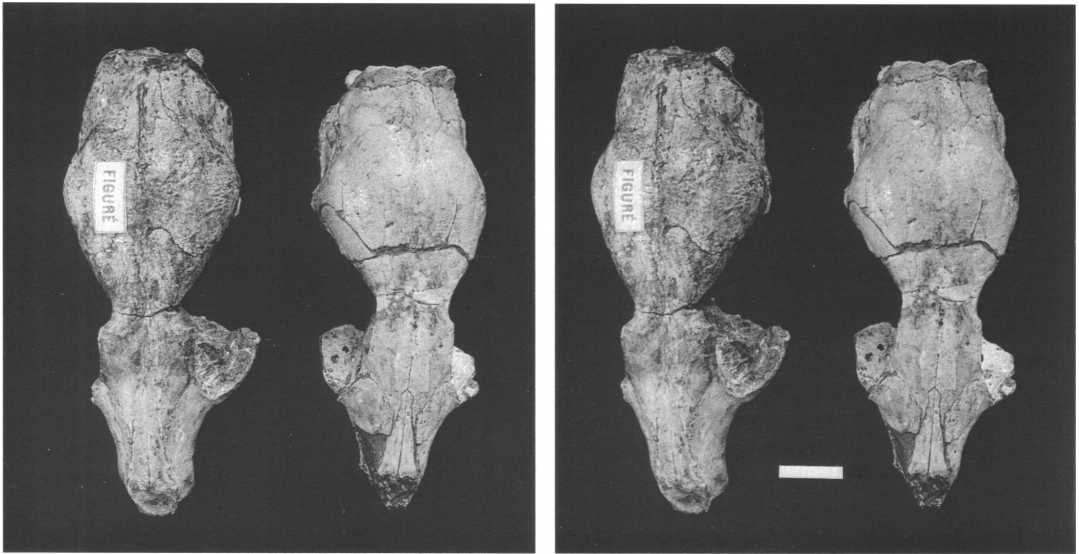


Fig. 10. Stereophotographs of crania of the Quercy aeluroid *Palaeoprionodon lamandini* in dorsal view (left, MNHN Qu 9370; right, MNHN Qu 9348).

However, no facet occurs on the promontorium in specimens of *Nandinia* that I have examined.

The promontorium of *Palaeoprionodon* is very large in comparison to the petrosals of many other small carnivorans. The petrosal is extended ventrad as a robust promontorial process, just as in *Nandinia* and *Stenoplesictis* (fig. 14; also Hunt, 1989: figs. 9, 10). This ventral process buttresses the basioccipital about midway along its lateral margin in all three genera. The petrosal is so large and ventrally protuberant in *Palaeoprionodon* that the ectotympanic cannot completely encompass it. Instead, the ectotympanic rests against the petrosal, creating the promontorial facet. Application of the moderately expanded ectotympanic to the petrosal encloses an anterior chamber of the middle ear.

The crura of the ectotympanic are anchored to the squamosal: as in *Nandinia* there is no mastoid contact. In Qu 9370, depressions for registration of the ectotympanic on the squamosal and alisphenoid can be observed. A deep pit for the anterior crus is present in the squamosal, and medial to it in the alisphenoid a wide shallow elliptical depression for the anterior face of the ectotympanic. The depression in the alisphenoid is well-defined just as in *Stenoplesictis* (BMNH

M1381, Hunt, 1989: figs. 9B, 10B), more so than in *Nandinia*, indicating the greater degree of development of an anteriorly expanded ectotympanic in the two Quercy aeluroids. Relative to *Palaeoprionodon* and *Stenoplesictis*, the plesiomorphic nature of *Nandinia*'s ectotympanic is demonstrated by its lack of expansion (inflation), absence of a conspicuous alisphenoid depression for a widened anterior face of ectotympanic, and the absence of strong ectotympanic contact with the petrosal promontorium (fig. 14A).

CAUDAL ENTOTYMPANIC: A small posterior chamber of the auditory region is enclosed by a caudal entotympanic element. The anterior chamber of the bulla formed by the ectotympanic bone measures 8.7 mm in length in Qu 9348 and 9.6 mm in Qu 9370, whereas the maximum length of the posterior chamber is only 6.8 mm and 7.5 mm, respectively (the length of the posterior chamber is measured from the tip of the ventral promontorial process to the rear wall of the auditory cavity). Thus, both *Palaeoprionodon* skulls have very small posterior chambers. This is certainly the case in the mature animal because Qu 9348 is an adult with fused basioccipital-basisphenoid suture and a fully erupted dentition.

The caudal entotympanic is not preserved

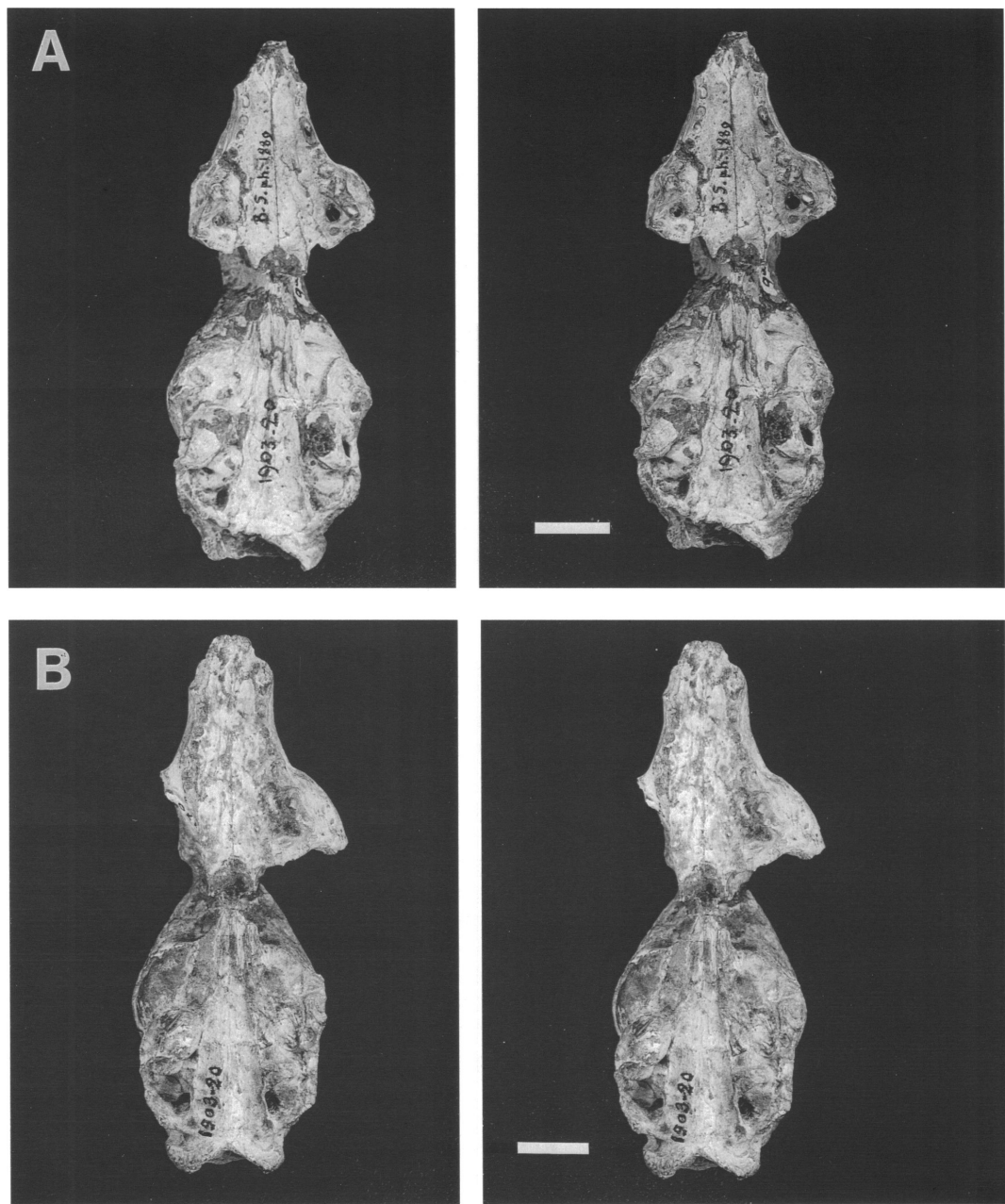


Fig. 11. Stereophotographs of crania of the Quercy aeluroid *Palaeoprionodon lamandini* in ventral view (A, MNHN Qu 9348; B, MNHN Qu 9370).

in any *Palaeoprionodon* skull, but its relative size and relationship to surrounding structures can be determined from its attachments to adjacent bones. In *Palaeoprionodon*, a cartilaginous or fibrous caudal entotympanic element was attached to the medial rim of

the ossified ectotympanic. The line of attachment is a roughened linear groove bordered by low bony ridges, developed as in living *Nandinia* (in which a hyaline cartilage caudal entotympanic produces a similar surface of attachment for the ectotympanic: see Hunt

TABLE 7
Cranial Measurements (in mm) of
Palaeoprionodon (Quercy), *Stenoplesictis* (Quercy)
and *Stenogale julieni* (St.-Gérand)

	MNHN Qu 9348	MNHN Qu 9370	UPM PQ 305	<i>S. julieni</i> holotype
Basilar length	67.4	71.7	84.8	(74) ^a
Braincase, greatest width	26.9	27.8	27.2	25.9
Width between post- orbital processes	13.1	15.3	17.3	17.4
Width between mastoid processes	24.6	24.9	27.8	29.0
Width between con- dyloid foramina	9.6	10.1	10.6	9.7

^a Estimated measurement.

1974, 1987). This line of attachment runs along the internal border of the ectotympanic, following the curve of the element (fig. 12B, indicated by x).

The caudal entotympanic would have covered the posterior auditory region and extended forward between ectotympanic and rostral entotympanic as a strip of cartilaginous or fibrous connective tissue; the anterior penetration of a strip of cartilage or fibrous tissue, separating the ectotympanic and rostral entotympanic elements (*athictic* state), occurs in living aeluroids only in neonatal and juvenile *Nandinia* (Hunt, 1987: figs. 6A, B, 15, 16A) and represents the plesiomorphic condition of the medial wall of the aeluroid bulla (Hunt, 1989). This athictic relationship is confirmed for *Palaeoprionodon* by the left auditory region of Qu 9348 in which the ectotympanic is seated on the petrosal in the life orientation (fig. 12B): in this position a space remains between the ectotympanic and the location of the rostral entotympanic element. Two observations support the inference that the athictic condition occurs in *Palaeoprionodon*: (1) the robust promontorium protrudes ventrad to such an extent that the ectotympanic can approach but cannot directly contact the rostral entotympanic, leaving a gap between the two bulla elements; (2) there is a roughened linear zone of attachment (fig. 12B, indicated by x) developed along the medial rim of ectotympanic for the caudal entotympanic element, and on the surface of the promontorium (anterior to

the ventral process), there is an area for the attachment of a small rostral entotympanic element. The gap between the ectotympanic and rostral entotympanic is configured as in the living *Nandinia*, where it is filled by a strip of hyaline fibrocartilage or dense fibrous connective tissue representing an anterior extension of the caudal entotympanic. Qu 9370, which also preserves the ectotympanic-petrosal relationship intact in the right auditory area, shows the same athictic condition.

The small size of the caudal entotympanic element and its peripheral attachment to surrounding basicranial bones (basi- and exoccipital, mastoid) is as in *Nandinia*, except that in *Nandinia* and in *Stenoplesictis* the mastoid and exoccipital bones are more developed, producing a mastoid-exoccipital shelf. In *Palaeoprionodon* the mastoid and exoccipital bones are thin and delicate in ventral view, as in the living linsang *Prionodon*, and are not developed as a wide, bony shelf.

The posterior part of the petrosal of *Stenoplesictis* (BMNH M1381, Hunt, 1989: fig. 9) displays a prominent flared margin, or "apron," to which the inflected posterior edge of the cartilaginous caudal entotympanic was attached. This petrosal apron slopes gradually caudad from the round window, and is also developed in Qu 9348, Qu 9370, and in *Nandinia*, but not to the degree seen in M1381. In *Nandinia* the anatomical relationship of the inturned edge of the cartilaginous caudal entotympanic attached to the flanged edge of the apron can be directly observed (Hunt, 1987: figs. 6, 16), and a similar situation can be inferred in the Quercy aeluroids *Palaeoprionodon* and *Stenoplesictis*, that is, the flanged margin of the petrosal apron marks the line of attachment of the caudal entotympanic.

When the promontorium of *Palaeoprionodon* (Qu 9348, 9370) is examined with a dissecting microscope, a narrow band of rugose bone is apparent along its medial margin, immediately anterior and posterior to the ventral promontorial process. This aspect of the promontorium is developed as in living *Nandinia* in which the rostral and caudal entotympanic cartilages attach to the surface of the promontorium along this linear feature.

ROSTRAL ENTOTYMPANIC: A discrete rostral entotympanic element is not well exposed in either Qu 9348 or Qu 9370, so its shape cannot be determined. However, in the right auditory region of Qu 9348, its ventral surface is evident but appears too fragile to prepare. In the left auditory region of Qu 9370 (which lacks the ectotympanic), a well-defined space, 1–2 mm in width, for the rostral entotympanic suggests that its form and placement were similar to the rostral element in *Nandinia*.

ARTERIES AND VEINS: The internal carotid artery in *Palaeoprionodon* most likely followed a transpromontorial course through the auditory region similar to its path in *Nandinia* (Chapuis, 1966) and that inferred for *Stenoplesictis* (Hunt, 1989: figs. 7,8). The artery apparently entered the auditory region by passing through the medial wall of the bulla formed by the cartilaginous caudal entotympanic. It is uncertain whether the artery would have penetrated the cartilage immediately posterior to the ventral promontorial process, near the apex of the process or anterior to it. The course of the artery is constrained by the barrier created by application of the ectotympanic to the promontorium; hence, the vessel cannot have ventured very far laterad on the promontorial surface. Its path on entering the middle ear probably followed a more medial course, turning only slightly laterad to run forward along the promontorium, then presumably traveling adjacent to the lateral face of the rostral entotympanic. Upon reaching the middle lacerate foramen the artery turned directly mediad and entered the cranial cavity to supply blood to the brain via the circle of Willis. There is no evidence of a stapedial artery.

The principal venous drainage utilized the internal jugular vein passing out of the skull at the posterior lacerate foramen, where there is an ample opening in the basicranium. The external jugular venous drainage was already reduced even in these early aeluroids: the postglenoid foramina are vestigial in Qu 9370 (as in *Stenoplesictis*, M1381). In Qu 9348 the left postglenoid foramen seems of moderate size, suggesting a patent vessel; on the right the foramen is of equal diameter, but it appears to be closed.

DISCUSSION: The larger skull of *Palaeo-*

prionodon (Qu 9370) confirms relations observed in the left auditory region of the smaller skull (Qu 9348) in which the ectotympanic shows no post-mortem displacement and is applied to the petrosal as in the living animal. Because the left auditory region of Qu 9370 lacks the ectotympanic, the roof of the middle ear and the unobstructed petrosal can be examined. The Qu 9370 petrosal is large and blocky, situated in the center of the auditory region, with its prominent ventral process applied against the basioccipital. The anterior and posterior faces of the promontorium slope gradually away from the ventral process, which is situated at the midpoint of the element. The location of this robust petrosal is important in establishing the relative volume of the anterior and posterior chambers of the bulla. In *Palaeoprionodon* the anterior chamber of the bulla is more voluminous than the posterior chamber.

The two Quercy skulls of *Palaeoprionodon* retain a more plesiomorphic auditory structure relative to the British Museum skull of *Stenoplesictis* (BMNH M1381, fig. 14B) and the Marseille *Stenoplesictis* skull (UPM PQ305, fig. 15) described by Piveteau (1943). In *Palaeoprionodon* the petrosal is large and centrally located within the auditory region, and the ventral petrosal process is robust and vertically aligned, not bladelike and anteriorly inclined as in most living viverrids. The caudal entotympanic chamber in *Palaeoprionodon* is small and has not encroached significantly on the paroccipital process or the mastoid region. The bulla is *athictic*, the ectotympanic and rostral entotympanic elements separated by a cartilaginous or fibrous anterior extension of the caudal entotympanic that penetrates into the anteromedial corner of the auditory region. The petrosal "apron" (a term used here for the smoothly sloping caudal surface of the promontorium posterior to the round window, prominently developed in some early aeluroids, figs. 12B,C, 13, 15) is plesiomorphic in its minimal degree of development, much as in *Nandinia*, and is not as derived as in *Stenoplesictis*. The more apparent differences relative to *Nandinia* are the slightly more chambered ectotympanic and the extensive contact between the rim of the ectotympanic and the promontorium in *Palaeoprionodon*,

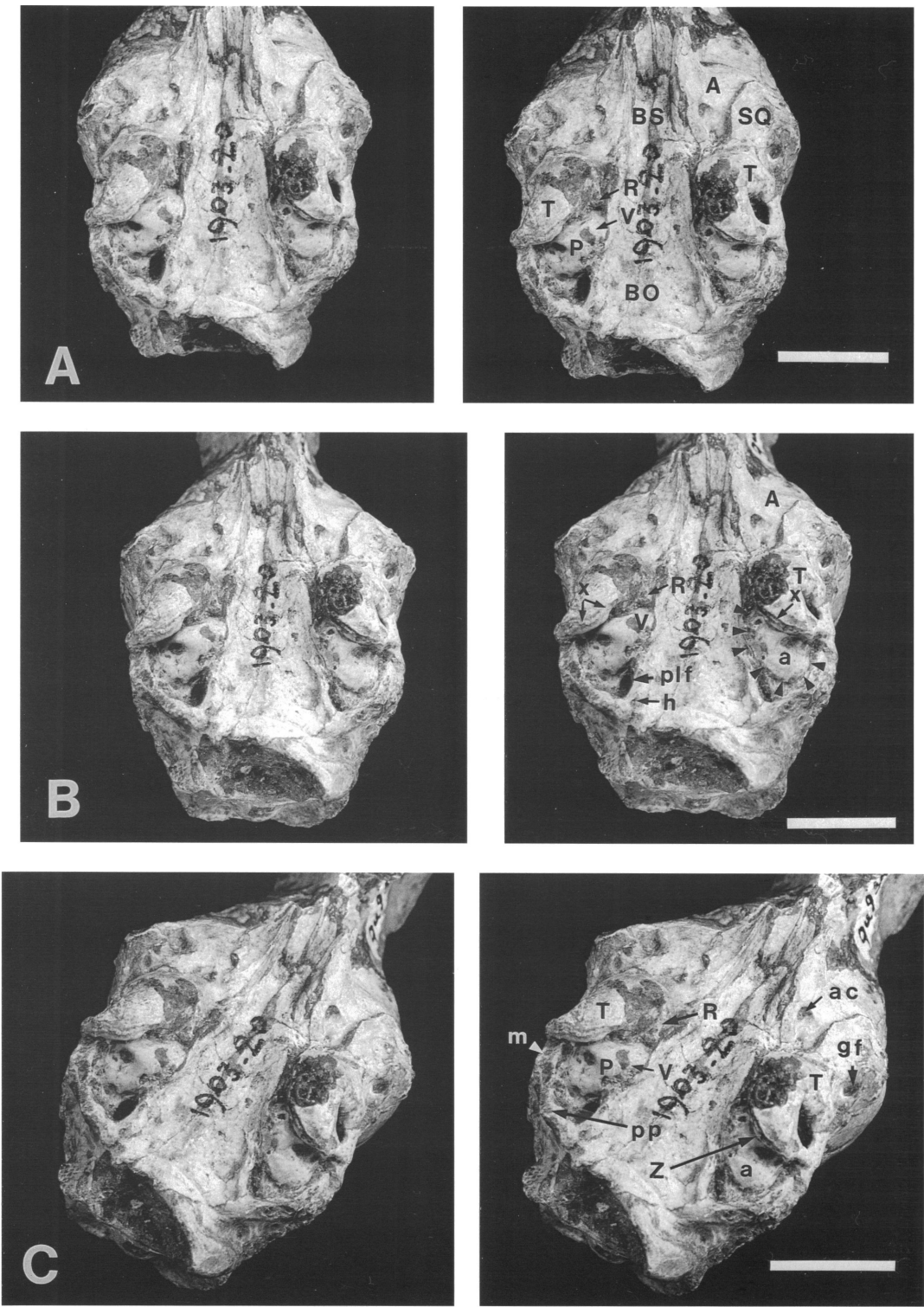


Fig. 12. Stereophotographs of the basicranium of *Palaeoprionodon* (MNHN Qu 9348) from Quercy:

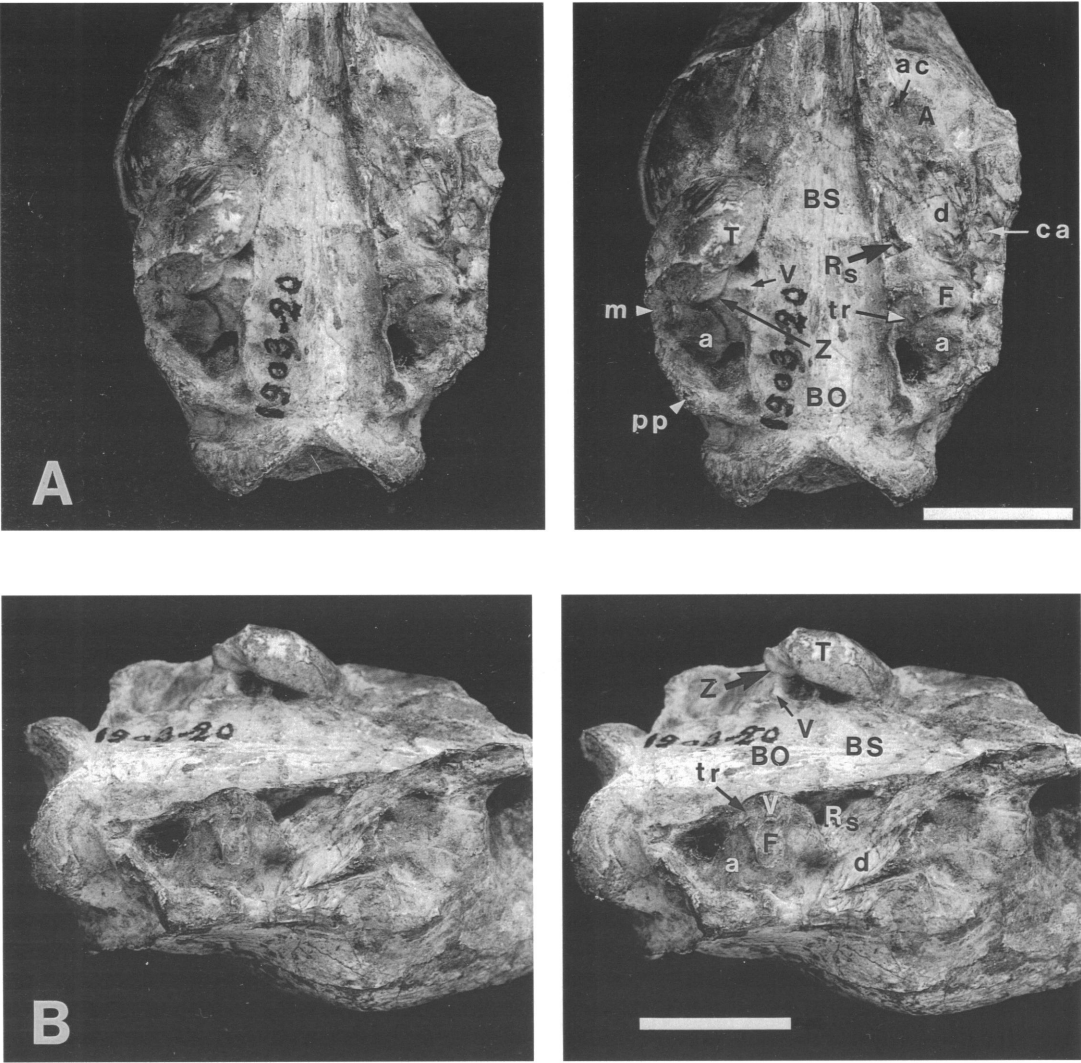


Fig. 13. Stereophotographs of the basicranium of *Palaeoprionodon* (MNHN Qu 9370) from Quercy: (A) ventral and (B) lateral views. Absence of the ectotympanic in the left auditory region allows an unobstructed view of the petrosal in this aeluroid.

both probably relating to the smaller body size of the Quercy genus. This contact is probably a derived trait common to many diminutive early aeluroids in which slight expansion of the bony ectotympanic mandates

contact with the promontorium in animals of small body size (the small living linsangs *Prionodon* and *Poiana* have the ectotympanic rim in strong contact with the promontorium).

←
(A) ventral, (B) posteroventral, and (C) posterolateral views. In (B) small black triangles indicate line of attachment of the caudal entotympanic to the margin of the petrosal. For abbreviations in this and subsequent figures, see p. 5.

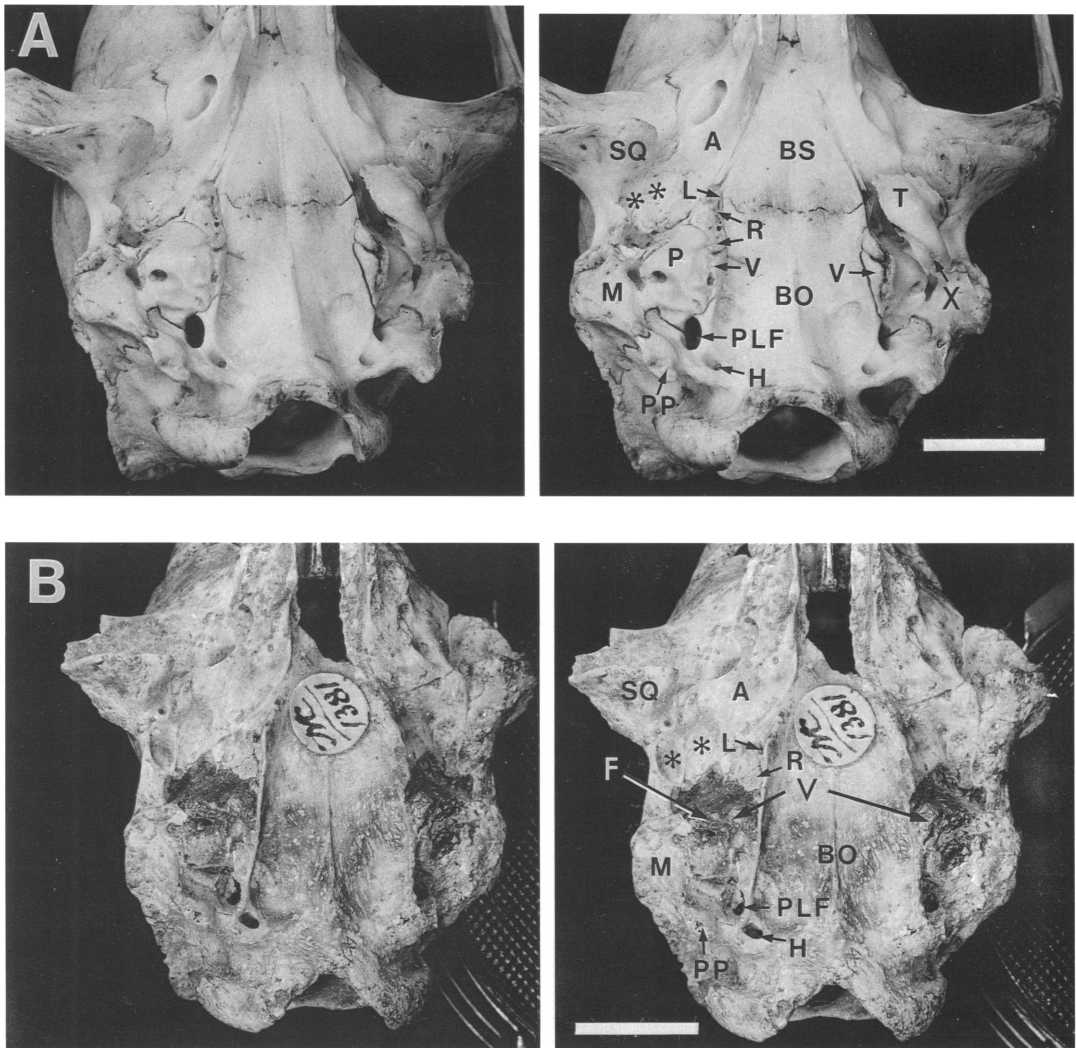


Fig. 14. Stereophotographs of the basicrania (in ventral view) of the living plesiomorphic aeluroid *Nandinia binotata* (AMNH-M 51492) and the Quercy *Stenoplesictis* (BMNH M1381). Asterisks indicate lateral and medial depressions for the anterior crus and anterior face of the ectotympanic, respectively. The ectotympanic is not preserved in this specimen of *Stenoplesictis*, permitting an unimpeded view of the petrosal and surrounding auditory region.

AUDITORY REGION OF *STENOPLESICTIS*

Piveteau (1943) described and illustrated a superb skull of *Stenoplesictis cayluxi* (UPM PQ305) from the collection of the Université de Provence, Marseille (fig. 4B). This uncrushed skull from Quercy (exact locality unknown) is remarkably well preserved (dimensions in table 7); it retains a complete upper dentition (lacking only the small M2s and left I1-2) in association with both man-

dibles and a nearly intact basicranium (fig. 15). The absence of any distortion in the cranium and mandibles allows accurate occlusion of the upper and lower teeth; the lower dentition compares well with the holotype mandible of *Stenoplesictis cayluxi* (figs. 7A, 8A). The dental formula is 3-1-4-2/?-1-4-2; M2 is extremely reduced in size. In the basicranium both ectotympanic bones are preserved *in situ*; the right ectotympanic has

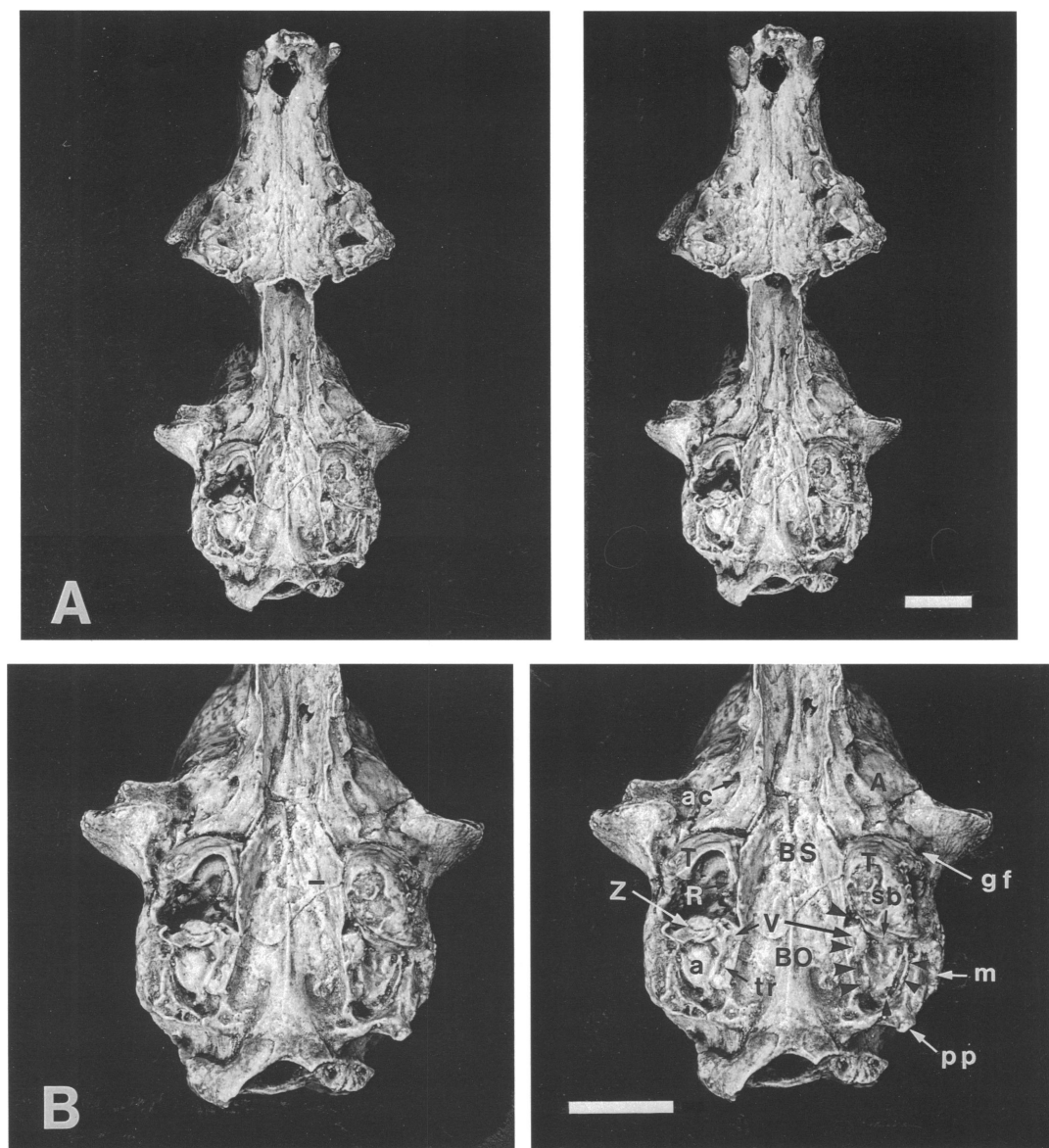


Fig. 15. Stereophotographs of casts of the (A) cranium and (B) basicranial structure of the Quercy aeluroid *Stenoplesictis cayluxi* (UPM PQ305, Marseille) in ventral view. The Marseille cranium, initially described by Piveteau (1943), preserves the ectotympanic element lost in the British Museum skull (BMNH M1381). Black triangles in (B) indicate the zone of attachment of the caudal entotympanic to the posterior and medial margin of the petrosal.

been opened to reveal the petrosal and anterior chamber of the middle ear.

In 1983 Fischer discussed and illustrated a less well-preserved *Stenoplesictis* skull without mandibles from the collection of A. Müller (P2004), Leipzig, that lacks the basi-cranium. The skull was found in Oligocene

sediments of the Weissester basin, south of Leipzig, Germany, which were deposited in a coastal environment (the sediments also preserve sirenian and shark remains). This specimen came from a phosphatic nodular horizon at the base of the Rupelton in the open-pit brown coal mine at Espenhain. On

the basis of this specimen, Fischer suggested that the skulls of *Stenoplesictis* and *Palaeoprionodon* cannot be distinguished from each other without the lower teeth.

During research at the British Museum (N.H.) in 1987 I was fortunate to discover an undescribed partial cranium from Quercy (BMNH M1381, Hunt 1989). This skull (fig. 14B) lacked the palate and teeth but its basicranial anatomy closely compared with the basicranium of the Marseille *Stenoplesictis* skull described by Piveteau (1943). A basicranial signature for *Stenoplesictis* could be identified with these specimens. A detailed examination of the basicrania of *Stenoplesictis* and *Palaeoprionodon* led to the conclusion that a distinctive basicranial structure is characteristic of each genus.

The following descriptive comparison is based upon the complete Marseille cranium (UPM PQ305) and the British Museum partial cranium (BMNH M1381).

ECTOTYMPANIC-PETROSAL RELATIONS: The ectotympanic in *Stenoplesictis* is a somewhat more inflated element than in *Palaeoprionodon*. The degree of ectotympanic inflation is evident when compared with the ectotympanic of *Nandinia*: in *Stenoplesictis* the anterior portion of the ectotympanic has expanded, increasing in width, so that it produces a prominent elliptical indentation where applied to the alisphenoid-basisphenoid surface and, in addition, the medial wall of the ectotympanic contacts the edge of the basicranial axis, pressing against a downturned flange of the basisphenoid-basioccipital. This flange forms a buttress applied against the inner (medial) wall of the ectotympanic in *Stenoplesictis* (a contact between ectotympanic and the basicranial axis does not occur in *Palaeoprionodon* because of the lesser degree of ectotympanic inflation).

In *Stenoplesictis* at the point where the inner (medial) wall of the ectotympanic turns laterad to become the posterior wall, the edge of the ectotympanic contacts and rests on the petrosal promontorium. The inturned edge of the ectotympanic (with an average width of ~1 mm) runs transversely across the apex of the promontorium for a distance of at least 3.3 mm in the Marseille skull. Application of the edge of the ectotympanic to the surface of the promontorium produces a conspicuous

transverse facet immediately anterior to the round window of the petrosal (fig. 15, Z). This facet extends over half the transverse width of the robust promontorium in these skulls, testifying to the marked degree of contact between the ectotympanic bulla and the petrosal. This is a derived condition not likely to be reversed during the evolution of this lineage; the descendants, if any, of *Stenoplesictis* probably retain this strong ectotympanic-petrosal contact and its concomitant structural byproduct, an anterior chamber of the bulla enclosed primarily by the bony ectotympanic.

The complete posterior wall of the ectotympanic is preserved in the left auditory region of the Marseille skull. Its surface demonstrates that a second bulla element shared an extensive contact with it: there is a moderately deep transverse indentation in the wall, slightly rugose, bordered above and below by smooth thickened bone. This is the surface of attachment for the cartilaginous or fibrous caudal entotympanic element, and this broad area of contact indicates a reasonable amount of inflection of the caudal entotympanic margin where it was applied to the bony posterior wall of the ectotympanic. This is the best evidence known to me among the Quercy aeluroids of an incipient bilaminar *septum bullae*, and is the oldest known example of this anatomical feature (fig. 15, sb). This also represents a more derived state than found in *Palaeoprionodon* in which the degree of inflection is minimal and the attachment of the caudal entotympanic to ectotympanic is essentially linear.

A prominent ventral process of the promontorium is developed in both the Marseille and British Museum skulls. It is pressed against the lateral flange of the basioccipital; however, the flange in the British basicranium extends slightly ventral to the process whereas in the Marseille cranium the process extends about 1 mm ventral to the edge of the basioccipital flange. In both individuals the robust promontorium descends well below the plane of the basioccipital surface so that the margin of the basioccipital must turn ventrad to buttress the process.

In *Stenoplesictis cayluxi* a broad posteriorly extended "apron" (fig. 15, at "a") is appended to the promontorium behind the

round window. In both the British Museum and Marseille skulls, the apron comprises a smooth sloping surface of considerably greater posterior extent than in *Nandinia* and *Palaeoprionodon*. The perimeter of the apron is marked by a channel for the attachment of the edge of the caudal entotympanic (fig. 15B, see black triangles).

CAUDAL ENTOTYMPANIC: The caudal entotympanic was a cartilaginous or fibrous connective tissue element covering the posterior chamber of the auditory region. Its inflected margin was attached to (a) the posterior wall of the bony ectotympanic, forming an incipient *septum bullae*; and (b) the perimeter of the petrosal apron. In the Marseille cranium the apron of the petrosal extends 5 mm posterior to the round window; the lateral and posterior margins of the apron are deeply grooved for the edge of the caudal entotympanic—the channel is about 0.5 mm in width. However, along the medial margin of the apron the edge of the caudal element attaches in a groove formed by both petrosal and basioccipital, and this channel continues anteriorly to the apex of the ventral promontorial process. Here the channel has a maximum width of about 1.5 mm. The posterior chamber of the auditory region, then, is of small volume and is fully enclosed by a caudal entotympanic that is attached at the periphery of the apron along a very narrow channel and is applied at its anterior end to the posterior wall of the ectotympanic. Thus, the margins of the caudal entotympanic were only moderately inflected, and are in a much more rudimentary condition than the strongly inflected margins of the inflated caudal entotympanics of living felids and viverrids.

The length of the anterior (ectotympanic) chamber of the bulla is 10.3 mm; the length of the posterior (caudal entotympanic) chamber is 5.1 mm, indicating the greater extent and volume of the anterior chamber in the Marseilles skull.

Additional evidence of the small volume and lack of expansion of the posterior chamber formed by caudal entotympanic is provided by the paroccipital process which is preserved in both the Marseille and British Museum skulls. In the Marseille skull, the process is a narrow rodlike element directed ventrad; there is no expansion or flattening

of the process to receive an inflated caudal entotympanic. The caudal entotympanic made contact only with the base of the process, which was free of any contact with the bulla. A low bony ridge extends from the base of the process anterolaterad to the mastoid shelf. A moderately wide mastoid shelf occurs in both *Stenoplesictis* skulls, differing from the narrow mastoid region of *Palaeoprionodon*.

ROSTRAL ENTOTYMPANIC: A bony rostral entotympanic occurs in the anterointernal corner of the auditory region. In both the British Museum and Marseilles specimens, it seems to have been separated by a gap from the inturned edge of the ectotympanic. In fact the rostral entotympanic in the British Museum skull is deeply recessed dorsal to the protruding lateral edge of the basioccipital (see Hunt, 1989: fig. 9B). This flanged edge of the basioccipital overhangs the rostral element to such an extent that it is unlikely that the ectotympanic margin could make contact. However, whether or not ectotympanic-rostral entotympanic contact occurred, intervention of the caudal entotympanic between the ectotympanic and the rostral element is improbable, due to the nearly complete enclosure of the anterior chamber of the bulla by the bony ectotympanic, seen in the left auditory region of the Marseilles skull (fig. 15). The caudal entotympanic would have been applied to the posterior wall of the ectotympanic and to the apex of the ventral process of the promontorium, but would have advanced no farther forward in the auditory region.

ARTERIES AND VEINS: A patent internal carotid artery probably existed in *Stenoplesictis*, but its exact path within the auditory region is uncertain. The artery most likely entered the auditory region by passing through the cartilaginous medial wall of the caudal entotympanic at the level of, or immediately anterior to, the ventral process of the promontorium. It then entered the middle ear cavity, traveling over the anterior slope of the promontorium (the anterior slope displays a sinuous channel in the Marseille skull that may indicate the course of the artery). The artery then left the anterior slope to run forward along the lateral face of the rostral entotympanic, turning mediad to enter the cra-

nial cavity through the middle lacerate foramen. The close apposition of the rim of ectotympanic to the promontorium would have prevented the artery from entering the anterior chamber of the bulla anywhere except in proximity to the ventral process.

As in *Palaeoprionodon* the internal jugular veins provided the principal venous drainage from the braincase via the posterior lacerate foramina. The postglenoid foramina are present, but they are very small, indicating a reduction of the external jugular drainage.

DISCUSSION: *Stenoplesictis* shows a somewhat more derived auditory anatomy relative to *Palaeoprionodon*. This is apparent in the: (1) greater inflation of the ectotympanic bulla; (2) incipient segregation of an anterior bulla chamber enclosed by the ectotympanic; (3) a laminar and somewhat recessed rostral entotympanic; (4) more pronounced posterior extension of the petrosal "apron"; and (5) development of the dependent flanges on the margins of basisphenoid and basioccipital to buttress the expanding bulla and the robust promontorial process. However, these features are superimposed on a plesiomorphic aeluroid auditory region that has retained the basic aeluroid petrosal form and a relatively unexpanded posterior chamber of the bulla, altered only to a slight degree relative to *Palaeoprionodon*. The auditory region of *Stenoplesictis* represents the first instance in an early aeluroid in which an anterior ectotympanic chamber of the bulla is becoming structurally separated from a caudal entotympanic chamber confined to the posterior part of the auditory area.

AUDITORY REGION OF *STENOGALE*

The near identity of mandibles and dentition of the Quercy aeluroid *Stenogale gracilis* and those of the holotype of *Stenogale julieni* from the Aquitanian of St.-Gérard make possible the identification of the basicranial anatomy of this genus. The mandibles of *S. julieni* are associated with a complete cranium including the auditory region, figured by Viret (1929: p1. XII, figs. 5, 8, 9), who believed it came from the locality of Chaveroche-sur-Besbre (fig. 16).

The skull is small, with an estimated basilar length of 7.4 cm (fig. 16A, measurements

in table 7). The most remarkable aspect of the skull is its short rostrum. The preorbital distance is estimated at ~18–19 mm (the premaxillae are broken), whereas the postorbital distance is 59.5 mm (yielding a pre- to postorbital ratio of ~1:3). A number of cranial sutures remain open, indicating that the animal was a young adult. The formula for the upper teeth is ?3-1-4-1; there is no M2 (fig. 16B). M1 is markedly reduced in size with para- and metacone tightly appressed, the metacone reduced, and a prominent parastylar region developed lateral to the paracone. M1 has a small but developed protocone basin and a V-shaped protocone; conules are not present. The upper carnassial is a shearing tooth with a parastylar cusp, a linguallly extended protocone, and is surrounded by a distinct cingulum. There is a deep pit in the palatal surface of the maxilla lingual to the shearing face of P4 for the trigonid of ml. P3 is a robust, well-developed premolar with a small prominent internal root in addition to the normal pair. There is a definite size break between P3 and a more petite P2; P2 is double-rooted. P1 is represented by a single alveolus and would have been a simple subconical tooth. The alveolus for the canine indicates a prominent stabbing tooth, nearly circular in cross-section; no incisors or their alveoli are preserved.

The basicranium is remarkably well preserved (fig. 16C). Sutures between basicranial bones are distinct and no distortion is evident. Sphenoid, periotic and occipital components of the basicranium are clearly identified; however, the anterior part of the squamosal, including the glenoid region, is missing on both sides. In the auditory region the bulla elements have been lost from the skull. The osseous ectotympanic and rostral entotympanic elements have been detached from the middle ear and, because of its probable cartilaginous composition, the caudal entotympanic is not preserved. However, the remainder of the auditory area is intact and shows considerable anatomical detail, allowing reliable inferences as to the nature of the ectotympanic and entotympanic elements. The ventral surface of the sphenoid records impressions of the ectotympanic and rostral entotympanic elements; the periotic displays registration marks for ectotympanic, rostral

and caudal entotympanics, and includes an intact tegmen tympani. The configuration of the exoccipital and basioccipital makes possible accurate reconstruction of the caudal entotympanic; a discrete paroccipital process separate from the bulla is slightly elongate and downturned. The mastoid-exoccipital region is developed as a broadened shelf, similar to the shelf of *Stenoplesictis*, but wider and more prominent than in *Palaeoprionodon*. As in both of the Quercy genera, a ridge extends onto the mastoid shelf from the base of the paroccipital process in *Stenogale*.

ECTOTYMPANIC-PETROSAL RELATIONS: In *Stenogale* the petrosal is large, robust, filling the central part of the auditory region. The promontorium protrudes ventrad, dividing the auditory area into anterior and posterior chambers that were enclosed, respectively, by the ectotympanic and caudal entotympanic. The marked similarity in form to the petrosals of *Palaeoprionodon* and *Stenoplesictis* is particularly apparent.

The promontorium of *Stenogale julieni*, however, differs in an important feature from the promontoria of the two Quercy genera. There is a prominent bladelike flange (fig. 16C, fp) developed on the medial margin of the promontorium which is pressed into the edge of the basioccipital. Although this animal must have been relatively young because of its open cranial sutures, the lateral margin of the basioccipital (and posterior part of the basisphenoid) already extends ventrad as a dependent lamina of bone. The thin flange of the promontorium is set deeply into this lamina and is bordered laterally by a shallow trough running along the medial margin of the promontorium; the pitted rugose surface within this trough indicates that the medial wall of the auditory bulla attached along its length (the identity of these bulla elements will be discussed in the next section). Lateral to the posterior part of the trough and the posterior limit of the flange, the ventral process of the promontorium (fig. 16C, V) extends ventrad to form the broad apex of the petrosal.

In contrast to *Stenogale julieni*, the promontoria of *Nandinia*, *Palaeoprionodon*, and *Stenoplesictis* are characterized by a plesiomorphic massive, medially placed, rather blunt ventral process of the promontorium

resting against the basioccipital margin. In these three genera there is no differentiation of the ventral surface of the promontorium into a medial blade, central trough, and laterally placed ventral process as seen in *Stenogale*.

Although the ectotympanic is not preserved in the *S. julieni* skull, its general form and relationship to the petrosal can be surmised from the impressions it created on the petrosal and adjacent basicranial bones. The anterior limb of the ectotympanic impressed the alisphenoid, evidenced by a shallow but pronounced elliptical depression similar to this feature in *Stenoplesictis* and *Palaeoprionodon*. The tip of the anterior crus must have been seated in the squamosal in a pit lateral to this depression, as in *Stenoplesictis* (fig. 14B), however this part of the squamosal has been broken and lost in this specimen of *Stenogale*. There is no indication that the ectotympanic contacted the bones of the basicranial axis but a prominent elliptical facet anterior to the round window of the petrosal shows that its posterior margin rested on the promontorium as in *Stenoplesictis* and *Palaeoprionodon*. The facet is medial to the point of attachment of the posterior crus of the ectotympanic; thus, the position of the ectotympanic's posterior limb relative to the petrosal must have been similar to *Palaeoprionodon*, *Stenoplesictis*, and the viverrid *Herpestides* (Hunt, 1991: fig. 5A).

In *Stenogale* the ectotympanic, together with a rostral entotympanic, would have enclosed a spacious anterior bulla chamber of somewhat greater volume than the posterior chamber. Whether the inner margin of the bony ectotympanic contacted the ventral edge of the rostral entotympanic is uncertain, because these two bony elements are not preserved in life orientation in any specimens. It is unlikely that these two elements were in contact in the early ontogenetic stages of bulla development in *S. julieni*. Considering the estimated size and location of the rostral element and the orientation of ectotympanic, the rostral entotympanic was probably separated from the inner edge of ectotympanic by a small gap filled by cartilage or fibrous connective tissue.

CAUDAL ENTOTYMPANIC: My description of the caudal entotympanic of *S. julieni* is an

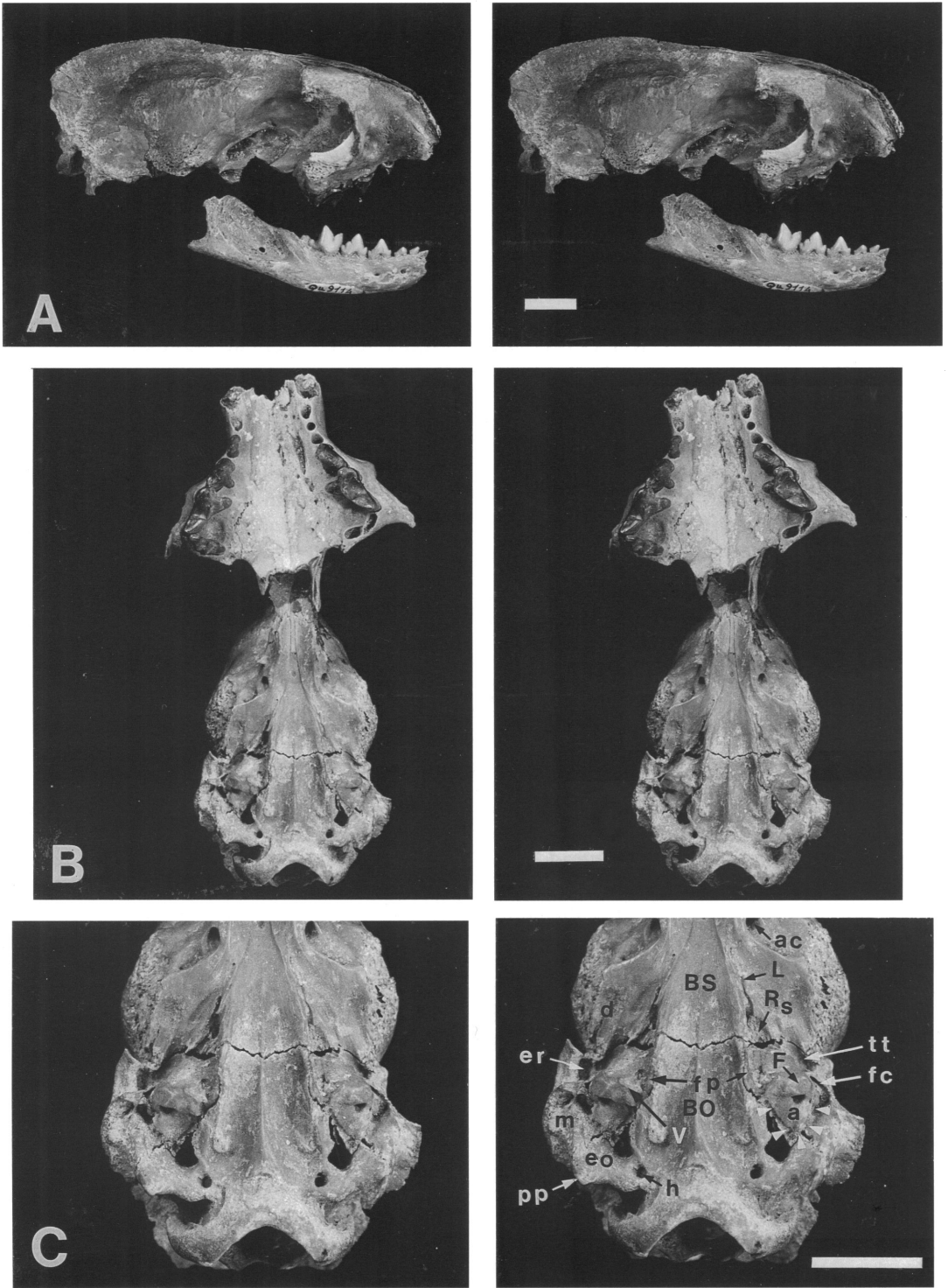


Fig. 16. Stereophotographs of the holotype cranium of the aeluroid *Stenogale julieni* from the Aquitanian of St.-Gérard: (A) comparison of holotype *S. julieni* cranium and unassociated Quercy mandible

interpretation based upon impressions made by the entotympanic on the petrosal and surrounding basicranial elements. Additional useful comparisons were made with the palm civet *Nandinia*; the felid *Proailurus lemanensis* from St.-Gérard; the Aquitanian viverrid *Herpestides antiquus*, also from St.-Gérard (Hunt, 1991); and with Quercy *Palaeoprionodon* and neonatal living aeluroids (illustrated in Hunt, 1987, 1991).

The caudal entotympanic of *Stenogale julieni* probably consisted of cartilage or of dense fibrous tissue and it enclosed the posterior chamber of the auditory region behind the promontorium. The posterior chamber was quite small—only slightly enlarged over that of *Palaeoprionodon*. The greatest length of the anterior chamber of the bulla (measured from the anterior limit of the alisphenoid depression for the ectotympanic to the apex of the promontorium) is 11.4 mm. The length of the posterior chamber measured from the apex of the promontorium to the estimated posterior limit of the caudal entotympanic on the exoccipital is about 7.1 mm.

The petrosal of *Stenogale* has the short sloping surface, or apron, posterior to the round window seen in *Palaeoprionodon* and *Stenoplesictis*. The sharply defined margin of the apron marks the line of attachment of the inflected dorsal edge of the caudal entotympanic (fig. 16C). *Stenogale julieni*, however, differs from *Palaeoprionodon* in having a slightly more expanded caudal entotympanic; in *Stenogale* this very limited posterior expansion of the caudal entotympanic is evidenced by its line of attachment to the mastoid, to the lateral margin of the basioccipital, and by the first indication of posterior deployment against the exoccipital (the bone is smoothly concave where the caudal entotympanic presses against it but the paroccipital process still remains distinct and free of the bulla).

ROSTRAL ENTOTYMPANIC: The auditory region of *Stenogale julieni* does not preserve

the rostral entotympanic but does show a wide well-defined space for this element. This is a roughened area, a small concavity, on the tympanic wing of the basisphenoid in the anterointernal corner of the auditory region. This small depression for the rostral entotympanic is bordered laterally by a low ridge situated along the basisphenoid-alisphenoid suture. The rostral entotympanic is likely to have been similar in form and placement to the rostral element in its Aquitanian contemporary *Herpestides* (Hunt, 1991: figs. 3B, 4B), and probably most closely approached the relationship to the petrosal seen in *Nandinia* (fig. 14A; also Hunt, 1987: figs. 6A, 6B, 16; Hunt, 1989: figs. 9A, 10A) in which the rostral element extends caudad a short distance along the medial edge of the promontorium but does not quite reach its apex. Based on detailed comparison with *Nandinia*, *Palaeoprionodon*, and neonatal stages of living aeluroids, the anterior part of the rugose strip visible along the medial edge of *Stenogale's* left petrosal (figs. 16C, 18B) was probably produced by attachment of the posterior part of the ossified rostral entotympanic. The posterior part of this rugose margin was for the anterior part of the cartilaginous caudal entotympanic, migrating forward to either closely approach or contact the rostral element.

ARTERIES AND VEINS: A large middle lacrate foramen occurs in the basisphenoid just anterior to the rostral entotympanic, suggesting a functional internal carotid artery. The artery most likely entered the auditory region through a cartilaginous medial wall of the caudal entotympanic 1–2 mm posterior to the ventral process of the promontorium. It either traveled lateral to the process (but medial to the promontorial facet for the ectotympanic) or within the trough on the medial margin of the promontorium. It then followed the anterior slope of the promontorium, maintaining contact with the rostral entotympanic and eventually turning medially to enter the mid-

←

(MNHN Qu 9114) of *Stenogale gracilis* in lateral view—the older Quercy and younger St.-Gérard species of *Stenogale* differ only slightly in size; (B) holotype cranium and (C) basicranium of *S. julieni* in ventral view. Five white triangles in (C) indicate the line of attachment of the caudal entotympanic to the posterior margin of the petrosal. The ectotympanics of *S. julieni* have been lost from the skull.

dle lacerate foramen. The relatively large posterior lacerate foramina indicate a developed internal jugular venous drainage from the cranium, but damage to the squamosal obscures the postglenoid foramina and, hence, the external jugular drainage.

DISCUSSION: In the ontogeny of certain living felids an anterior migration of the caudal entotympanic occurs, pushing forward between the rostral entotympanic and ectotympanic, thereby creating the *bradynothictic* condition of the bulla in early development (Hunt, 1987: 27, fig. 11B). In many living felids a contact between the ventral edge of the rostral entotympanic and the inner margin of the ectotympanic eventually occurs in the adult. This ontogenetic pattern identified in living felids resulted from a progressive enlargement and anterior migration of the caudal entotympanic element during felid phylogeny. The auditory region of *S. julieni* possibly documents an early stage in this process of caudal entotympanic development. In this small aeluroid the surface of the petrosal promontorium has been modified from the plesiomorphic state found in *Palaeoprionodon* and *Nandinia*. In *S. julieni* the part of the caudal entotympanic in contact with the ventral process has impressed the promontorium, altering its shape. The plesiomorphic ventral process (as exemplified by *Palaeoprionodon*) has been divided by the invading entotympanic into a medial bladeliike flange and a lateral blocky remnant of the original ventral process. The developing caudal entotympanic produced a narrow rugose trough on the petrosal promontorium of *S. julieni* directly medial to the ventral process and lateral to the prominent vertical flange. Lavocat (1952) believed that this trough transmitted the carotid artery. However, although the artery may have passed through the area, the pitted rugose texture of the trough tells us that a bulla element attached along the medial margin of the promontorium; comparison of the auditory region with that of the larger contemporaneous felid *Proailurus lemanensis* establishes a strong argument for the identity of the unknown element as the caudal entotympanic.

Lavocat (1952) was impressed by the marked anatomical similarities between the

basicrania of *P. lemanensis* and *S. julieni*. In *P. lemanensis* the medial margin of the promontorium has been invaded and completely overgrown by the anterior part of caudal entotympanic; the anatomical relations leave no doubt as to the presence of the caudal entotympanic in this location (fig. 17). Moreover, the anatomical features of this part of the auditory region can be matched in detail to those of *S. julieni*, suggesting a close relationship between these two aeluroids as suggested by Lavocat. However, the auditory region of *Proailurus* represents an anatomical advance beyond the *Stenogale* condition: in *Proailurus* the anterior part of caudal entotympanic was much larger and more inflated than in *Stenogale*, and has actually pushed deeply into the basioccipital margin, indenting it, and in so doing has flattened the medial flange of the promontorium (fig. 17, fp). The expanding caudal entotympanic has overgrown and thereby depressed the flange, forcing it from the parasagittal into the frontal plane, so that the caudal entotympanic completely covered the flange in *Proailurus*.

In *Stenogale julieni* we can identify an earlier phylogenetic stage in this process: the relatively less voluminous caudal entotympanic chamber of *Stenogale* has just begun to push forward along the medial border of the auditory region adjacent to the edge of the basioccipital. In so doing, it has modified the surface of the petrosal, indenting the promontorium to segregate the thin flange which becomes pressed into the margin of the basioccipital by the advancing entotympanic element. Unfortunately, the exact relationship of the caudal to the rostral entotympanic is uncertain: without the bulla I cannot determine if an anterior extension or lamina of the caudal entotympanic of *Stenogale* intervened between the rostral element and the ectotympanic (athictic state) as seen in living *Nandinia* or, alternatively, if the caudal element may have been largely restricted to the posterior auditory region. In this latter scenario the caudal entotympanic might have approached the posterior edge of the rostral element (or made only a rudimentary contact, perhaps slightly overlapping it) but would not have intervened between the ectotympanic and rostral elements. Discovery of an intact auditory bulla in a species of *Stenogale*

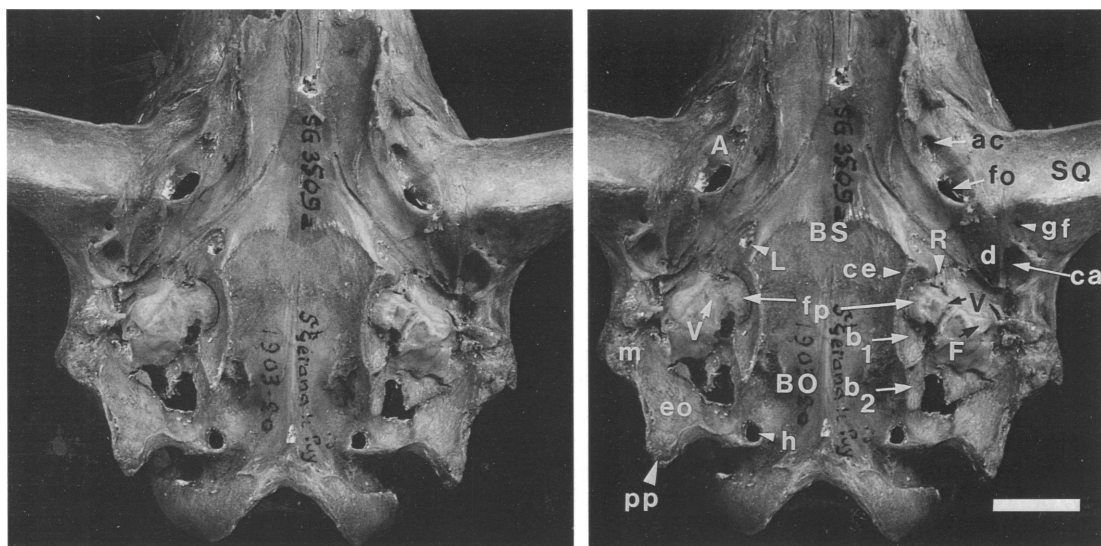


Fig. 17. Stereophotographs of the basicranium of *Proailurus lemanensis* (MNHN S.G. 3509a) from the Aquitanian of St.-Gérard. This proailurine cat and the early viverrid *Herpestides antiquus*, also from St.-Gérard, are the earliest aeluroids to show a marked inflation of the caudal entotympanic element of the auditory bulla. In *Proailurus* this inflation is indicated by deep registration marks of the caudal entotympanic on adjacent basicranial bones (b_1 , b_2 , eo, advancing as far forward in the auditory region as ce).

will be necessary to choose between these alternatives.

AUDITORY REGION OF *PROAILURUS*

The auditory region of the aeluroid *Proailurus lemanensis* from St.-Gérard was described by Lavocat (1952), who commented on the marked basicranial similarities with *Stenogale julieni*. I studied and photographed the *P. lemanensis* basicranium in the Paris Museum (figs. 17, 18C), where it bears the number MNHN S.G. 3509a (earlier I had illustrated and discussed a cast of this basicranium as Paris Museum 1903–20, which is a second number also inscribed on the cranium; see Hunt, 1989: figs. 11, 12). The maxillae and mandibles associated with this basicranium were figured by Viret (1929: pl. X, figs. 3–4, 6–7). As noted by Lavocat, this is a larger carnivore than *Stenogale*, *Palaeoprionodon* or *Stenoplesictis*, with an estimated basilar length of 10–12 cm, about the size of a lynx. A relatively complete skeleton was described by Filhol (1881). Ginsburg (1983) presents a cogent summary of the probable relationships of this early felid to later and

better known felids such as *Pseudaelurus* and its descendants.

The basicranium of *Proailurus* (MNHN S.G. 3509a) lacks the auditory bullae which have been lost from the skull, although remnants of the rostral entotympanics are still present. The bullae, however, have left impressions on the surrounding basicranial bones so that reliable inferences can be made concerning the elements making up the bulla.

ECTOTYMPANIC-PETROSAL RELATIONS: Despite the larger body size of *Proailurus lemanensis*, its petrosal retains the same basic form as the previously described genera. The robust *Proailurus* petrosal is situated in the central part of the auditory region, dividing it into anterior and posterior chambers (fig. 17). The anterior chamber of moderate size was enclosed primarily by a bony ectotympanic; the posterior chamber was enclosed by a moderately inflated caudal entotympanic which had considerably enlarged relative to its size in *Stenogale*, *Palaeoprionodon*, and *Stenoplesictis*.

The petrosal promontorium of *Proailurus* is most similar to that of *Stenogale*; the ven-

tral process of the promontorium is an identifiable landmark in both genera. Medial to the ventral process of the promontorium in *Proailurus* is an arcuate rugose bony process (fig. 17, fp) pressed into the lateral margin of the basioccipital. This process appears to be the homologue of the bladelike flange in *Stenogale* which occupies the same position. In *Proailurus* this flange has been entirely overgrown by the enlarging caudal entotympanic, converting the flange into a low, rugose buttress that remains in contact with the basioccipital.

The anterior slope of the promontorium is somewhat more steeply inclined in *Proailurus* relative to *Stenogale*; in both, the rostral entotympanic element fits in a pocket or concavity formed at the junction of the anterior slope and the sphenoid. The rostral entotympanic is positioned so that its anterior part rests on the sphenoid, while the posterior part contacts the anterior slope of the promontorium, the entotympanic taking the form of a wedge inserted between sphenoid and petrosal.

The posterior slope of the promontorium in *Proailurus* displays the apron common to *Stenogale julieni* and the two Quercy genera. The apron, configured as a smooth, sloping surface in *Palaeopriondon*, *Stenopleistcis*, and *Stenogale*, is more irregular in *Proailurus* where the posterior margin of the apron is deeply emarginated for the attachment of the inflected dorsal margin of the caudal entotympanic. In addition, the apron is posteriorly prolonged to form a thin, bony roof for the posterior bulla chamber; this extension of the apron is the direct result of the posteriorly expanding caudal entotympanic element and is also seen in the St.-Gérard viverrid *Herpestides* (Hunt, 1991: fig. 7B) in which the caudal entotympanic has enlarged in the same manner as in *Proailurus*.

From impressions on the squamosal, alisphenoid, and petrosal, the ectotympanic was a moderately inflated capsular bone enclosing an anterior bulla chamber of moderate volume. The deep pit in the squamosal for the tip of the anterior crus, and the immediately adjacent elliptical depression in the tympanic wing of the alisphenoid for the anterior wall, indicates an ectotympanic of some size, slightly inflated and broadened.

The posterior crus of the ectotympanic was attached to the post-tympanic process of the squamosal, which forms the posterior wall of the bony auditory meatus. Posteromedial to the posterior crus, the left auditory region preserves the attached tympanohyal. Medial to the tympanohyal and anteromedial to the round window of the petrosal is an elliptical facet on the promontorium produced by the posterior margin of the ectotympanic. The location of the facet is in the same place as in *Stenogale*. From the facet the dorsal edge of the ectotympanic must curve in the anterior direction toward the anterointernal corner of the auditory region. It is evident that the margin of the ectotympanic would have been situated directly adjacent to the ventral margin of the rostral entotympanic. Although it is not possible to determine whether the two elements were in contact, it is clear that they were in close relationship.

CAUDAL ENTOTYMPANIC: One of the most interesting aspects of the auditory region of *Proailurus lemanensis* is the evident expansion or inflation of the caudal entotympanic, indicated by deep impressions in the basioccipital, exoccipital, mastoid, petrosal, and even a small penetration into the basisphenoid. There is a considerably greater amount of caudal entotympanic inflation relative to the more plesiomorphic auditory region of *Stenogale julieni*. During ontogeny the posterior part of caudal entotympanic pushed caudad into the exoccipital and mastoid, producing a smoothly confluent, curved surface on the internal face of these bones. Despite the close apposition of the entotympanic to the paroccipital process, the tip of the process remained free of the encroaching bulla, not yet attaining the more complete incorporation of the process seen in modern cats. The dorsal edge of the entotympanic also deeply impressed the caudal apron of the petrosal along its posterior border. However, the most striking feature of caudal entotympanic expansion, relative to the state of the element in *Stenogale*, is the medial and anterior penetration of caudal entotympanic into the lateral margin of the basioccipital and into the basisphenoid. The lateral margin of the basioccipital records two concave impressions for the caudal entotympanic, the smaller one (~7 mm in length, fig. 17, b₂) directly medial

to the posterior lacerate foramen, the larger one (11.5 mm in length, fig. 17, b₁) medial to the petrosal promontorium. The former houses the medial wall of the enlarged posterior part of the caudal entotympanic; however, the latter receives the anteromedial expansion of the caudal entotympanic, which is beginning its penetration into the anterointernal corner of the auditory region, a process that reaches its culmination in living felids such as the domestic cat (*Felis catus*). This emargination of the basioccipital is also seen in the contemporary aeluroid *Herpestides* (Hunt, 1991: fig. 3B), but it is not as developed as in *Proailurus*. Basioccipital emargination is so extensive in *Proailurus* that the entotympanic pushes forward to impress the posterointernal corner of the basisphenoid. It is this strongly developed anteromedial invasion by the advancing caudal entotympanic that has suppressed the medial flange of the promontorium in *Proailurus lemanensis*, covering it as the entotympanic grows forward into the basioccipital-basisphenoid margin. Caudal entotympanic inflation in *P. lemanensis* is the most pronounced of any aeluroid carnivoran known up to this time (Aquitanian of western Europe); it is approached, however, by a nearly equivalent degree of expansion in the contemporary viverrid *Herpestides* (Hunt, 1991).

ROSTRAL ENTOTYMPANIC: Remnants of the rostral entotympanic are present on both right and left sides. The rostral entotympanic was situated in a well-defined space at the medial margin of the rather steep anterior slope of the promontorium where its anterior border rested against, and in some cases fused with, the sphenoid. Its shape was essentially triangular with the apex directed dorsad, contacting the petrosal-sphenoid suture as in other aeluroids. The inner edge of the anterior slope of the promontorium is marked by a rugose surface of attachment for the rostral entotympanic. This attachment surface is steeply inclined, rising to the apex of the ventral process of the promontorium, which is faceted by this surface. Because the ventral part of the rostral entotympanic is lost on both sides of the specimen, it is uncertain whether the rostral element actually extended to the limit of this facet, but this arrangement appears probable. Whether the rostral ento-

tympanic made contact with the inturned edge of the ectotympanic in this adult cannot be determined.

ARTERIES AND VEINS: The internal carotid artery probably entered the auditory region at the boundary between the anterior and posterior caudal entotympanic emarginations of the basioccipital. It then appears to have traveled anterolaterally to the posterior slope of the promontorium where it followed a groove across the ventral process (fig. 17). The artery next coursed along the anterior slope of the promontorium, running on or adjacent to the rostral entotympanic. At the anterior margin of the rostral element the artery followed a shallow groove in the sphenoid to the middle lacerate foramen.

The prominent posterior lacerate foramina demonstrate a well-developed internal jugular venous outflow from the cranium; the reduced state of the postglenoid foramina indicates a near loss of the external jugular drainage.

DISCUSSION: The auditory region of *P. lemanensis* is associated in MNHN S.G. 3509 with a proailurine dentition. The auditory region, because of its undistorted preservation, allows a relatively complete reconstruction of the nature and relationships of the bulla elements. The auditory bulla as reconstructed is a type predicted from earlier studies of bulla ontogeny in living felids (see Hunt, 1974, 1987): one of its most characteristic features is a marked inflation and migration of the caudal entotympanic into the anterointernal corner of the auditory region. This penetration by the caudal element is also seen in the bullae of a number of species of living cats. In these particular felids the anterior migration of the caudal entotympanic overgrows the rostral entotympanic and ectotympanic to a degree seen in no other fossil or living aeluroid carnivoran (Hunt, 1987: fig. 10A, fig. 14, stage 1).

In addition, the documented overgrowth of the medial process of the promontorium in *Proailurus lemanensis* by the migrating caudal entotympanic supports the inference that the process has been suppressed in the evolution of felids but was retained in other aeluroids (viverrids, herpestids, hyaenids). The evolution of the *Proailurus* petrosal can be visualized as a series of steps, beginning with

a plesiomorphic petrosal similar to *Palaeoprionodon*, progressing to stages represented by *Stenogale julieni* and finally *Proailurus lemanensis*. Caudal entotympanic growth progressively altered the form of the promontorium, transforming a massive ventral process that buttressed the basioccipital into a subdivided promontorial apex. This subdivided promontorium comprises a laterally placed ventral process and a medially placed thin vertical flange, the latter inset into the margin of the basioccipital. In the final stage the medial flange was depressed dorsad by the expanding caudal entotympanic yet still maintained contact with the basioccipital.

SUMMARY AND CONCLUSIONS (AUDITORY REGION): The auditory regions of the early aeluroids from Quercy and St.-Gérard-le-Puy display a considerable anatomical similarity, reflecting a not-too-distant common ancestry. In particular, the type of petrosal is unique to the group and serves as a derived feature distinguishing the basal aeluroids from contemporary arctoid carnivorans. The form of the petrosal is apomorphic relative to arctoids but plesiomorphic relative to many living aeluroids. In its most plesiomorphic form as seen in *Nandinia* and *Palaeoprionodon*, the aeluroid petrosal is a blocky massive element with a prominent ventral process applied to the lateral margin of the basioccipital. Modification of the primitive aeluroid petrosal, chiefly the shape of the promontorium, occurs in the different genera (fig. 18). Not only do these modifications permit explicit recognition of these genera, they also reveal that ontogenetic growth patterns of the auditory bulla elements in the different lineages are responsible for modification of petrosal shape.

Of the four European aeluroid genera under consideration, *Palaeoprionodon* possesses the most plesiomorphic auditory region (fig. 18A): the ectotympanic is only slightly inflated, the caudal entotympanic element is quite small and unexpanded, and the petrosal essentially in its plesiomorphic form. Only the living *Nandinia binotata* of Africa has a more plesiomorphic auditory structure, and shares with *Palaeoprionodon* the athictic type of bulla.

The petrosal of *Palaeoprionodon* closely approximates a plesiomorphic aeluroid state

and is not as derived in form as is the petrosal of *Stenoplesictis*. This type of petrosal in conjunction with other related aspects of auditory anatomy confirms several points concerning the nature of the plesiomorphic aeluroid auditory region:

(1) the petrosal is very large relative to the chambers fore and aft; hence, the ectotympanic bone cannot easily enclose it (the petrosal must attain relatively large size early in ontogeny for this situation to exist);

(2) the posterior chamber of the bulla, enclosed by a presumably cartilaginous caudal entotympanic, was small in volume in its initial state in early aeluroids. The caudal entotympanic element enclosed the open space situated directly behind the robust promontorium, surrounded by occipital, petrosal, and mastoid bones. At first in these early aeluroids the caudal entotympanic did not expand outward to create pockets or depressions in the basioccipital or exoccipital. It was a simple cartilage or fibrous lamina covering the posterior chamber and extending forward to intervene between ectotympanic, petrosal, and bony rostral entotympanic, as in living *Nandinia* (Hunt, 1974: pl. 1; 1987, figs. 6, 15). Eventually, in a number of aeluroids, significant growth of the caudal entotympanic accompanied the inflation of the posterior chamber, resulting in deformation of surrounding basicranial bones;

(3) the *athictic* condition of the ectotympanic relative to the rostral element was probably the primitive aeluroid state;

(4) a large space is present for a rostral entotympanic element (fig. 13, R.), of considerable width and bordered laterally by a raised bony ridge on the sphenoid;

(5) in *Palaeoprionodon* (fig. 12) and *Nandinia* (fig. 14A), the flanged margins of the basioccipital do not extend ventrad below the ventral process of the promontorium as they do in *Stenoplesictis*, the lack of pronounced lateral flanges on the basioccipital is regarded as plesiomorphic. The condition seen in *Stenoplesictis* (figs. 14B, 15B) in which the edges of the basioccipital are strongly downturned is probably derived, as is the posterior elaboration of the apron on the M1381 petrosal.

(6) the paroccipital process of Qu 9348 and Qu 9370 is free of the caudal entotym-

panic element (in Qu 9370 the base of the process extends anterolaterad as a ridge not as evident in Qu 9348). This independent paroccipital process also appears in *Nandinia* and *Stenoplesictis*, and is the plesiomorphic state in these early aeluroids. These early aeluroid skulls lack the flattened and expanded paroccipital process present in most living viverrids; such a process represents a derived state that evolved as an inflating caudal entotympanic grew backward and was applied to the process. The living linsang *Prionodon* is most similar to *Palaeoprionodon*, but its paroccipital process is applied to the caudal entotympanic along its entire length, indicating that the caudal entotympanic chamber has expanded caudad to a greater degree than in the Quercy genus.

The auditory region of *Stenoplesictis cayluxi* (figs. 14B, 15) is somewhat more derived relative to *Palaeoprionodon*. Its ectotympanic is more expanded, resting against the basicranial axis; the petrosal is more extended caudad, and the caudal entotympanic chamber of the bulla is somewhat more inflated. Although the caudal entotympanic does not extend into the anterointernal part of the auditory region, the athictic condition of the ectotympanic/rostral entotympanic appears to be present; however, application of the caudal entotympanic's anterior face to the broad posterior wall of the ectotympanic has produced an incipient bilaminar septum bul-lae.

The auditory region of *Stenogale julieni* (fig. 18B) is only slightly evolved beyond that of *Palaeoprionodon*. It retains a very small caudal entotympanic chamber, only modestly enlarged beyond the state of *Palaeoprionodon*. Impressions on surrounding bones indicate a slightly wider ectotympanic in *Stenogale*. However, the promontorium of *Stenogale* displays a unique configuration not seen in either *Palaeoprionodon* or *Stenoplesictis*. A bladelike flange appears on the medial margin of the promontorium, bordered laterally by an anteroposteriorly oriented trough that separates the flange from the main body of the ventral promontorial process. This anatomical situation is unique to *Stenogale* and is a hallmark of its basicranium.

The auditory region of *Proailurus lemanensis* (fig. 18C) is morphologically similar to, in fact possibly evolved from, the more primitive auditory region of *Stenogale julieni*. The anteroposterior trough on the medial promontorium of *Stenogale*, situated directly lateral to the flanged process, has expanded into a broad depression in *Proailurus* to house the anteriorly migrating and enlarging caudal entotympanic. This entotympanic element in *Proailurus* has grown over the medial flange of the promontorium, covering it and flattening it. The depressed flange still continues to buttress the deeply indented margin of the basioccipital. In addition, the caudal entotympanic chamber is greatly inflated in *Proailurus*, strongly impressing the surrounding basicranial bones. A moderately inflated ectotympanic element also can be inferred. The only other Aquitanian aeluroid with a well-inflated caudal entotympanic is the viverrid *Herpestides* (Hunt, 1991). *Herpestides* differs from *Proailurus* in retaining a plesiomorphic ventral process of the petrosal which has not been altered or transposed by overgrowth of the caudal entotympanic.

Intervention of a laminar caudal entotympanic between the ectotympanic and the rostral entotympanic is a plesiomorphic aeluroid trait (athictic condition, Hunt, 1987: 31–32, 39), and is well developed among living aeluroids only in the living *Nandinia binotata*. In *Palaeoprionodon* the caudal entotympanic was positioned as in *Nandinia*, and was similar in form and in relationship to surrounding structures. The only significant distinction is that in *Nandinia* the ectotympanic does not create a facet on the promontorium, whereas in *Palaeoprionodon* it does. Thus, the auditory region of *Palaeoprionodon* differs only slightly from *Nandinia*, and represents an extremely plesiomorphic grade of aeluroid basicranial evolution, one that could evolve into certain extant species of the Viverridae (Asian *Prionodon pardicolor*, *P. linsang*). These living species of *Prionodon* also retain dentitions similar to *Palaeoprionodon*, including the marked reduction of p2 anterior to p3 in the mandible.

The caudal entotympanic in *Palaeoprionodon*, *Stenoplesictis*, and *Stenogale* was extremely similar in its size relative to the ectotympanic, and in its form and anatomical

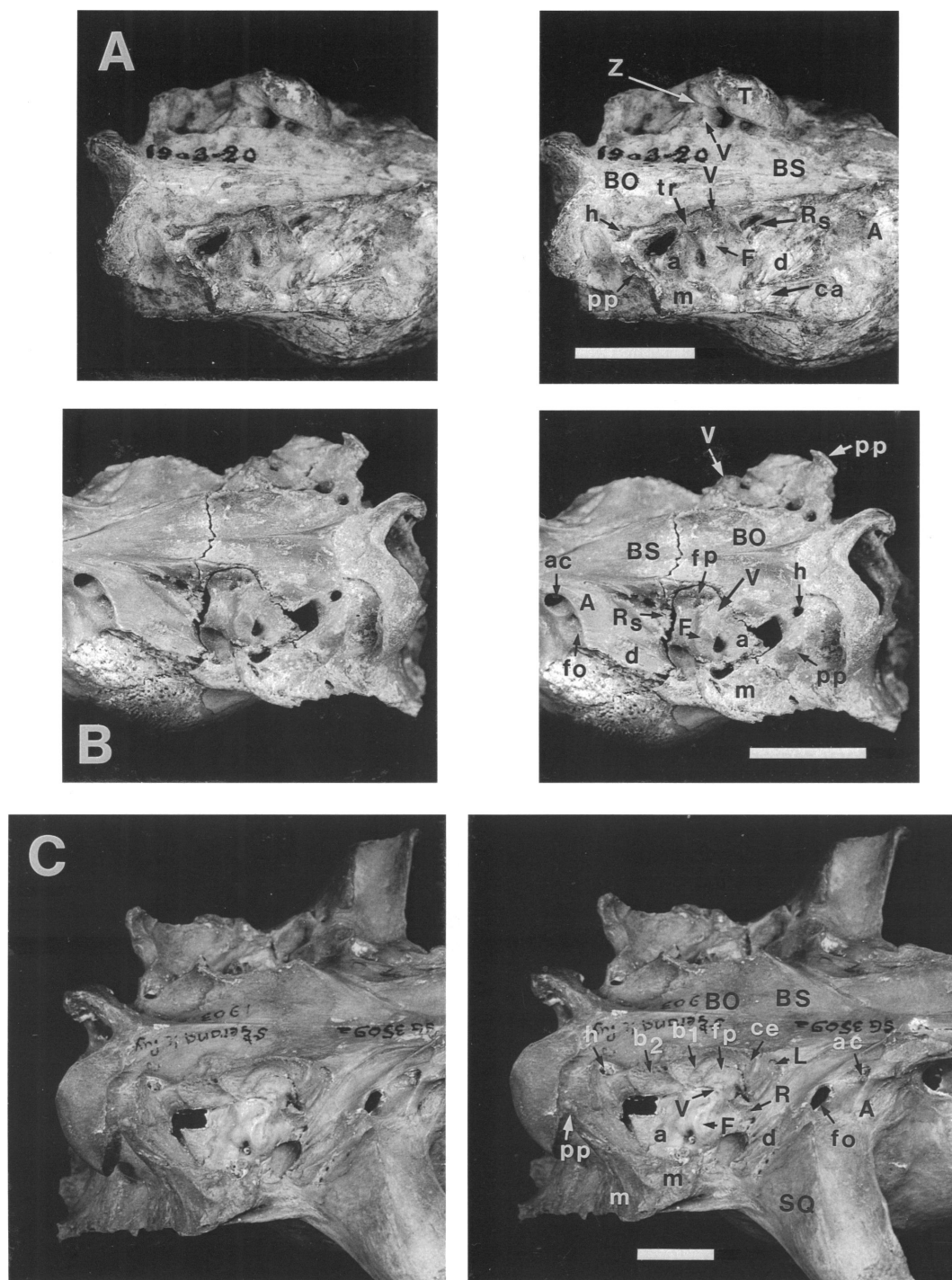


Fig. 18. Modification of the form of the petrosal promontorium in early aeluroids from Quercy and St.-Gérard, France (in lateral view): (A) basicranium of *Palaeoprionodon lamandini* (Quercy, MNHN Qu 9370); (B) holotype basicranium of *Stenogale julieni* (St.-Gérard); (C) basicranium of *Proailurus lemanensis* (St.-Gérard, MNHN S.G. 3509a). The unmodified promontorium with its robust process in

relationships. It displays a rudimentary stage of development relative to living felids and viverrids, and was very likely composed of hyaline cartilage because: (1) delicately attached ectotympanic bones remain in place in these skulls but the caudal entotympanic is never present, and (2) the rugose surfaces of attachment for the caudal element in the fossil crania are identical to those produced by the hyaline cartilage caudal entotympanic of the living *Nandinia*. However, the caudal entotympanic of *Palaeoprionodon* is the smallest and least expanded of any fossil European aeluroid, and vies with *Nandinia* as the most plesiomorphic state of the caudal entotympanic element known in any fossil or living aeluroid carnivoran.

BASICRANIAL ANATOMY OF THE EARLIEST NORTH AMERICAN FELIDS

The Eurasian genus *Proailurus* is often included among the earliest felids. Its skull form, dentition, and postcranial skeleton present no barriers to its placement as an early felid, but whether the genus is directly ancestral to later felids such as *Pseudaelurus* has been questioned (Ginsburg, 1983). *Haplogale* has also been considered an early felid, but its long-snouted skull without facial reduction is more similar to certain viverrids and lacks derived features allying it with *Proailurus* and other early felids. Discovery of its basicranium would improve our understanding of its phylogenetic position.

In Europe the genus *Pseudaelurus* Gervais is considered either a close relative or descendant of *Proailurus*, and its several species mark the beginning of the Neogene felid radiation (Ginsburg, 1983; Beaumont, 1978; Heizmann, 1973). Although it is often assumed that *Proailurus* was ancestral to *Pseudaelurus* and the later felids based on dental evidence, no detailed comparison of their

basicrania has yet been made. The most commonly encountered fossils of these Oligocene and Miocene cats are jaw fragments which, even at this early stage in the history of the Felidae, are monotonous in tooth form and mandibular features. Because hypercarnivorous dentitions have evolved in parallel on a number of occasions during the Cenozoic in marsupials, creodonts, and in different groups of Paleogene and Neogene carnivorans, the accurate recognition of lineages can benefit from the discovery of relatively complete basicranial and even postcranial remains.

Parts of the skeleton having a uniquely derived anatomical pattern are particularly useful in the tracking of felid lineages, especially during the early phase of felid diversification in the Miocene. The structure of the petrosal, auditory bulla, and surrounding basicranium of *Proailurus lemanensis* provides such an anatomical marker identifying this particular felid lineage. The development of the distinctive flange on the medial margin of the petrosal (and the structural relationship of this flange to surrounding basicranial elements) could serve as a synapomorphy for the Felidae. Member taxa of this lineage either retain the distinctive flange (*Stenogale*), or modify it (*Proailurus*), either by reduction or by transformation to another configuration. I have earlier remarked that living felids examined in this study lack this flange of the petrosal that has either been suppressed or reoriented if these carnivores descend from felids such as *Proailurus*. Examination of additional Old World Neogene felids is required to determine the variety of petrosal and other basicranial modifications that occurred in the evolution of the living Felidae.

Crania of European *Pseudaelurus* (supposedly ancestral to many of the later Neogene felids) were not available for this study,

←

Palaeoprionodon is the plesiomorphic aeluroid condition. In *Stenogale* the promontorium has developed a vertical bladeliike flange inset in the margin of the basioccipital. In *Proailurus* this flange has become depressed dorsally, penetrating deeply into the basioccipital, where it was entirely overgrown by an expanding caudal entotympanic element. The three genera (A to C) reflect a progressive inflation and anterior migration of the enlarging caudal entotympanic in these early aeluroids. In addition, the derived structural features of the basicrania provide distinctive synapomorphies useful in the recognition of each of these early aeluroid lineages.

but when basicrania of this genus can be obtained, the form of the petrosal and its relations with surrounding cranial elements should supply critical information on its relationship to *Proailurus*. *Pseudaelurus* is also reported from Asia, but no crania are known (Ginsburg, 1983; Qiu, 1989).

The earliest published occurrences of New World felids are early Barstovian fossils from western Nebraska placed in *Pseudaelurus* (Ginsburg, 1983; Macdonald, 1954; Matthew, 1918, 1924; Sinclair, 1915). Actually, however, the oldest North American felids are undescribed specimens in the Frick collection of the American Museum. These specimens were found at three localities, all of late Hemingfordian age: (1) quarries of the Sheep Creek Formation, Sioux Co., Nebraska; (2) Ginn Quarry, Dawes Co., Nebraska; and (3) East Cuyamungue locality, near Española, New Mexico, possibly from the Nambe Member of the Tesuque Formation, Santa Fe Group.

The Sheep Creek quarries are dated at ~ 16.5 Ma and have produced two undescribed felid species, a small lynx-sized animal and a larger form the size of a small leopard. These fossils were collected by field parties of the Frick Laboratory from 1934 to 1942. The Cuyamungue locality in New Mexico yielded a single individual, represented by a crushed but complete skull, associated mandibles and most of the postcranial skeleton (FAM 62128), collected in 1939. The larger species from the Sheep Creek Formation and the Cuyamungue felid are probably the same species. The associated skeleton of the Cuyamungue cat has articulated forefeet that show the reduced metacarpal 1 of living felids, as well as retractile claws and asymmetric median phalanges. A maxilla of the larger Sheep Creek cat was also associated with a reduced metacarpal 1 of the same type as the Cuyamungue animal. No basicrania are included among the felid sample from the Sheep Creek quarries. Unfortunately, the basicranium of the New Mexican felid is too damaged to provide good anatomical data on the auditory region.

This situation is remedied by the Ginn Quarry occurrence: a skull with intact basicranium, but lacking mandibles or postcra-

nials (fig. 19). Through the courtesy of Dr. R.H. Tedford, American Museum (New York), I was able to dissect the auditory region of the Ginn Quarry cranium to learn if the auditory pattern of *Proailurus* was present.

The Ginn Quarry cat is the oldest New World felid, represented by a complete cranium (FAM 61847), collected in 1935 by Ted Galusha of the Frick Laboratory. Ginn Quarry occurs in Dawes County, northwestern Nebraska, a few miles north of the Niobrara River (Galusha, 1975: 56). The quarry was excavated in a fluvial channel fill that produced a fauna of Hemingfordian age, believed by Galusha to be intermediate in time between the oldest late Hemingfordian faunas of the Sheep Creek Formation, and the fauna from the subjacent Box Butte Formation of Nebraska. The age of the cranium can be estimated from recent dating of the late Hemingfordian of Nebraska and California: (1) the Sheep Creek ash in the type area of the Sheep Creek Formation, Sioux County, Nebraska, has produced a fission-track age of 16.5 ± 0.6 Ma (Tedford et al., 1987); (2) the Kinnick Tuff, Bopesta Formation, California, which underlies the late Hemingfordian Phillips Ranch fauna, has been dated by the K-Ar method (biotite, hornblende) at 16.5 ± 0.2 Ma and 16.5 ± 0.8 Ma (Coles et al., 1997). No dates are available from the Box Butte Formation, but a tuff in the upper part of the underlying Runningwater Formation (early Hemingfordian) has been dated by the fission-track method, suggesting the end of Runningwater deposition occurs at 17–17.5 Ma. Thus, an estimated age for the Ginn Quarry felid is ~ 16.5 –17 Ma.

No Old World *Proailurus* is known to be as young as the Ginn Quarry felid, yet the latter animal retains a number of dental features more typical of the proailurine grade. The Ginn Quarry cranium (basilar length, 14.2 cm) is somewhat larger than the skull of *Proailurus lemanensis* from St.-Gérard (basilar length, ~ 13.4 cm), and is also more robust with much larger canines. Reduction of the anterior premolars, often a criterion in classification of early felids, is more advanced in the Ginn Quarry cat: it retains a small peglike single-rooted P1 and a very reduced (yet still double-rooted) P2 whereas *P.*

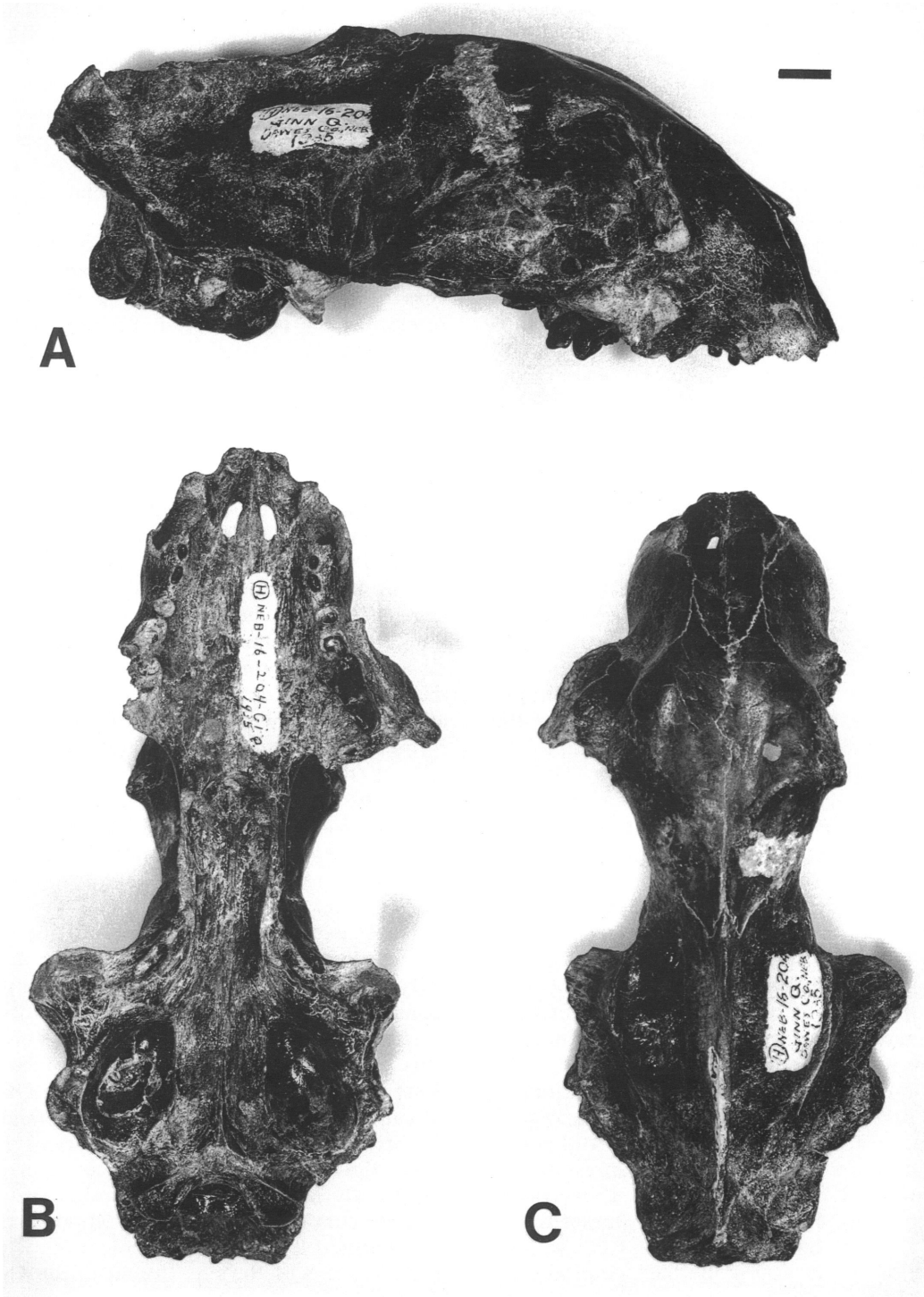


Fig. 19. Cranium of the Ginn Quarry felid (FAM 61847), Dawes County, Nebraska, ~16.5–17 Ma: (A) lateral, (B) ventral, (C) dorsal views. This is the oldest evidence of the Felidae in the New World.

lemanensis has a more robust single-rooted P1 and a much less reduced, well-developed P2. *Pseudaelurus* is recognized in the Old World by loss of P1/p1 (Ginsburg, 1983); the Ginn Quarry cat has not yet attained that grade of premolar reduction.

BASICRANIUM OF THE GINN QUARRY FELID: The remarkably preserved adult skull includes the basicranium with both auditory regions (fig. 19). The right auditory bulla was previously windowed through the caudal entotympanic. We enlarged this opening to reveal the internal structure and relationships of the bulla and middle ear. The ectotympanic and caudal entotympanic chambers of the bulla are positioned as in living felids (Hunt, 1974, 1987), differing only in that the caudal entotympanic has not penetrated as far into the anterointernal corner of the auditory region as it has in the bullae of some living felids. Also, the ectotympanic and caudal entotympanic elements are not as fully fused as in most living adult felids. The ectotympanic displays a prominent styliiform process that contributes to the anterior bulla wall. Internally, the inner margin of the ectotympanic rests on the surface of the petrosal promontorium, creating a thickened flange along the edge of the ectotympanic. The contact of the ectotympanic flange with the promontorium occurs 5 mm anteromedial to the round window along the transverse crest of the promontorium (lateral to this linear contact the ectotympanic margin approaches within 0.3–0.4 mm of the ridged apex of the promontorium, but does not make contact with it). This pattern differs from the Quercy and St.-Gérard aeluroid petrosals described above in which the point of ectotympanic contact is far laterad on the promontorium just anterior to the round window.

The configuration of the promontorium of the Ginn Quarry felid is of particular importance. In a previous study of aeluroid petrosal structure (Hunt, 1989), representative members of the living families (Viverridae, Herpestidae, Hyaenidae) were shown to retain a prominent ventral process of the promontorium buttressing the basioccipital margin. Living felids, however, are the exception among living aeluroids: they lack a robust ventral process applied against the side of the basioccipital, and rather, are characterized by

a wide bony shelf forming the medial margin of the petrosal. This shelf is separated by a narrow gap from the lateral margin of the basioccipital (e.g., domestic cats, *Panthera pardus*, *Panthera leo*). Earlier I suggested that the process must become suppressed and/or reoriented at some time in the lineage(s) leading to living felids, relative to its state in *Proailurus* (Hunt, 1989).

In the Ginn Quarry felid, dissection revealed a plesiomorphic robust ventral process of the petrosal, buttressing the lateral margin of the basioccipital (fig. 20), similar to the vertically-oriented ventral processes in other living aeluroid families. Directly lateral to the ventral process, in fact applied to the base of the process, is the ectotympanic flange, here fused to the posterior terminus of the bony rostral entotympanic. The tabular process of the petrosal stands in near-vertical alignment against the basioccipital, and thus differs markedly from the medial margin of the promontorium in *Proailurus lemanensis* (figs. 17, 18C), where the depressed petrosal flange fills a prominent gap between the basioccipital and promontorium. The shape of the promontorium in the Ginn Quarry felid also differs from that of *Proailurus*: in the former there is a more anteroposteriorly compressed narrow promontorium, but in the latter the promontorium is more plesiomorphic, blocky, and robust. The promontorium of *Proailurus* is most similar in form to the promontoria of *Palaepriodon*, *Stenoplesictis* and *Stenogale*.

These two types of promontoria indicate two distinct neofelid lineages—the geologically older *Proailurus* petrosal retains a plesiomorphic promontorium, but it has evolved a derived bony flange on its medial border. This anatomical configuration precludes its designation as an ancestor of the Ginn Quarry cat in which the promontorium retains a primitively configured ventral process. Because the Ginn Quarry felid occurs in the latest early Miocene, we can predict that its predecessors during the earlier Miocene can be identified by a plesiomorphic ventral petrosal process of the type found in the Ginn Quarry skull.

BASICRANIUM OF THE ECHO QUARRY FELID: No well-preserved basicrania of other late Hemingfordian felids are known in North

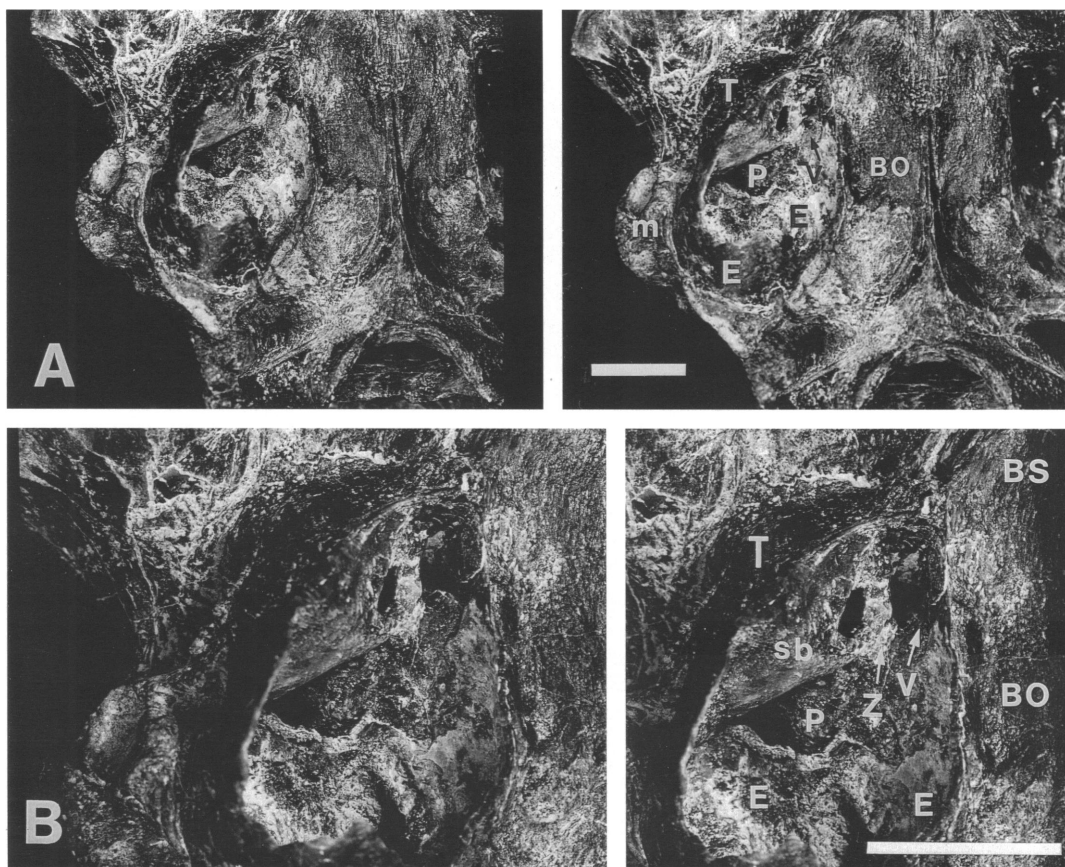


Fig. 20. Auditory region of the Ginn Quarry felid (FAM 61847), same individual as in figure 19, showing the dissection of the right auditory bulla in distant (A) and close (B) ventral views. The floor of the bulla was removed to open the posterior chamber. The caudal entotympanic covering the petrosal promontorium was detached, revealing the ventral process of the promontorium (V) in the anterointernal corner of the auditory region, buttressing the lateral margin of the basioccipital. Note the ectotympanic resting on the surface of the promontorium (Z), and the perforation of the septum bullae.

America, but in the early Barstovian several felid crania of good quality in the collections of the American Museum retain intact basi-crania and bullar structure. Perhaps the most exceptional preservation occurs in an undescribed cranium (FAM 61835, Echo Quarry, fig. 21) found in the Olcott Formation, Sioux County, western Nebraska in 1938. This is a robust felid skull with a basilar length of 19.2 cm, the size of a large leopard. The left auditory region had been opened previously by removal of the floor of the posterior chamber of the bulla (fig. 21A). The ectotympanic and caudal entotympanic chambers of the bulla are developed much as in the Ginn Quarry felid. As in that animal, the flanged medial

edge of ectotympanic rests on the promontorium, here along its entire length. The portion of the caudal entotympanic covering the medial margin of the petrosal was removed by dissection (figs. 21B, C), revealing a flange-like medial extension of the promontorium (resting against the basioccipital) that is similar to the medial process in the same location in *Proailurus*. Considering the much larger body size of the Echo Quarry cat, the process is relatively less developed, but was in the same relationship to the caudal entotympanic that impressed and covered it in both animals. Application of the caudal entotympanic against the promontorium created a shallow depression in the petrosal between

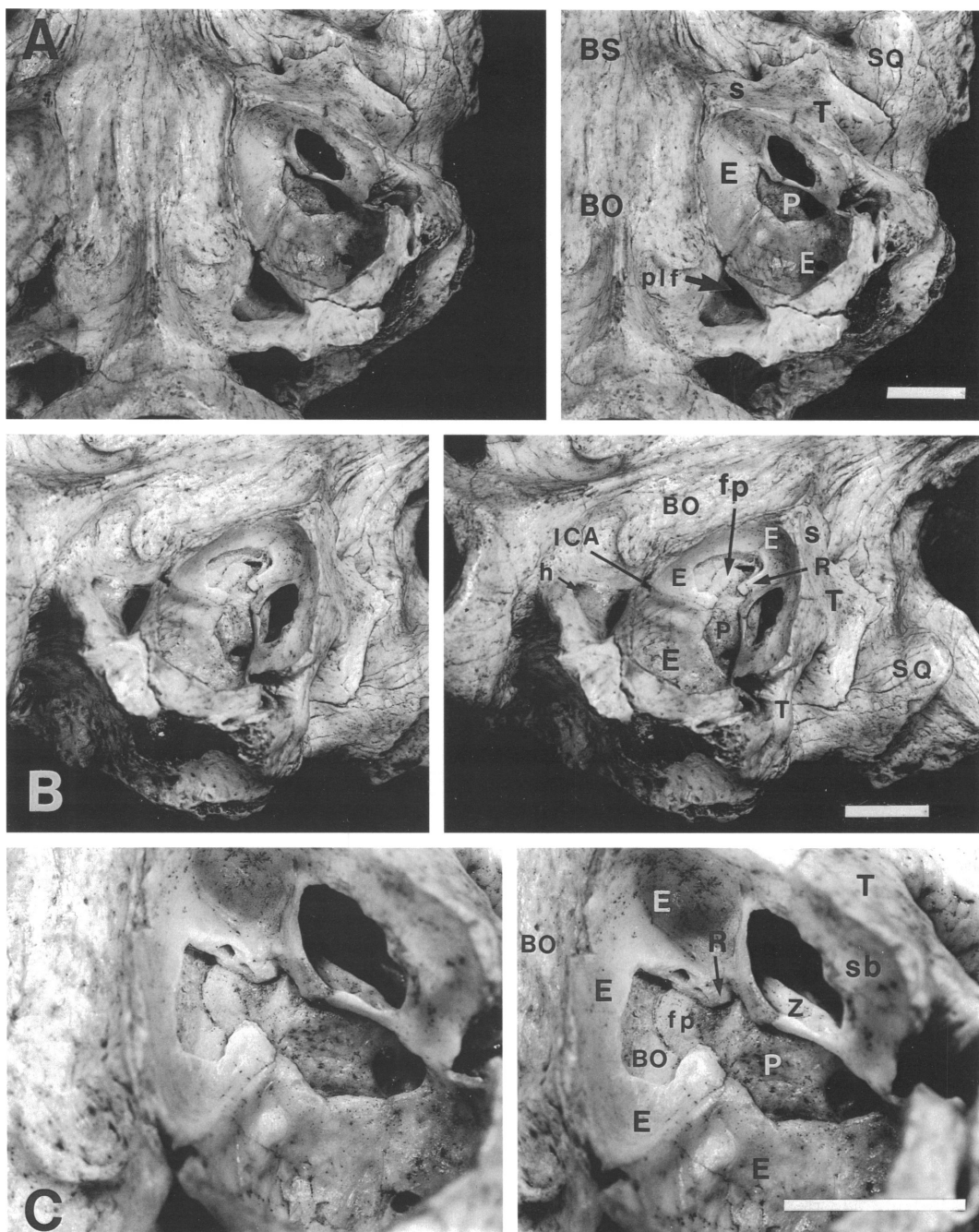


Fig. 21. Auditory region of the Echo Quarry felid (FAM 61835), early Barstovian, Olcott Fm., Sioux County, Nebraska: (A) left auditory bulla with posterior chamber opened and perforation cut in septum bullae, prior to our dissection; (B) interior of the auditory region after removal of the caudal entotympanic plate that covers the flangelike process (fp) of the petrosal promontorium, resting on the basioccipital; (C) close view of the dissection shown in (B)—note window cut in caudal entotympanic plate revealing the medial process (fp) of the promontorium resting against the basioccipital. Note also the flanged edge of ectotympanic resting on the apex of the promontorium, and the posterior terminus of the rostral entotympanic situated in the depression on the surface of the promontorium.

the medial process and the main body of the promontorium. The posterior terminus of the rostral entotympanic rests in the anterior part of this depression and does not continue further caudad. Consequently, the petrosal structure of the Echo Quarry cat is of the archaic type, similar to *Proailurus*, and is not like that of living felids. The Echo Quarry cat demonstrates that in the early Barstovian (mid-Miocene) of North America the *Proailurus*-type petrosal with ventral process and the depressed flange was maintained in at least one felid lineage. In addition, an auditory region of the North American Clarendonian felid *Nimravides pedionomus* (FAM 61855, late Miocene) contains a flanged petrosal indicating derivation from earlier Miocene ancestors with similar anatomy.

Thus, the oldest commonly acknowledged neofelid of the Old World (*Proailurus*) and the oldest New World neofelid (Ginn Quarry) both retain plesiomorphic petrosal structure, yet each of these taxa is distinctive. The petrosal of the St.-Gérard proailurine is similar to plesiomorphic aeluroid petrosals found in *Palaeoprionodon*, *Stenoplesictis* and *Stenogale*, yet it also shows a derived feature, an arcuate flange forming a medial extension of the promontorium, which is strongly impressed and covered by the encroaching caudal entotympanic. The Ginn Quarry cat, however, lacks the derived flangelike process of *Proailurus*, and retains a vertical robust ventral process of the promontorium interpreted to be even more plesiomorphic. Thus, the two crania suggest the existence of at least two early Miocene lineages of felids.

Dissections of living felids (domestic cats, African lion and leopard) demonstrate a much different petrosal form in which the ventrally directed process of the promontorium is absent (or reoriented in such manner that it can no longer be recognized). In these living cats a wide, low shelf occupies the medial margin of the petrosal along its entire length; the shelf continues into the anteroinferior corner of the auditory region to become the low triangular apex of the petrosal. Where and when the transition occurred in felid evolution between the archaic petrosal structure of the Miocene felids and the modern type of petrosal of the living species remains to be determined. The petrosal and

bullae structure of Old World *Pseudaelurus* species is of considerable interest. Do the various Old World *Pseudaelurus* species have a petrosal structure like that of *Proailurus*; do they retain more plesiomorphic petrosals similar to the Ginn Quarry felid, or do some lineages possess the derived petrosal morph of living cats?

DIVERSITY OF AELUROID CARNIVORA AT HSANDA GOL

Among the rare carnivoran fossils from the Hsanda Gol Formation in the Valley of the Lakes, Tsagan Nor basin, Mongolia, recovered in the 1920s by the Central Asiatic Expeditions (CAE) of the American Museum, were fragmentary dentitions of several aeluroids. These fossils were initially described by W. D. Matthew and Walter Granger (1924) and later reviewed by Mellett (1968). Restudy of these specimens and the discovery of previously undescribed material in the museum collections, together with review of the aeluroid samples from Quercy, permits a reallocation of taxa from Hsanda Gol to three genera: *Proailurus* Filhol, *Asiavorator* Spassov and Lange-Badré, and *Shandgolictis*, new genus. The first of these genera is also found in the Quercy fissures.

The Valley of the Lakes occupies the fault-bounded Tsagan Nor basin, bordered on the south by the Altai range and on the north by the Uskuk uplift or block (Berkey and Morris, 1924). Neogene tectonism has deformed the Cretaceous-Tertiary basin fill which includes the Hsanda Gol Formation. Recent field studies by M. C. McKenna and colleagues (in manuscript) have reviewed earlier geologic work in the region, and more accurately defined the geologic setting, stratigraphic limits, and areal extent of the Hsanda Gol Formation. A highly deformed Precambrian to Mesozoic basement complex is unconformably overlain by dinosaur-bearing Cretaceous beds of the Ondai Sair Formation. In unconformable contact with these Cretaceous rocks are unfossiliferous Tertiary arkosic sands and gravels of the Elegen Formation (Berkey and Morris, 1924; Berkey et al., 1929). These sands and gravels are apparently conformably overlain by the red beds of the Hsanda Gol Formation. Initial es-

timates of formation thickness by CAE geologists in the Tsagan Nor basin in thousands of feet have been revised to a few tens of meters (McKenna et al., MS). Their restricted stratotype of the formation south of the CAE camp at Loh is ~60 meters thick.

Fossiliferous localities of the Hsanda Gol Formation occur along the principal ephemeral drainages, Shand Gol and Tatal Gol, where measured sections have been located in extensive badland exposures. Both the original stratotype of the CAE geologists and the restricted stratotype to be designated by McKenna and his associates are in Shand Gol; an important reference section occurs at Tatal Gol ("Grand Canyon" of the CAE). A basalt within the Hsanda Gol Formation was sampled in 1994 in Shand Gol 0.6 km north of the well at Loh; the $^{40}\text{Ar}/^{39}\text{Ar}$ method produced a date of 31.2 ± 0.06 Ma (McKenna et al., MS) within the early Oligocene, in general agreement with the earlier K/Ar dates (31.3, 32.0 Ma) reported by Evernden et al. (1964).

The fossil carnivorans from the Hsanda Gol Formation include the oldest assemblage of Asian aeluroids. The aeluroid fossils were found at three localities: (1) *Loh*—the exact meaning of Loh on field labels remains uncertain. Most likely Loh refers to the location of the CAE camp at Loh which was about 10 miles downstream from Ondai Sair on the Shand Gol (Berkey and Granger, 1923). The designation probably includes fossils from the vicinity of the camp as well as outlying areas. The holotypes of *Cynodictis? elegans* and *Viverravus constans* Matthew and Granger (1924), identified in this report as aeluroids, are reported to come from Loh (CAE field numbers 69, 77); (2) *2 miles southwest of Loh*—McKenna (in manuscript) notes that this locality is the principal source of "Loh" small mammals that resemble those from the lower faunal level of the Hsanda Gol Formation (Ulaan Khongil fauna) at Tatal Gol. The isolated teeth and partial skeleton of "*Palaeoprionodon*" *gracilis* Matthew and Granger (1924) are from this locality (CAE field no. 91). In addition, the holotype mandibles of the aeluroid *Asiavorator altidens* Spassov and Lange-Badré (1995) were reported from 1.5–2 km south of the well at Loh in the Shand Gol drainage

and probably also come from rocks yielding the Ulaan Khongil fauna (McKenna, personal commun.); (3) *Tatal Gol*—the deeply incised drainage of Tatal Gol (Grand Canyon), west of Shand Gol, exposes important outcrops of the Hsanda Gol Formation that produced CAE field numbers 531 (*Proailurus*, AMNH 21674) and 532 (*Asiavorator*, AMNH 21629). The exact stratigraphic level yielding these two important aeluroids remains uncertain.

Carnivorans collected by the Central Asiatic Expeditions from the Hsanda Gol Formation do not include any fossils referable to *Palaeoprionodon*, *Stenoplesictis*, *Stenogale* and *Haplogale*. The only Asian occurrences of these Quercy genera are reported in a recent publication by Dashzeveg (1996) in which he records, but does not describe or illustrate, the genera *Palaeoprionodon* and *Stenogale* from the Hsanda Gol Formation, Mongolia. This author also identifies *Stenoplesictis* in the Hsanda Gol Formation based upon the specimens from Loh attributed by Matthew and Granger (1924) to *Cynodictis? elegans* and *Viverravus constans*. From Paleogene exposures approximately 450 miles east of the Valley of the Lakes, Dashzeveg (1996) has also identified *Stenoplesictis* in the early Oligocene Ergilin Member of the Ergilin Dzo Formation, and at the late Eocene Alag Tsab locality, both in the southeastern Gobi region. These occurrences are from sediments reported by Dashzeveg (1993, 1996) to be stratigraphically beneath the Hsanda Gol Formation. There is also a recent report of *Palaeoprionodon* from Ulan-tatal, China (Huang, 1993), a locality yielding a fauna considered to be age-equivalent to the fauna from Hsanda Gol (Spassov and Lange-Badré, 1995). These fossils from Ulan-tatal are limited to rare dental remains; illustrations are inadequate to determine their referral to a Quercy taxon.

The following account of the Hsanda Gol Formation aeluroids is based upon previously described as well as undescribed American Museum specimens found by the Central Asiatic Expeditions:

PROAILURUS: A fragment of the right mandible (AMNH 21674) with m1 and the small single alveolus for m2 is referable to a small species of *Proailurus* (fig. 22). This speci-

men was not included in Matthew and Granger's (1924) publication; however, the genus *Proailurus* was included in a faunal list by Mellett (1968), but no reference to a particular fossil was made. It was collected in 1925 from the Tatal Gol locality (Grand Canyon), north of Tsagan Nor, Mongolia, and bears AMNH field number 531.

The m1 is 10.3 mm in length, 4.6 mm in width, and has already achieved the cusp pattern of the carnassial of a hypercarnivore. The paraconid-protoconid are fully developed as a shearing blade, including a tight carnassial notch; the metaconid is lost, its place represented by only a weak swelling at the base of the protoconid; the m1 talonid is strongly reduced, with a weak hypoconid bordered lingually by a shallow talonid basin. The hypoconid is continued anteriorly by a low crista obliqua that abuts the posterior wall of the prominent trigonid. Lateral to the crista is a ventral wear groove produced by the paracone of M1. The m2 alveolus is single-rooted, nearly circular, measuring 1.9 mm in length, and 1.4 mm in width. There was no m3.

Among all Hsanda Gol and Quercy aeluroids, this individual shows the greatest degree of reduction of the m1 metaconid. Even the Quercy mandibles assigned to *Proailurus* (MNHN Qu 9437, Concats; Qu 9438, Bach) retain a tiny vestigial metaconid. Also, the m1 talonid of AMNH 21674 is not as reduced in size as in the Quercy *Proailurus* carnassials. Thus this animal, while very likely an early example of *Proailurus*, differs in details of its m1 from the European species, suggesting geographic and/or temporal variation in the evolution of hypercarnivorous dentitions in this genus. The m1 of AMNH 21674 is smaller than any currently reported specimen of *Proailurus lemanensis* (Ginsburg, 1983; fig. 1), falling into the lower part of Ginsburg's range for the genus.

SHANDGOLICTIS, new genus: Among the specimens from Hsanda Gol described and illustrated by Matthew and Granger (1924: 9, fig. 6F) was a fragment of a right mandible with m1-m2 (AMNH 19130), which they made the holotype of a new species, *Viverravus constans* (fig. 23). In the same publication on the preceding page, Matthew and Granger also described a partial right man-

dible (AMNH 19016) with the premolars and canine preserved (1924: 8-9, fig. 6A), which they designated the holotype of a second species, *Cynodictis? elegans*. Although they recognized the possibility that these two specimens might belong to the same species on the basis of size, they could not demonstrate this with the available material because only molars were present in the holotype of *constans* and only premolars in the type of *elegans*.³

Both AMNH 19016 and 19130 were collected in 1922 from the Loh locality; their field numbers (AMNH 19016, field no. 69; AMNH 19130, field no. 77) are in proximity, and they represent an individual of the same size.

Until the molars of *Viverravus constans* (AMNH 19130) are found in association with the premolars of *Cynodictis? elegans* (AMNH 19016), it seems unwise to unite them as a single species. In fact, the molars of *V. constans* differ from all other early aeluroids in these features: (1) m1 is much larger than in Quercy *Stenoplesictis*, *Palaeoprionodon*, and *Stenogale*; a tall m1 trigonid is accompanied by a low, short, reduced talonid; the prominent metaconid is not retracted behind the protoconid; the talonid is not basined, differing from *Stenoplesictis*, and is dominated by a laterally placed hypoconid ridge; the m1 labial cingulum becomes particularly thick at the base of the trigonid, rising nearly vertically at the front of the tooth; (2) m2 is double-rooted (in contrast to Quer-

³ There are actually two mandibular fragments numbered as AMNH 19016. One of these, a right partial mandible, definitely corresponds to the holotype of *Cynodictis? elegans* figured by Matthew and Granger; however, this specimen lacks p2 and the canine (fig. 24A). The second mandibular fragment (fig. 24B) represents the anterior part of a left mandible with canine, p1-2, and on the basis of size could belong to the same individual as the figured specimen. It is probable that these two specimens cataloged as AMNH 19016 are preserved today exactly as they were in 1924, and therefore that Matthew and Granger created a composite illustration, restoring the canine and p2 in the figured specimen. The canine and p2 in the unillustrated fragment are identical to these teeth in Matthew and Granger's illustration. Nevertheless, both fragments cataloged as AMNH 19016 represent the same species, if not the same individual; the fact that they were given the same number implies their close association when discovered in the field.

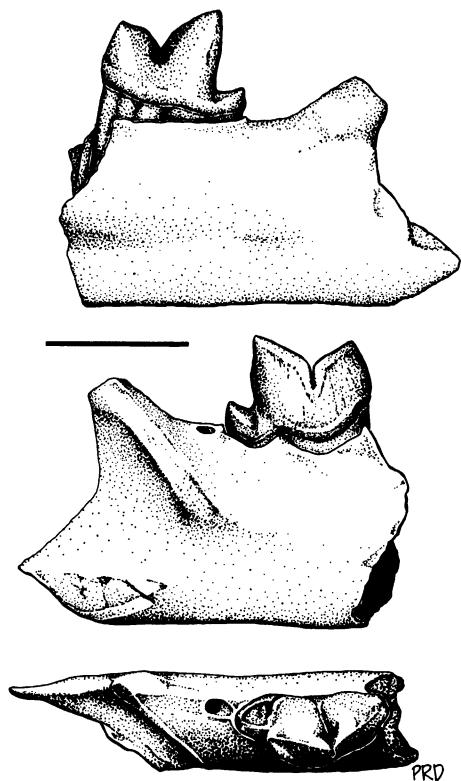


Fig. 22. Mandibular fragment with m1 and m2 alveolus of *Proailurus* sp., Hsanda-Gol (AMNH 21674, field number 531), collected in 1925 from Tatal Gol, north of Tsagan Nor, Mongolia. From the top: lingual, labial, and occlusal views.

cy *Stenoplesictis* species, whose m2 is single-rooted), with a small, sharply defined trigonid and a low, distinct talonid; the trigonid has a tall V-shaped protoconid whose flat medial surface slopes into a shallow basin bordered by the low metaconid and somewhat lower paraconid, these last two cusps being close set and connected by a low ridge; the m2 cingulum is thickened anterior and lateral to the protoconid; the m2 talonid tapers posteriorly and displays a low hypoconid ridge; there is no m3. The m1-2 differ from those of the common Quercy genera (*Palaeoprionodon*, *Stenoplesictis*, *Stenogale*, *Haplogale*), yet they show some similarity to the more plesiomorphic molars of *Anictis simplicidens*. AMNH 19130, the holotype of *Viverravus constans*, is removed from that genus and placed in the new genus *Shandogolictis*, and hence AMNH 19130 is design-

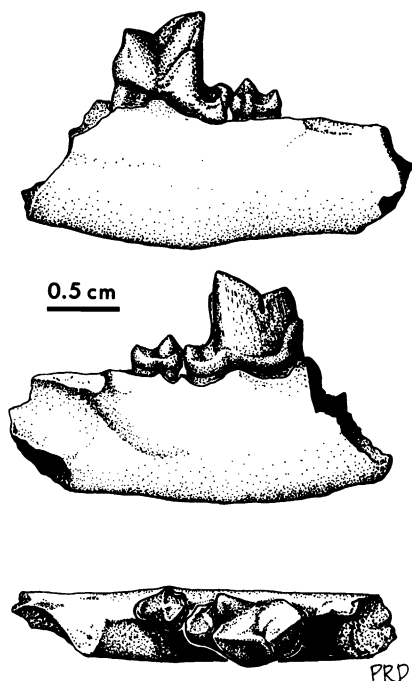


Fig. 23. Mandibular fragment with m1-2 of *Shandogolictis constans*, Hsanda Gol (AMNH 19130, field no. 77), collected in 1922 from the Loh locality, Mongolia. Originally described by Matthew and Granger (1924) as the holotype of *Viverravus constans* (see text for discussion).

nated in this study *Shandogolictis constans* (Matthew and Granger, 1924). If in the future the premolars of *elegans* (AMNH 19016) can be shown to belong to this aeluroid, the species *elegans* will have page priority.

ASIAVORATOR: Spassov and Lange-Badré (1995) recently described a pair of associated mandibles recovered by a Soviet-Mongolian expedition from Oligocene sediments in the Valley of the Lakes, southern Mongolia, as a new genus, *Asiavorator*. The holotype mandibles are numbered FM 487-95 in the collections of the National Museum of Natural History, Sofia, Bulgaria. The single species, *A. altidens*, is known only from the holotype, collected in the "Svita Shand Gol, à environ 1.5-2 km Sud de Loh-us Huduk . . . situé dans le bassin de la rivière Shand Gol." Spassov and Lange-Badré (1995) believe the site of collection is probably the same as the Loh locality of Matthew and Granger.

In 1925 the Central Asiatic Expedition col-

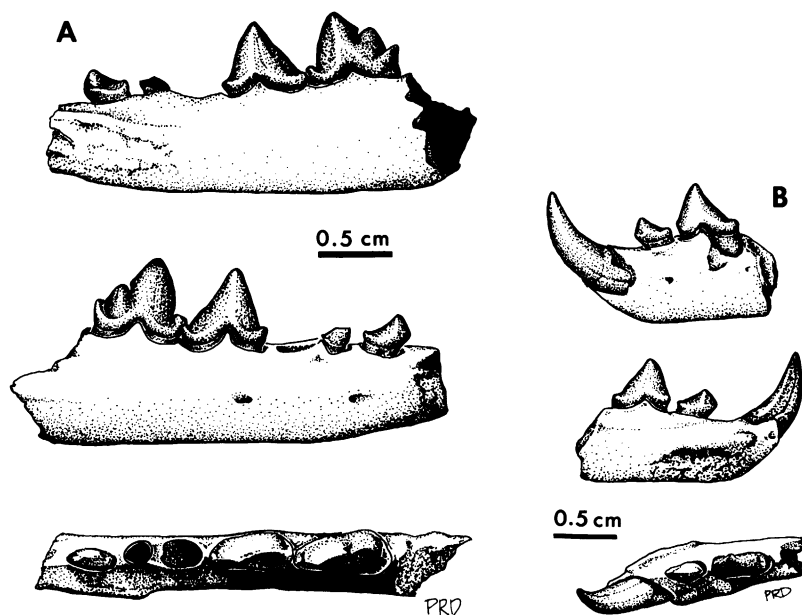


Fig. 24. (A) Mandibular fragment with right p1, p3-4 and alveoli for p2 of a small aeluroid, Hsanda Gol (AMNH 19016, field no. 69), collected in 1922 from the Loh locality, Mongolia. Originally described by Matthew and Granger (1924) as the holotype of *?Cynodictis elegans* (see text for discussion). (B) Mandibular fragment with left canine, p1-2 of *elegans*, (AMNH 19016, field no. 69), from the same locality and presumably the same individual as (A); both (A) and (B) were used to create a composite figure of the holotype by Matthew and Granger (1924; fig. 6A). At present the generic assignment of this small aeluroid is indeterminate.

lected from the Tatal Gol ("Grand Canyon") locality an isolated left mandible (fig. 25) with p3-4 and the m1 trigonid, and alveoli for C, p1-2 (AMNH 21629, field no. 532), representing a long-jawed aeluroid distinct from *Anictis*. This aeluroid was never described by Matthew and Granger and remained unnoticed in the American Museum collections. There is no doubt upon dental and mandibular comparisons with the illustrations of the holotype of *Asiavorator* that this mandible is referable to that genus and species, and represents the first remains of the genus recovered. Its field number (532) is very close to the field number (531) of the *Proailurus* mandibular fragment (AMNH 21674), also from Tatal Gol, and the two specimens may have been found in 1925 at about the same time, perhaps in geographic proximity.

Among the distinguishing features of AMNH 21629 is the slender, elongate mandible (p1 and p2 are separated from adjacent teeth by diastemata as in the holotype), the well-developed elongate p2, the slender, lat-

erally compressed p3-4, both with a particularly strong anterior cingulum cusp and posterior accessory cusp, and the sharply defined labial cingula on p3-4 and on the m1 trigonid. The m1 trigonid is laterally compressed and bladellike, and despite the loss of the posterior part of m1, it is evident that the metaconid was low, retracted, and reduced in size, as in the holotype carnassial of *A. altidens*. The dimensions of the p3, p4, and m1 in AMNH 21629 are also similar to those of the holotype (AMNH 21629, length \times width: p3, 8.0 \times 2.8 mm; p4, 8.2 \times 3.0 mm; m1 trigonid, 7.5 \times 4.6 mm; FM 487-95, holotype: p3, 7.7 \times 3.0 mm; p4, 7.8 \times 3.3 mm; m1 trigonid, 7.1 \times 4.1 mm). The placement of the mental foramina is as in the holotype. However, the shallow longitudinal groove developed along the lingual side of the holotype mandible is not present in AMNH 21629.

These specimens of *Asiavorator* are most similar in dental and mandibular features to the aeluroid *Stenoplesictis* which displays

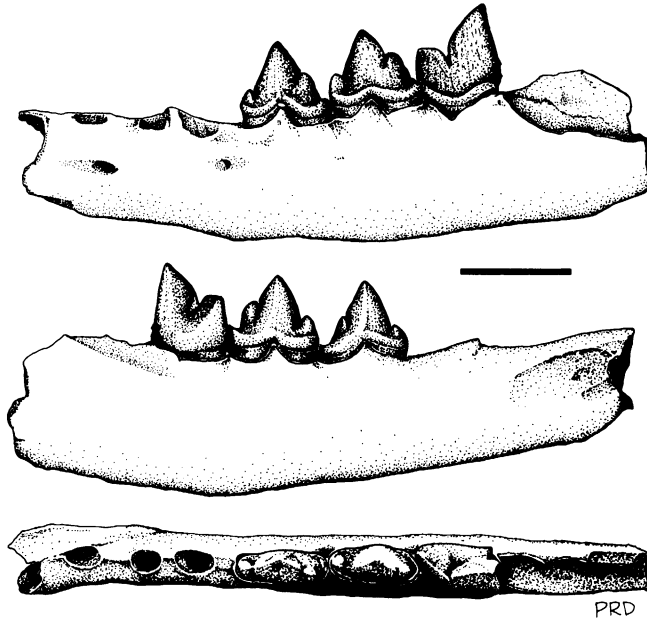


Fig. 25. Mandible with p3-4, partial m1, and alveoli for p1-2 of *Asiavorator gracilis*, Hsanda Gol (AMNH 21629, field no. 532), collected in 1925 from Tatal Gol, north of Tsagan Nor, Mongolia. From the top: labial, lingual, and occlusal views.

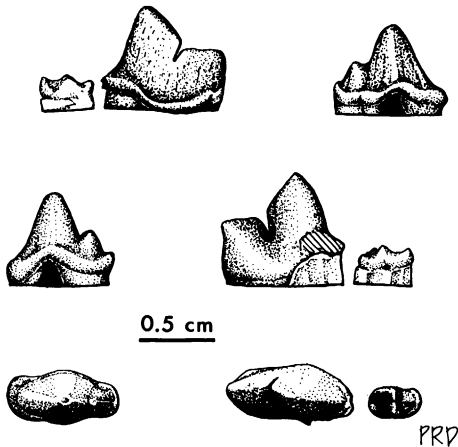


Fig. 26. Isolated m2 and partial m1 of *Asiavorator gracilis*, Hsanda Gol (AMNH 19123), collected in 1922 from the Loh locality, Mongolia. These teeth were originally described by Matthew and Granger (1924) as the holotype of *Palaeoprionodon gracilis* (see text for discussion). The isolated premolar illustrated here was also attributed to the holotype (AMNH 19123), but is not regarded in this study as belonging to this species.

many of the distinguishing traits of *A. altidens* but in a more subdued manner. *Asiavorator* differs from *Stenoplesictis* species in its larger, more prominent p2, in the stronger emphasis on the p3-m1 labial cingula, and in its generally greater overall dimensions (toothrow length, C-M1, in the *Asiavorator* holotype is 45.9 mm, and is estimated to be 42.6 mm in AMNH 21629). Some specimens of *Stenoplesictis cayluxi* (e.g., AMNH 10094) are somewhat similar but smaller versions of AMNH 21629.

STATUS OF "*PALAEOPRIONODON*" *GRACILIS* FROM HSANDA GOL: One of the most enigmatic fossil aeluroids described by Matthew and Granger (1924) from the Hsanda Gol Formation was AMNH 19123, their holotype of *Palaeoprionodon gracilis* (fig. 26), based on "lower teeth and parts of skeleton." These teeth, all isolated, comprised an m1 lacking the talonid, a complete small m2, two canines, and a premolar described as p4. Reference to *Palaeoprionodon* was provisional because the

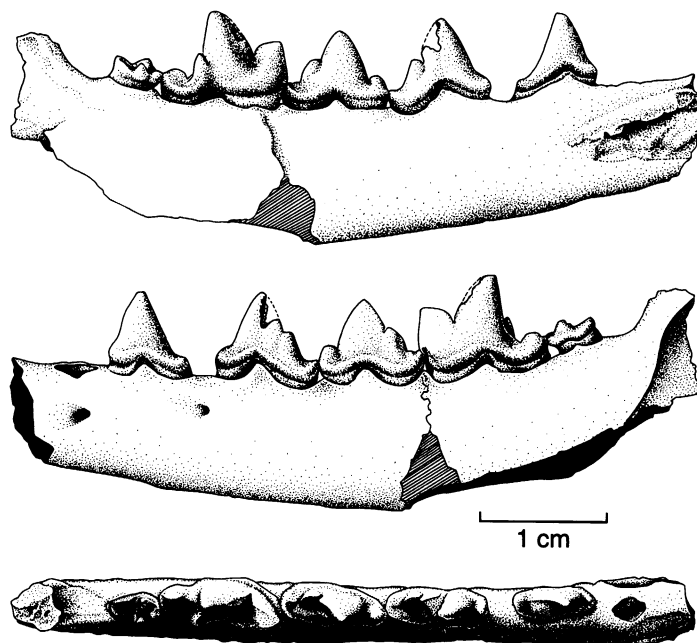


Fig. 27. Mandible with p2-m2 of *Asiavorator gracilis* (AMNH field no. 86, see text), collected in 1991 by the Mongolian-American Museum Expeditions in the Hsanda Gol Formation, Mongolia (through the courtesy of M. C. McKenna).

dentition was so poorly represented. The postcranial skeleton, which will be subsequently discussed in more detail, was said to include the humerus, radius, ulna, astragalus, calcaneum, and metatarsals. Unfortunately, Matthew and Granger (1924) do not comment on the nature of association of the teeth and the postcranials; presumably they were confident of this because Granger is reported to have collected the specimen in 1922.

Collecting in 1991 by American Museum field workers at Tatal Gol recovered rare aeluroid dental remains, including a well-preserved left mandible (fig. 27, Mongolian-American Museum Field Expeditions, field no. 86, collected 4 August 1991 by J. Clark) with single-rooted p1 alveolus, p2-4, m1-2; there is no m3. Also present is the right m1-2 and left M1-2 of the same individual. This specimen clarifies a long-standing problem in the identification of the Hsanda Gol "*Palaeoprionodon*" and demonstrates that "*P.*" *gracilis* (AMNH 19123) and AMNH 21629 are referable to a species of *Asiavorator*; which appears to be relatively common at the Hsanda Gol localities. The mandible even-

tually will be given a number of the Mongolian Academy.

The mandible (field no. 86) is directly comparable with AMNH 21629 in size and form of the mandible and in dental traits. Because AMNH 21629 lacked the m1 talonid and the m2 it was difficult to evaluate relative to other early aeluroids. This problem was solved with the discovery of field no. 86, which retains these teeth. The m1 is a rather narrow bladelike carnassial, the metaconid quite small and low on the trigonid, the talonid somewhat reduced and less basined than in the more plesiomorphic m1 of *Anictis*. This carnassial is incipiently hypercarnivorous, and directly corresponds to the m1 of the *A. altidens* holotype described by Spassov and Langé-Badre (1995). The m2 is small, but it retains a plesiomorphic structure, with the three trigonid cusps at the corners of an equilateral triangle, and a well-developed m2 talonid, similar to the plesiomorphic m2 of *Anictis*.

Comparison of field no. 86 with AMNH 21629 shows no differences in p1, p4 or m1. On p3 the anterior cingulum cusp is not as

developed in field no. 86. Also, the p2 is slightly shorter in field no. 86 relative to the spacing of the p2 alveoli in AMNH 21629, however, the latter is a somewhat larger individual.

It is the m2 of field no. 86 that supplies the critical link to the holotype of *Palaeoprionodon gracilis*. The small m2 of the holotype (AMNH 19123) as well as the partial m1 closely match these same teeth in field no. 86. Thus, (1) the holotype m1–m2 of “*Palaeoprionodon*” *gracilis* (AMNH 19123) from 2 miles southwest of Loh, (2) the holotype mandibles of *Asiavorator altidens* from at or near the Loh locality, (3) the undescribed mandible (AMNH 21629) from Tatal Gol, and (4) the newly found mandible with nearly complete dentition (field no. 86), also from Tatal Gol, probably belong to a single species of aeluroid carnivoran. This animal would have had a basilar skull length of ~9–10 cm, about the size of the living *Viverricula*. It would also have a long snout; well-developed premolars with diastemata between the canine and anterior premolars; a prominent p2 (not reduced as in many contemporary aeluroids); a p3–4 with developed accessory cusps; an m1 trending toward a hypercarnivorous form but retaining a low metaconid and a small talonid with sharp hypoconid ridge; a small plesiomorphic m2 that retained the three trigonid cusps and a developed unreduced talonid. This is a taxon obviously different from the more hypercarnivorous *Proailurus*, and much larger than the small hypercarnivores *Palaeoprionodon* and *Stenogale*. It approaches *Stenoplesictis* and *Haplogale* from Quercy, yet it differs from the former in its prominent p2, more elongate mandible, and larger size, and from the latter in its plesiomorphic m2 and in retaining a more developed m1 talonid with hypoconid ridge (the m1 talonid is quite short and flat in *Haplogale*).

One of the teeth of the “P.” *gracilis* holotype figured and briefly described by Matthew and Granger appears to be mistakenly identified. The isolated premolar (fig. 26) that they describe as p4 is more likely the right P3 of *Asiavorator* or an unknown carnivoran. This tooth carries a basal swelling medial to its posterior root and also displays a fine ridge running down the anterior face

and curving linguad at its terminus. Both of these features indicate that the tooth cannot be a lower right premolar, but if it were from the lower jaw, it would have to be a left. The basal swelling, however, seems more in keeping with a P3, but it is unlike any aeluroid P3 at my disposal.

The upper molars of *Asiavorator* were not preserved among the holotypic material described by Spassov and Lange-Badré. However, field no. 86 includes an associated M1–2. M1 is triangular with a broad stylar shelf on its labial margin, and a well-developed parastylar region. The paracone is taller than the metacone, and the protocone is large and projecting; a protocone basin occupies the center of the tooth; the overall form of M1 is typical of many living viverrids. M2 is much smaller than M1; its occlusal form is as M1 but simply reduced in size. This carnivoran was in the process of reducing m2/M2 and developing a more hypercarnivorous dentition while maintaining its full complement of premolars.

There is, then, probably a single aeluroid carnivoran represented by a hypodigm made up of AMNH 21629, 19123, field no. 86, and FM 487–95 (table 8). This animal has been found in the vicinity of the Loh locality and at Tatal-Gol. The specimens are referable to the genus *Asiavorator*; the species name with priority is *A. gracilis* (Matthew and Granger).

POSTCRANIAL SKELETON OF THE OLDEST ASIAN AELUROID

The teeth of the holotype of *Asiavorator gracilis* (AMNH 19123) are associated with a relatively complete postcranial skeleton, found by Walter Granger 2 miles southwest of Loh, Mongolia. This is the oldest known aeluroid skeleton from Asia, and therefore it both merits a comparison with the skeletons of living aeluroid Carnivora and provides insight into the functional anatomy of this Oligocene aeluroid.

Matthew and Granger (1924) initially described under AMNH 19123 only a humerus, radius, ulna, astragalus, calcaneum, and metatarsals. The bones of the forelimb were illustrated, as was a third metatarsal. They believed that the limb elements compared

TABLE 8
Measurements (in mm) of the Lower Dentition of *Asiavorator gracilis*
(Matthew and Granger) from Mongolia (Hsanda Gol)

	AMNH f.n. 86	FM 487-95	AMNH 21629	AMNH 19123
Length × width				
p1	(2.7 × 1.8) ^a	2.5 × —	(2.7 × 1.4)	—
p2	6.2 × 2.7	6.1 × 2.7	(6.9) × —	—
p3	7.9 × 3.0	7.7 × 3.0	8.0 × 2.8	—
p4	8.0 × 3.5	7.8 × 3.3	8.2 × 3.0	—
m1	9.9 × 4.1	9.7 × 4.1	— × 4.6	(9.7) × 4.1
m2	3.8 × 2.6	—	—	3.8 × 2.2
Length				
p1-4	27.9	(28.1)	30.5	—
p1-m2	41.2	—	(44.8)	—

^a Estimated measurements in parentheses.

TABLE 9
Postcranial Elements Attributed to
Asiavorator gracilis (Matthew and Granger) 1924,
from 2 miles Southwest of Loh, Mongolia,
Hsanda Gol Formation (AMNH 19123, 82310)

AMNH 19123	AMNH 82310
Humerus (r)	Humerus (l), proximal end absent
Radius (r)	Radius (l), proximal end only
	Ulna (l); ulna (r), proximal
	Scapula (r), glenoid only
	Magnum (l, r)
	Carpal cuneiform (l, r)
	Unciform (r)
	Metacarpal 1 (l)
	Metacarpal 3 (l)
	Metacarpal 4 (l), proximal only
	Metacarpal 5 (l, r)
	Metapodials (2), distal ends only
	Patella
	Fibula (l), proximal end absent
Cuboid (r)	Cuboid (l)
Astragalus (r)	Astragalus (l), proximal only
	Calcaneum (l, r)
Navicular (r)	
Metatarsal 2 (l)	
	Metatarsal 3 (r), proximal
Metatarsal 4 (l)	Metatarsal 4 (r), proximal
Metatarsal 5 (r)	
	Proximal phalanges (5)
	Proximal phalanx (1), pathologic
	Intermediate phalanges (3)
	Ungual phalanges (2)
	Axis vertebra, partial
Caudal vertebrae (2)	Caudal vertebrae (4)

(l) = left; (r) = right.

with those attributed by Schlosser to *Palaeoprionodon* from Quercy.

When a search was made of the American Museum collection for unidentified aeluroid material from Hsanda Gol, additional postcranial bones were discovered under the number AMNH 82310. Although AMNH 82310 was not mentioned by Matthew and Granger (1924) in their descriptions of Hsanda Gol carnivorans, it almost certainly represents the remainder of the postcranial skeleton of AMNH 19123. Both AMNH 19123 and 82310 bear the same field number (91), and were collected at the same locality (2 miles southwest of Loh) in the same year (1922). There is no duplication of postcranial elements, the bones correspond to an animal of the same size, and the color, degree of mineralization, and residual sediment on various bones appear similar. The elements of the skeleton are listed in table 9.

Enough of the skeleton is present to make useful comparisons with fossil and living carnivorans. The fore- and hindlimbs are relatively complete with the exception of the femur, tibia, and some tarsal and carpal bones. Vertebral column, scapulae, and innominates are poorly represented. The limb and foot bones, partial scapula, axis and caudal vertebrae are closely comparable to the skeleton of the living Lesser Oriental Civet (Viverridae, *Viverricula indica*, 2–4 kg) and to the skeletons of living genets (Viverridae,

Genetta, 1–3 kg). However, the skeleton of *Asiavorator* differs from genets in its more robust limb elements, in its larger feet, and in a lengthened tarsus (the calcaneum and astragalus in particular display longer distal segments than seen in genets).

The postcranials of *Asiavorator* are most similar in size and form to those of *Viverricula*, but some differences exist. The radius of *Asiavorator* is longer than the radius of *Viverricula indica* (Szechuan province, China, AMNH 58327, male) although the humerus is the same length, indicating a proportionately longer forelimb in the fossil aeluroid. The calcanea of the two carnivores are almost identical in size and form, both with a lengthened distal segment. The *Asiavorator* astragalus is slightly more elongate, with better developed proximal trochlear ridges, and the sustentacular facet more dorsoventrally extended and aligned—hence a somewhat elongated tarsus in *Asiavorator* with evidence of more restricted astragalar motion relative to the distal tibial articulation.

Metapodials of the hindfoot (metatarsals 2–5) in *Asiavorator* are markedly lengthened relative to those of *V. indica*. In the forefoot, metacarpal 3 of *Asiavorator* is about the same size and length as in *V. indica*, metacarpal 5 is somewhat larger and longer, and metacarpal 1 is much reduced in size, but not to the extent seen in *Viverricula*. The tarsus and metatarsus of *Asiavorator* are much longer relative to its carpus-metacarpus, with the fourth metatarsal nearly twice the length of the third metacarpal. Thus *Asiavorator* had a somewhat lengthened lower forelimb, but without elongation of the manus, yet in the hindlimb, the metatarsals, calcaneum and astragalus indicate an elongation of the hindfoot relative to *Viverricula*.

Of some interest are the phalanges of *Asiavorator* (table 9): representative proximal, intermediate, and ungual phalanges are similar to these bones in genets, but the intermediate phalanges are only moderately asymmetric in form, and the ungual phalanges are more robust and not as laterally compressed. Therefore, it is unlikely that claw retractility was developed to the degree evident in living genets. Genets are both arboreal and terrestrial; their retractile claws are useful in climbing trees.

Viverricula indica also can climb, but is generally considered to be more terrestrial, inhabiting grasslands and forests (Nowak; 1991). The skeleton of *Asiavorator* indicates similar habits but the terrestrial mode may have been more strongly emphasized, based on its overall skeletal robustness and the proportions and anatomy of the feet. The similarity of the *Asiavorator* skeleton to those of living viverrids demonstrates the antiquity of the viverrid postcranial skeleton as retained in genets, civets, and other small generalized viverrid carnivores.

PALEOGENE AELUROIDS FROM MONGOLIA: RECENT DISCOVERIES

Dashzeveg (1996) has recently described partial mandibles of two small aeluroid carnivorans from the Alag Tsab (late Eocene) and Ergil Obo (early Oligocene) localities of Mongolia that he referred to *Stenoplesictis*. The European aeluroid genera *Palaeoprionodon*, *Stenogale* and *Stenoplesictis* were also reported, but not described, from younger horizons within the Hsanda Gol Formation (early Oligocene). All three genera are said to occur both below (Tatal Member) and above (Shand Member) the dated basalt (31–32 Ma) within the Hsanda Gol Formation (Dashzeveg, 1996). As Dashzeveg points out, the occurrence of these three aeluroid genera accompanied by the small carnivoran *Palaeogale*, the amphi cynodont *Amphicyonodon*, and the nimravid cat *Nimravus* demonstrates affinity with the Oligocene assemblage of small carnivorans from the fissures at Quercy. None of these small aeluroids have been found in North America.

Huang (1993) has also described several fragmentary mandibles of small carnivorans from the Oligocene locality of Ulantatal, Nei-Mongol, China. Some of these specimens undoubtedly represent small aeluroids, but generic referrals are uncertain.

The oldest reported Asian aeluroids are the two mandibles of *Stenoplesictis* described by Dashzeveg (1996) from Alag Tsab and Ergil Obo in the southeastern Gobi (Mongolia). A new species, *Stenoplesictis indigenus*, is represented at Alag Tsab only by the holotype, a mandibular fragment with p4-m1, and the alveoli for a two-rooted m2. The form of p4-

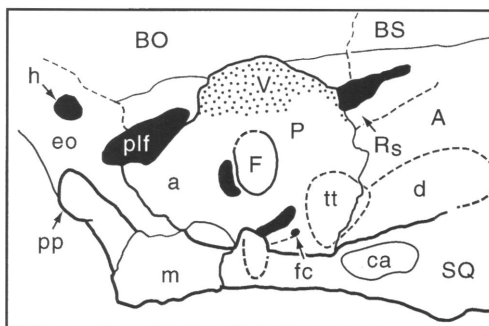
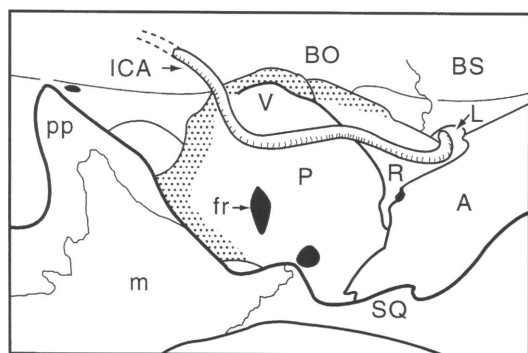
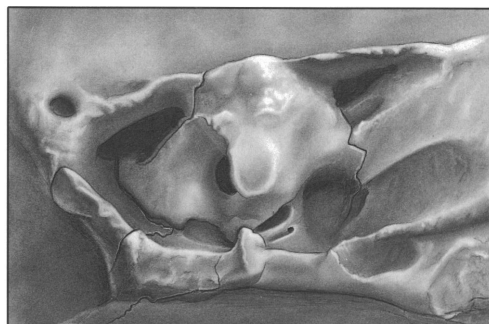


Fig. 28. Auditory region of the living African palm civet *Nandinia binotata*, showing the plesiomorphic aeluroid petrosal and rostral entotympanic. The cartilaginous caudal entotympanic has been removed but the area of attachment of its dorsal margin is indicated by stipple.

Fig. 29. Auditory region of the Quercy aeluroid *Palaeoprionodon lamandini*, showing the plesiomorphic aeluroid petrosal with promontorial facet and robust ventral process. The area of attachment for the caudal entotympanic along the medial margin of the promontorium is indicated by stipple.

m1 is most similar to these teeth in early aeluroids. The Alag Tsab locality is said to be late Eocene in age, hence this is the oldest Asian aeluroid. However, there are some distinctions from typical Quercy *Stenoplesictis* (*S. cayluxi*, *S. minor*): the two Quercy species possess a reduced m2 which is essentially single-rooted. In the Alag Tsab mandible, the m2 was not as reduced, remained two-rooted (based on alveoli), and was longer relative to m1 length.

The second species of *Stenoplesictis* (*S. simplex*) described by Dashzeveg from Ergil Obo is a slightly larger carnivore and, although stratigraphically younger, could belong to the same lineage as *S. indigenus*. The species *S. simplex* is known only from the holotype mandible with p4-m2. The form of m2 is distinctive in many of these early aeluroids (fig. 6)—in the Ergil Obo mandible the m2 has two

roots, and is proportionately shorter relative to m1 length than m2 in *S. indigenus*.

Referral of the Alag Tsab and Ergil Obo mandibles to *Stenoplesictis* draws attention to the defining dental features of the genus: (1) the Quercy species of *Stenoplesictis* (holotype species *S. cayluxi* and referred *S. minor*) possess a single-rooted m2 that, when removed from the jaw, leaves only a single small oval to circular alveolus—in the two Mongolian species the m2 remains two-rooted even in *S. simplex*, which is larger than either of the Quercy forms; (2) the m2 cusp pattern in *S. cayluxi* and *S. minor* (fig. 6) is relatively plesiomorphic among early aeluroids in retaining three trigonid cusps distributed at the points of an equilateral triangle—these cusps surround a shallow trigonid basin. A small weakly basined talonid is appended, reflecting the basined talonid of m1. The m2 of *S. simplex* appears to differ from

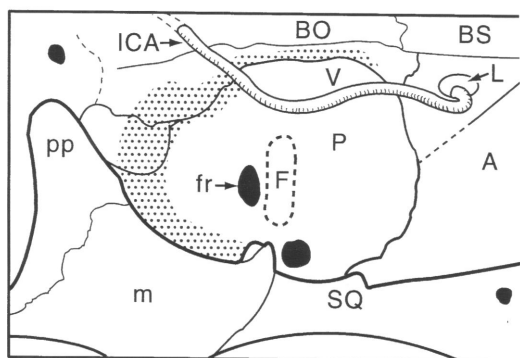
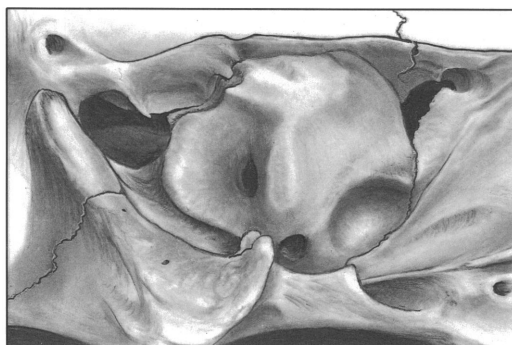


Fig. 30. Auditory region of the Quercy aeluroid *Stenoplesictis cayluxi*, showing the robust petrosal with promontorial facet, the ventral process, and the posteriorly directed "apron" behind the round window. The stipple pattern indicates the area of attachment of the dorsal margin of caudal entotympanic to the petrosal.

the Quercy m2s in lacking the cristids connecting the trigonid cusps in the Quercy species (table 3), and in having the hypoconid moderately developed on the talonid.

These considerations suggest that if these Mongolian fossils are correctly referred to *Stenoplesictis*, the lineage in Asia is distinguished from the Quercy species at least by features of m2. Complete mandibles of these Mongolian aeluroids would significantly clarify their relationships with the European species since the form of the premolars, together with the molar pattern, effectively define these small early aeluroids.

A better comparison of the Alag Tsab and Ergil Obo "*Stenoplesictis*" molars is with the mandibular fragment with m1-2 (AMNH 19130) from the Loh locality, Hsanda Gol Fm., Mongolia, initially described as the type

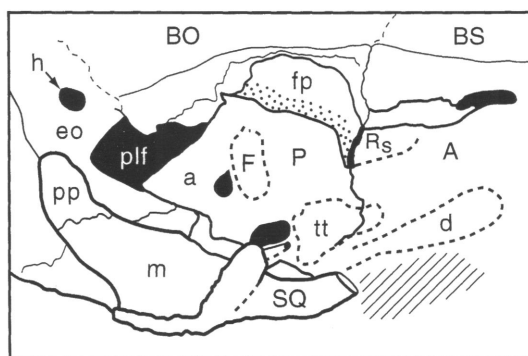
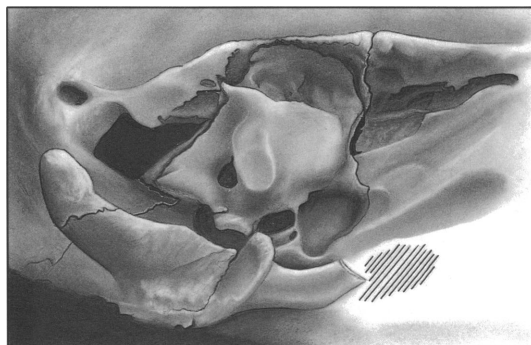


Fig. 31. Auditory region of the St.-Gérard aeluroid *Stenogale julieni*, showing the promontorial facet, the vertical flange (fp) pressed into the side of the basioccipital, and the area lateral to the flange for the attachment of the edge of the caudal entotympanic (stipple pattern). The caudal entotympanic is slightly inflated in the posterior part of the auditory region in comparison to the more plesiomorphic uninflated state found in *Nandinia* and *Palaeoprionodon*. Note prominent depression for the rostral entotympanic element (R_s).

of *Viverravus constans* by Matthew and Granger (1924), and named here as the holotype of *Shandgolichtis constans*. The marked similarity of the type of *constans* (AMNH 19130) to the Alag Tsab and Ergil Obo fossils suggests that these jaw fragments may represent an independent late Eocene-early Oligocene Asian lineage of small aeluroids. However, before the Alag Tsab and Ergil Obo mandibles can be referred to *Shandgolichtis*, more complete dental and cranial material is necessary to evaluate the diversity of small aeluroid carnivorans in Asia relative to those of western Europe.

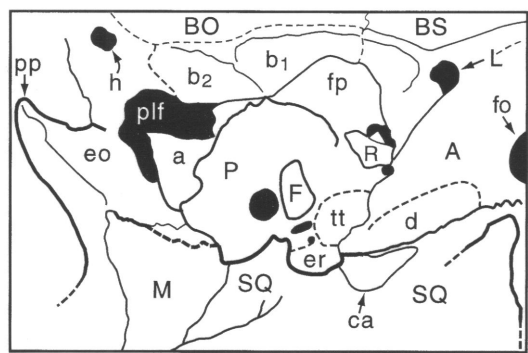
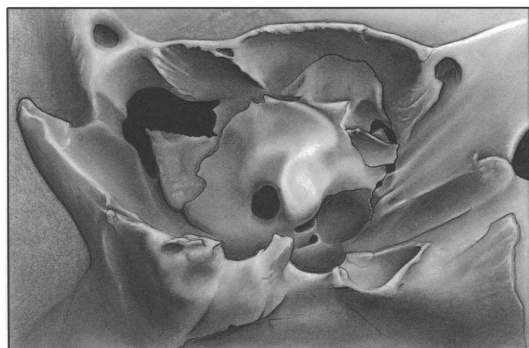


Fig. 32. Auditory region of the St.-Gérand aeluroid *Proailurus lemanensis*, showing the promontorial facet, the depressed flange of the promontorium (fp), the prominent posteriorly directed "apron" of the petrosal, and the excavated margins of the basioccipital (b_1 , b_2) and exoccipital (eo) for the expanded caudal entotympanic. This auditory region is morphologically similar to that of *Stenogale julieni* but is more derived in its greater degree of caudal entotympanic inflation.

SUMMARY

The karst fissures of the Quercy district (France) and the sediments of the Hsanda Gol Formation (Mongolia) preserve the earliest assemblages of aeluroid carnivorans. These localities lie near the western and eastern extremes of Eurasia at approximately 45° N latitude. Six aeluroid genera (*Anictis*, *Palaeoprionodon*, *Stenoplesictis*, *Stenogale*, *Haplogale*, *Proailurus*) are known from Quercy, and three from Hsanda Gol (*Proailurus*, *Asiavorator*, *Shandgolicteis* n.gen.). Recently reported occurrences of *Palaeoprionodon*, *Stenoplesictis*, and *Stenogale* in eastern Asia are of much interest but require confirmation. The paucity of aeluroid specimens

from Mongolian and Chinese sites are the result of the scarcity of aeluroid fossils in the interior basins of central Asia relative to the more prolific and intensively collected Quercy fissures.

These earliest aeluroids share small body size (< 5 kg), a tendency to develop a hypercarnivorous dentition, and a basicranial homogeneity (at Quercy and St.-Gérand where skulls are available) suggesting a relatively recent common ancestry. Four European aeluroid genera (*Palaeoprionodon*, *Stenoplesictis*, *Stenogale*, *Proailurus*) that have representative species occurring at Quercy can be placed in a cladogram employing basicranial morphology. The most primitive aeluroid auditory region known among fossil and living carnivorans remains that of the living African palm civet, *Nandinia binotata* (fig. 28). The fossil European basicrania from Quercy and St.-Gérand could have been derived from this or a similar morphotype. The most plesiomorphic basicranial structure occurring in a Quercy aeluroid is found in *Palaeoprionodon* (fig. 29), in which the ectotympanic is rudimentary, the posterior chamber of the bulla is small in volume, and in all likelihood enclosed by a cartilaginous caudal entotympanic. Significantly, as in *Nandinia*, the caudal entotympanic of *Palaeoprionodon* intervened as a lamina between the ectotympanic and the rostral entotympanic (athictic state). The somewhat more derived basicranium of *Stenoplesictis* (fig. 30) can be interpreted as a modification of the plesiomorphic *Palaeoprionodon* basicranial pattern. In *Stenoplesictis*, the ectotympanic is more inflated and appears to exclude the caudal entotympanic from the anterior chamber of the bulla, yet the posterior chamber of the bulla formed by the caudal entotympanic remains small in volume. Although the anatomical distinctions between *Palaeoprionodon* and *Stenoplesictis* are slight, *Stenoplesictis* is uniquely derived in some morphological features (enlarged ectotympanic forming anterior chamber of the bulla, caudal entotympanic largely excluded from anterior chamber, posteriorly elongated petrosal apron, ventrally extended basioccipital margins), and does not appear to serve as a plausible antecedent stage for other Quercy or St.-Gérand aeluroids.

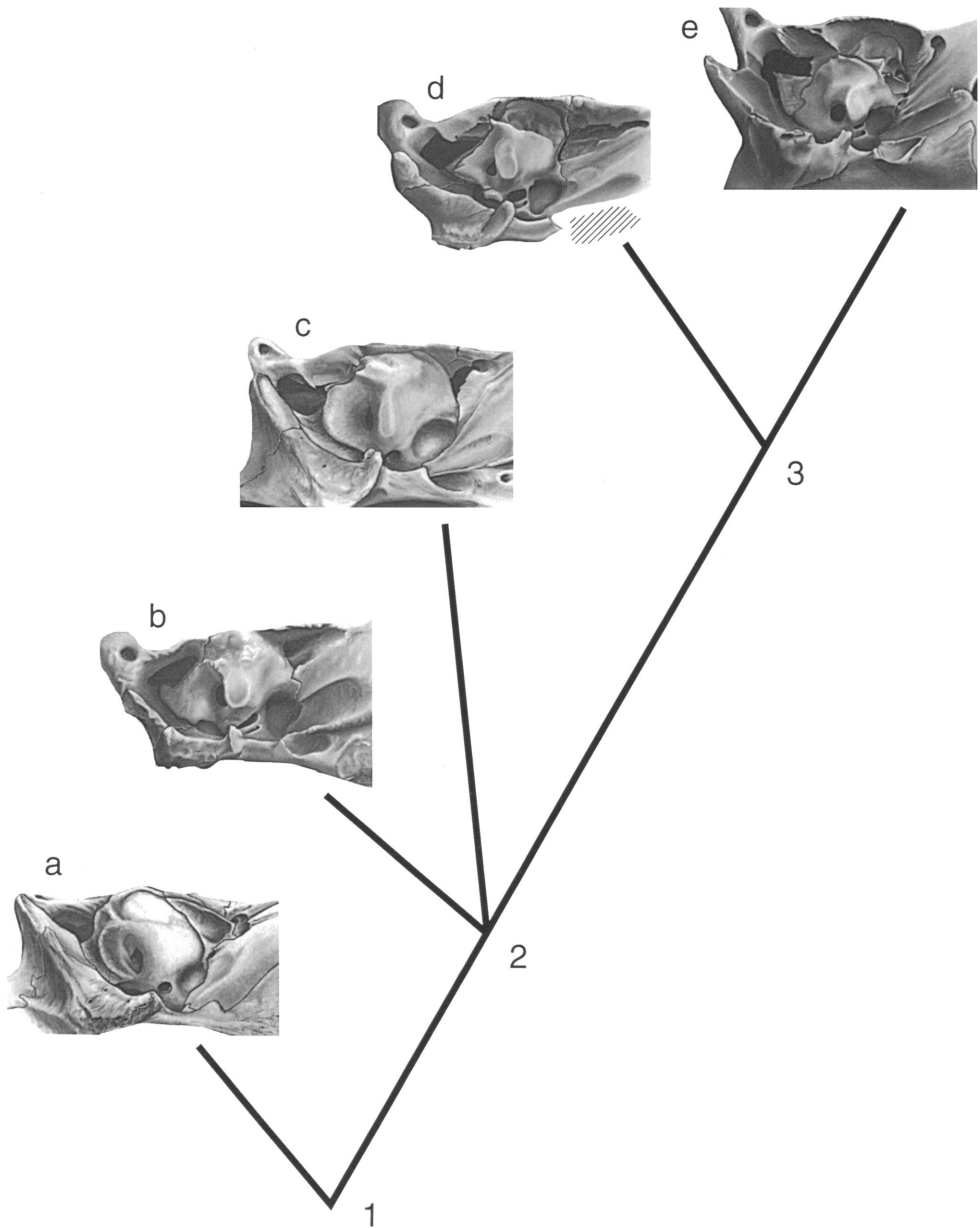


Fig. 33. Hypothetical relationships among plesiomorphic aeluroid carnivorans employing basicranial and auditory anatomy: **Node 1**, robust blocky petrosal with ventral promontorial process buttressing the lateral margin of basioccipital; discrete ectotympanic, rostral, and caudal entotympanic bulla elements inferred. **Node 2**, elliptical facet developed on lateral face of promontorium anterior to round window; slight expansion or widening of the bony ectotympanic (initiation of an ectotympanic capsule); development of a modest petrosal apron. **Node 3**, development of a bladelike flange or process on the medial margin of the promontorium inset in the edge of the basioccipital; initiation of an anterior migration of the inflated caudal entotympanic into the anterointernal corner of the auditory region; additional inflation of the ectotympanic to form a more expanded anterior chamber of the bulla (this exceeds the degree of inflation found in *Nandinia* and *Palaeoprionodon*). Autapomorphies of **(a)** *Nandinia*: none in auditory region. Autapomorphies of **(b)** *Palaeoprionodon*: widened zone along medial margin of promontorium for attachment of entotympanic cartilage. Autapomorphies of **(c)** *Stenoplesictis*: ectotympanic forms

The basicranium of *Stenogale julieni* (fig. 31) from the Aquitanian of St.-Gérard is regarded in this study as representative of the genus, given the absence of Quercy basicrania of *Stenogale*. The marked similarity of mandibles of the genus from Quercy and St.-Gérard suggests these were carnivorans of similar body size and, presumably, cranial anatomy. In *S. julieni*, the petrosal and inferred bulla structure are more derived than in *Palaeoprionodon*, yet the *Stenogale* auditory region could have developed from the more conservative pattern of Quercy *Palaeoprionodon*.

A derived petrosal with a prominent vertical bony flange on the medial margin of the promontorium distinguishes *Stenogale julieni*. The bladelike flange of the petrosal is actually inset into the edge of the basioccipital, and this arrangement constitutes an autapomorphy of the species, and presumably of the other species in the genus (*S. gracilis*, *S. intermedia*). The *Stenogale* basicranium can be hypothesized as a plausible (even necessary) morphological antecedent to that of *Proailurus lemanensis* (fig. 32) from St.-Gérard, a resemblance noted earlier by Lavocat (1952).

As in the case of *Stenogale*, mandibles of *Proailurus lemanensis* from Quercy and the Aquitanian sites of St.-Gérard are nearly indistinguishable, suggesting the basicranial pattern of Quercy and St.-Gérard *Proailurus* is probably similar. *Proailurus lemanensis*, like *Stenogale*, also has a distinctive petrosal in which a medial flange of the promontorium is present, but the flange is depressed dorsad by a migrating caudal entotympanic. The derived features of the auditory region of *Proailurus* identify a Neogene felid clade.

The cladogram of figure 33 rests on an inferred transformation of the petrosal promontorium's ventral process: in the plesiomorphic state the process is robust, vertical, and applied directly to the basioccipital (*Nandinia*, *Palaeo-*

prionodon, *Stenoplesictis*)—a thin bladelike flange is not developed. In the intermediate state a thin vertically oriented bony flange becomes separated from the process and is inset into the basioccipital margin (*Stenogale*). In the most derived state this vertical flange is overgrown and depressed dorsad by an enlarging caudal entotympanic (*Proailurus*).

Stenogale julieni is considered in this study as the sister taxon to *Proailurus*, based on interpretation of the flangelike medial process of the petrosal promontorium as a shared derived trait of the two St.-Gérard aeluroids. The subfamily Proailurinae could be restricted to *Proailurus* and its descendants, or it could be employed for all taxa above node 3 in figure 33 (*Stenogale*, *Proailurus*, and descendant species). In the former case, the defining derived trait would be the dorsally depressed petrosal flange of *Proailurus lemanensis* (and the correlated anterior expansion of the caudal entotympanic); in the latter, the synapomorphy would be the development of a vertical bladelike medial flange of the promontorium as in *Stenogale julieni*, which then becomes reoriented (depressed dorsad) by the enlarging caudal entotympanic in *Proailurus*.

The use of a subfamily Stenoplesictinae for *Palaeoprionodon* and *Stenoplesictis* seems no longer valid since such a paraphyletic category would serve no useful purpose. A plausible scenario based on figure 33 might regard *Stenoplesictis* as an early side-branch developing from the plesiomorphic *Palaeoprionodon* basicranial pattern.

The absence of crania from Hsanda-Gol or elsewhere in Asia prevents comparison with the Quercy/St.-Gérard aeluroids. However, the pronounced dental similarities shared among these Mongolian and European species suggest such skulls when discovered probably will exhibit an aeluroid basicranial

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anterior chamber of the bulla without participation of the caudal entotympanic; expanded medial wall of ectotympanic rests against lateral flanged margin of basioccipital; posterior extension of the petrosal apron; slight inflation of the caudal entotympanic without anterior penetration or expansion. Autapomorphy of (d) *Stenogale*: development of a vertically oriented medial flange of the promontorium. Autapomorphies of (e) *Proailurus*: medial flange of the promontorium depressed dorsad by expanding caudal entotympanic element; prominent inflation of the posterior (caudal entotympanic) chamber of the bulla, accompanied by migration into the anteromedial corner of the auditory region.

pattern. Despite the antiquity of the Quercy crania, none are as plesiomorphic in their auditory anatomy as the living palm civet *Nandinia binotata*. Therefore an even more primitive aeluroid basicranial pattern must have existed in the late Eocene or earliest Oligocene from which these early Eurasian aeluroids and *Nandinia* were derived.

Basicranial evidence indicates that the aeluroid Carnivora are a monophyletic group, stemming from small Eurasian carnivorans displaying the aeluroid morphotypic basicranial structure (Hunt, 1996: fig. 15.10; Hunt and Tedford, 1993: fig. 5.7). All modern aeluroids share distinctive synapomorphies of the auditory region that indicate derivation from this ancient aeluroid stock. The viverrid and felid basicranial patterns are recognizable in the Quercy and Aquitanian fossils, and the ancestors of these families lie within or in phylogenetic proximity to the fossils of *Palaeoprionodon* (Viverridae) and *Stenogale/Proailurus* (Felidae). The distinctive basicranial structure of the Herpestidae is not recognizable in these Oligocene species, yet the aeluroid traits of the herpestid basicranium leave no doubt that mongooses are closely related to these other aeluroids. Hyaenids can be traced to mid-Miocene fossils that show the hyaenid auditory pattern but, as with herpestids, the ancestral stage is not clearly indicated at Quercy or at the St.-Gérard or other European localities of equivalent age. Of interest is that the bulla of *Stenoplesictis* shows a pattern that might be expected in an ancestral hyaenid. The enlarged ectotympanic chamber that excludes the caudal entotym-

panic from participation in the anterior chamber of the bulla, and the small caudal entotympanic (posterior) chamber are plausible anatomical correlates of the hyaenid bulla. This possibility lacks confirmation because of the temporal hiatus between the earliest hyaenid basicrania of mid-Miocene age and the Quercy *Stenoplesictis*. Crania of early Miocene hyaenids, at present unknown, are necessary to resolve this issue.

Among all living aeluroids, felids lack a typical ventral process of the petrosal promontorium. However, a ventral process is present in the early felid *Proailurus lemanensis*. Thus, at some time in the Neogene, the ancestor of living felids must reorient or lose this petrosal process. Dissection of the oldest New World felid from the latest early Miocene of Nebraska revealed an archaic petrosal similar to the European *Proailurus*, but in an even more plesiomorphic state. In *Proailurus lemanensis* this process has been modified in form, overgrown and depressed dorsad, by encroachment of an enlarging caudal entotympanic element. This anatomical condition differs from the form of the petrosal in the oldest North American felid (Ginn Quarry), in which the ventral petrosal process remains in a more plesiomorphic vertical orientation than seen in *Proailurus*. Hence, the North American Ginn Quarry felid must be derived from an aeluroid with a more plesiomorphic petrosal anatomy than found in European *Proailurus*. An ancestral felid must exist in the early Miocene of Holarctica with a petrosal form and bulla structure more plesiomorphic than that of *Proailurus lemanensis* from St.-Gérard.

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