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## Felid Phylogenetics: Extant Taxa and Skull Morphology (Felidae, Aeluroidea)

LEANDRO O. SALLES<sup>1</sup>

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<sup>1</sup> Graduate Student, Department of Mammalogy, American Museum of Natural History, and City University of New York, The City College. Present address: Muséum National d'Histoire Naturelle, Paleontologie, CNRS 12, 8 rue Buffon, 75005 Paris.

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## ABSTRACT

Relationships among extant felid taxa are controversial. A historical appraisal addresses component congruence among statements on felid phylogenetic relationships, and monophyly of generic ranks proposed for felids is discussed.

Felid cranial morphology (especially the masticatory apparatus, basicranium, and rostral regions) is examined, and 44 characters are postulated for 39 taxa. Internal congruence for these characters is evaluated and 27 components are suggested. Parsimony analysis, using the successive weighting option of Hennig86, of the 44 cranial characters plus 13 other morphological features yields 29 components in a "modified Nelson" consensus cladogram.

Two basal, well resolved clades are hypothesized in the total morphology analysis; under par-

enthetical notation the first is: (*Hepailurus yagouaroundi* (*Puma concolor* (*Acinonyx jubatus* (*Uncia uncia* (*Neofelis nebulosa* (*Panthera tigris* (*P. onca*, *P. leo*, and *P. pardus*)))))). The second clade is: (*Profelis temmincki* (*P. badia* (*Pardofelis marmorata* ((*Caracal caracal* (*Lynx rufus* (*L. lynx* (*L. pardina* (*L. canadensis*)))) (*Felis chaus* (*F. lybica* (*L. cafra* (*L. silvestris* (*F. bieti* (*F. nigripes* (*F. margarita* (*Otocolobus manul*)))))))))). *Prionailurus planiceps* and *P. viverrina* formed another group which is suggested as the basal branch of the felid phylogeny.

The results of this study do not support monophyly of *Leopardus* Gray, 1841; *Profelis* Severtzon, 1858; and *Prionailurus* Severtzon, 1858. A better supported, more highly resolved, felid phylogenetic tree is needed.

## INTRODUCTION

For the last two centuries various zoologists and paleontologists have focused attention on the Felidae. Despite this, generic relationships among extant felids have remained controversial. One cause of con-

trovery is the abundance of errors in evaluating character distributions (levels of generality across taxa). Often characters were proposed based on a partial examination of this family, focused in a particular faunal region. Most empirical evidence regarding the morphology of extant felids was revealed by the English zoologist, R. I. Pocock. His publications date from the beginning of this century to the 1950s. In 1978, Hemmer attempted a synthesis. That study represents an important literature review, but no directed and detailed character analysis was performed. A second review of extant felid relationships (after that of Pocock, 1917b) was performed by Herrington (1986) in an unpublished Ph.D. dissertation. In view of the lack of general concordance between Herrington's statements of homology and those advocated here, a reappraisal of extant felid phylogenetics is appropriate.

Absence of phylogenetic resolution within the Aeluroidea (Flynn et al., 1988) is shown in figure 1. The felid outgroup node is represented by a polytomy in which three other aeluroid taxa, the Herpestidae, Hyaenidae,

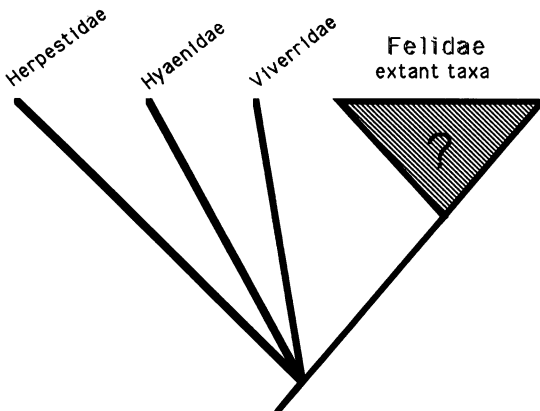


Fig. 1. Cladogram (Flynn et al., 1988), representing phylogenetic relationships within Aeluroidea, shows that the study of extant felid phylogenetics developed here suffered from the absence of outgroup resolution.

and Viverridae, are rooted. This lack of resolution is a main problem of the phylogenetic study developed here, directly affecting character polarizations. This problem is addressed under Methods.

The present study is a cladistic character survey of cranial morphology in extant felid. A morphological data matrix is constructed and analyzed. A number of components are proposed and evidence supporting these statements of relationship is discussed.

#### ACKNOWLEDGMENTS

As an undergraduate student in the early 80s at Universidade Federal do Rio de Janeiro and trainee of Museu Nacional, Rio de Janeiro, I became interested in taxonomy and geography of extant neotropical cats. Working as a visitor at the British Museum (Natural History) in 1986, I began the systematic part of this research. In 1987, as a graduate student of The City University of New York, City College and working at the Department of Mammalogy of the American Museum of Natural History (AMNH), I continued and expanded it.

I would like to express gratitude to my Brazilian colleagues who directly participated in the beginning of this study, especially João Alves de Oliveira. I also want to acknowledge encouragement received from Alfredo Langguth.

I am deeply indebted to my advisor, Sydney Anderson, for his support of my research in New York.

As a graduate student working at the AMNH, I was privileged to become acquainted with a number of researchers in systematics and evolution. I express special gratitude to Gareth Nelson for his dedication in bringing the beauty of the science of comparative biology to graduate students at the AMNH.

My systematic research on felids has benefited from fruitful discussions with graduate students at the AMNH, including Gregory Edgecombe and Mário de Pinna.

This work was courteously supported by the following individuals (and institutions) who allowed me to study felid collections in their care: G. Musser, American Museum of Natural History; I. Bishop and D. Hills, Brit-

ish Museum (Natural History); B. Patterson and W. Stanley, Field Museum of Natural History; G. Storch, Forschungsinstitut Senckenberg, Natur-Museum Senckenberg, Frankfurt; H. Kuhn, Georg-August-Universität; U. Caramaschi, Museu Nacional; M. Tranier, Museum National D'Histoire Naturelle; C. Handley and L. Gordon, National Museum of Natural History, Smithsonian Institution; L. Werdelin, Swedish Museum of Natural History. Special gratitude goes to the personnel of the Department of Mammalogy, AMNH.

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This manuscript has been greatly improved by critical readings of Sydney Anderson, Gareth Nelson, Michael Novacek, Gregory Edgecombe, Mário de Pinna, Lars Werdelin, Andre Wyss, John Flynn, and Nancy Simmons. Credits for photographs go to Andrew Modell and Peling Fong.

Finally, I thank friends who not only tolerated my every day preoccupation with cats but also helped me in various ways.

#### MATERIAL EXAMINED

This study is restricted to skull morphology of extant felids, and focuses on teeth, rostrum, and auditory region. Most of this work is based on the collection of the Department of Mammalogy of the American Museum of Natural History (AMNH), New York. Specimens listed below under AMNH are those most carefully studied. (Nearly every felid skull in this collection was at least superficially examined.) Other collections visited and from which loans were received are: British Museum (Natural History) (BMNH), London; Field Museum of Natural History (FMNH), Chicago; Forschungsinstitut Senckenberg, Natur-Museum Senckenberg (NMS), Frankfurt; Georg-August-Universität (UG), Göttingen; Museu Nacional (MNRJ), Rio de Janeiro; Museum National D'Histoire Naturelle (MNHN), Paris; National Museum of Natural History, Smithsonian Institution (USNM), Washington; Swedish Museum of Natural History

(SMNH), Stockholm. A photograph from a specimen of *Leopardus jacobita* of the Museum of Vertebrate Zoology, Berkeley (MVZ) is also used here.

Terminal taxa, species, and generic names are mostly based on the works of Pocock (1917b), Hemmer (1978), and Herrington (1986). Usage of generic names here does not necessarily imply their monophyly (choice of ranks used is largely arbitrary); in fact, cases of generic paraphyly are here detected in the current classification. Unavailability of specimens of *Mayailurus iriomotensis* prevented its inclusion in this study. The 415 specimens (of extant felid taxa) examined are:

*Leopardus pardalis*: AMNH 214743, 24855, 98608, 96175, 128130, 248728, 148992, 18947, 71264, 24652, 14858, 92835, 41226, 70333; FMNH 10940, 14177, 14175, 25351, 41220.

*Leopardus wiedii*: AMNH 80351, 64113, 141989, 172714, 133961, 123385; FMNH 92213, 94321; NMS 33 267.

*Leopardus tigrina*: AMNH 69166, 139224, 93323, 143896; FMNH 70571, 70570.

*Leopardus geoffroyi*: AMNH 205907, 205909, 205910, 205911, 41553, 41551, 94331; FMNH 24360.

*Leopardus guigna*: AMNH 33280, 33283, 33285, 33286, 33288; FMNH 24359, 24357; USNM 391855; BMNH 1905.2.4.1, 1903.7.9.1.

*Leopardus colocolo*: AMNH 243110, 133976; FMNH 52488, 68318, 28335, 24358; BMNH 1927.11.1.6.7, 1901.11.18.1; NMS 15 726; MNRJ 24904.

*Leopardus jacobita*: UG 2337, photograph of MVZ 116317.

*Profelis aurata*: AMNH 51994, 51998, 54332, 51996; FMNH 99025; BMNH 25.10.7.13.

*Profelis temmincki*: AMNH 84393, 84396, 17103, 84395, 13709; FMNH 75826, 31778; BMNH 22.12.22.1, 50.515, 79.11.21.631.

*Profelis badia*: FMNH 8378; USNM 198073; BMNH 95.5.7.3, 88.8.13.1.

*Prionailurus bengalensis*: AMNH 102880, 3833, 102183, 57066, 57119, 47870, 84397, 84000, 87352, 58372, 107131, 60053, 60093, 90339, 107132, 27598, 38334, 59960, 87357, 59931, 59957, 26601, 90338; FMNH 32549, 39340, 35669, 35670.

*Prionailurus viverrina*: AMNH 70128, 102691, 102084, 106323, 101627, 11093; FMNH 105561, 105562, 99533; USNM 395757, 253538; BMNH 46.221, 43.1.12.120.

*Prionailurus planiceps*: AMNH 173515, 35398; FMNH 58951, 60476; USNM 49973, 196607,

145594, 14419, 48942; BMNH 79.11.21.627, 8.7.17.11, 5.3.1.7, 46.8.3.8.

*Prionailurus rubiginosa*: FMNH 96335, 95037, 96333, 96334; BMNH 34.4.17.2, 20.2.8.5, 75.2.11.2, 1937.3.24.20.

*Felis lybica*: AMNH 180102, 180104, 180103, 55852, 116513, 116520, 169457, 55043, 185174, 83634, 116519, 51059, 55854, 51954, 51961, 51956, 207508, 89007, 89820, 51061, 51955; FMNH 123383, 101877, 105529, 107295, 107296.

*Felis cafra*: AMNH 42042, 80893.

*Felis silvestris*: AMNH 160967, 80212, 169493, 41338, 169494.

*Felis nigripes*: AMNH 214380, 214381, 146838; USNM 381275, 395135, 395519; BMNH 39.679, 2.12.1.5; NMS 50 170.

*Felis chaus*: AMNH 54759, 184683, 54553; FMNH 97866, 97864, 105560, 103997.

*Felis margarita*: FMNH 107299, 60613, 60169; USNM 396080; BMNH 59.634; NMS 55 529, 47 691, 44 749, 55 532, 55 525, 55 526; MNHN 1962 2919.

*Felis bieti*: SMNH A585295, A595165.

*Caracal caracal*: AMNH 24220, 116512, 83764; FMNH 32945, 105607; USNM 182310; BMNH 2.9.1.20.

*Otocolobus manul*: AMNH 185371, 180268; FMNH 135319, 60611, 121278; BMNH 79.11.21.540, 5.4.5.1; NMS 44816; MNHN 1895 524.

*Herpailurus yagouaroundi*: AMNH 126978, 173911, 147577, 150010, 98602, 98649, 145961, 24250, 17457, 2691/3418, 64111; FMNH 88479, 51865, 79924.

*Puma concolor*: AMNH 24686, 24688, 1338, 6295, 11062, 164117, 11067, 78554; FMNH 16024, 51862.

*Acinonyx jubatus*: AMNH 35998, 36426, 80125, 80618, 80619, 80866; FMNH 29634, 29635, 1453.

*Leptailurus serval*: AMNH 11873, 167487, 51983, 36009, 27837, 85166, 81673, 79135, 205151, 51980, 51981, 51973, 51972, 51971, 51066; FMNH 27164, 27165, 95093.

*Lynx rufus*: AMNH 245534, 8304, 135163, 254478, 254480, 147441, 255672, 146633, 22804, 1348, 208423, 138409, 208421, 1351/2507, 138409, 208421; FMNH 48866, 84432, 72834, 51644.

*Lynx canadensis*: AMNH 29045, 239797, 147754, 239787, 239760; FMNH 43111.

*Lynx lynx*: AMNH 41337, 69502, 196; FMNH 51820; USNM 0850; BMNH 98.8.5.1, 2.3.9.1; NMS 16 252.

*Lynx pardina*: AMNH 169432; USNM 152619, 152618; BMNH 95.9.4.1, 8.3.8.2.

*Neofelis nebulosa*: AMNH 35808, 22916, 35273,



- 35113, 27620; FMNH 42583, 75830, 75831; NMS 19527; MNHN 1985, 2017.
- Pardofelis marmorata*: AMNH 102844, 106615; FMNH 68728, 104901; USNM 239326, 325000; BMNH 55.1645, 61.1277, 99.12.9.13.
- Uncia uncia*: AMNH 35529, 207704; FMNH 41604, 122235; BMNH 33.7.20.2, 46.712.
- Panthera tigris*: AMNH 54845, 119632, 54605, 119633, 90298, 87349, 113743, 117420, 6254, 6255, 6256, 1253, 135954, 90298, 85404, 85405, 87349, 113744, 119632, 119633, 54605, 54460, 54845.
- Panthera onca*: AMNH 38126, 2306, 64, 25010, 11083, 37504, 22915, 22919, 3812, 100111, 2306, 110, 133963, 11083, 147512.
- Panthera leo*: AMNH 83623, 60, 35088, 35087, 35122, 35276, 81838, 83618, 13904, 83622, 83625, 81842, 52076, 14027, 16875, 14028, 35276, 35122, 35087, 35088, 21516, 22706, 36241.
- Panthera pardus*: AMNH 43091, 87350, 52016, 52023, 52035, 57009, 70553, 52029, 81303, 52034, 52028, 52001, 52021, 52045, 81302.

#### ABBREVIATIONS

##### *Masticatory Apparatus*

ad	anterior dentary
fs	fossa angular
dP <sup>4</sup>	upper fourth deciduous premolar
dP <sup>3</sup>	upper third deciduous premolar
dP <sup>2</sup>	upper second deciduous premolar
dP <sub>3</sub>	lower third deciduous premolar
dC	upper deciduous canine
dc	lower deciduous canine
C	upper canine
c	lower canine
M <sub>1</sub>	lower first molar
P <sup>4</sup>	upper fourth premolar
P <sub>4</sub>	lower fourth premolar
P <sup>3</sup>	upper third premolar
P <sup>2</sup>	upper second premolar
la	lateral accessory cusp
lr	labial ridge
clc	lower canine labial cavity
Clr	upper canine labial ridge
pr	protocone
ps	parastyle cusp
sps	secondary parastyle cusp
ms	metastyle cusp
pa	paracone
pc	paraconid crest
po	protoconid
pi	paraconid
fpa	first posterior accessory cusp
spa	second posterior accessory cusp
psr	parastyle root
msr	metastyle root

##### *Basicranial*

p	palatine
sq	squamosal
zp	zygomatic process of the squamosal
gc	glenoid cavity
pg	postglenoid process
oc	occipital
occ	occipital condyles
epf	external pterygoid fossa
fr	foramen rotundum

##### *Auditory Region*

mt	processus mastoid (of petrosal)
et	entotympanic (rostral and caudal)
ect	ectotympanic
pct	posterior crus ectotympanic
eam	external auditory meatus
gfs	groove for stylomastoid foramen
fs	stylomastoid foramen
ml	malleus
pm	processus muscularis
pb	processus brevis
i	incus
ihm	incus inferior head with malleus
pt	petrosal
tr	tympanic roof
iam	internal auditory meatus
ms	marginal surface (of the iam)
lor	longitudinal ridge
sf	subarcuate fossa

##### *Rostrum*

m	maxilla
pm	premaxilla
n	nasal
l	lacrimal
j	jugal
lro	lower rim of the orbit
pp	postorbital process
jap	jugal anterior process
rc	rostral constriction
if	infraorbital foramen
fnd	frontonasal depression
f	frontal
fd	frontal depression

##### *Frontal Sinus*

fs	frontal sinus
asc	anterodorsal frontal sinus cavity
fe	first caudal ethmoturbinate scroll
pfe	posterior wall of the first caudal ethmoturbinate scroll

Museum abbreviations are under Materials Examined (p. 3–4) and taxonomic abbreviations are in Appendix 1 (p. 64).

## METHODS

Statements of topographical correspondence (Rieppel, 1988) of the felid cranial morphology were proposed on the basis of qualitative observations, and assisted by a few measurements. Internal cranial morphology was assessed by examination of cut (and broken) skulls as well as by the use of x-rays. Postulated homologies (synapomorphies) were tested by internal overall congruence among statements of topographical sameness. The Hennig86 (version 1.5) computer program (Farris, 1988) was used to perform analysis of strict (or simple) parsimony. The combination of two branch-swapping algorithms, namely *mhennig\** and *bb\**, was used for all analyses of parsimony. Procedures for the parsimony analysis are detailed under "Cranial Osteology, Internal Congruence" and "Phylogenetic Relationships of Felidae." Consistency indices were calculated with all the autapomorphies present in the data matrix (table 1). Identity of extant felid species is still a primary matter of felid phylogenetics. In order to maximize component information, two modified Nelson consensus trees, analogous to "general cladograms" of Nelson (1979), were put forward. The two modified Nelson consensus trees are further discussed under the two sections mentioned above.

Most proposed character states were based on degree of development of a given trait, or they seemed to be part of a continuum where the plesiomorphic state is one extreme. It is assumed here that similarity (among states) alone satisfies the criterion for hypothesizing the order of a transformation series. For a few characters this assumption is considered inapplicable, and the characters were left unordered; these cases are discussed later.

Outgroup comparison (Maddison et al., 1984) and ontogenetic criteria (Nelson, 1978, 1985) were applied in character polarizations. Based on dentition eruption and wear as well as degree of ossification of cranial sutures (primarily basisphenoid and presphenoid sutures) four ontogenetic stages are considered—infant, juvenile, subadult, and adult. These stages were used as references for direction of ontogenetic change.

Characters polymorphic for the presence

of the derived state, unless the sample has an extremely low percentage of individuals with the derived state, are considered nonproblematic. Absence of a trait in some individuals of a population (or taxon) does not have any effect on the fact that this population displays the trait. Therefore, such cases are considered here as having the derived state. The justification for this view is that if each individual has an ontogeny each individual's parts are necessarily polymorphic with respect to the presence of any given state. An interesting case involves sexual dimorphism as a source of polymorphism of the derived state. Females of *Panthera* have the frontal sinus cavity placed in the position derived for felids, that is, the cavity is centralized in the region of the postorbital processes (see character 27 in "Character Topographical Correspondence and Polarization" section for further details), whereas males display the plesiomorphic state. Weitzman and Fink (1985) interpreted sexual maturation as just another case of ontogenetic transformation, in dealing with cases of sexual dimorphism evolving the presence of derived state in Characidae. This position is in total agreement with that argued here. The *Panthera* example has the peculiarity also of involving neoteny.

As mentioned in the introduction, one of the problems of polarizing characters in felids is the lack of phylogenetic resolution within Aeluroidea. This has specifically affected polarity assessment for characters numbered 2, 9, and 25. These are three cases of a single problem. In all three, both plesiomorphic and derived states are present within one of the three outgroup families, and no internal resolution in any of the three families is considered (or indeed available in the literature). Assuming this problem, the worst possible scenario for character polarity within the clade Felidae would be: (1) if the basal node of the outgroup family in question is unambiguous for the presence of the "derived state"; and (2) if this family is assumed to be the sister taxon of Felidae. However, even if these two situations are hypothesized, the state at the felid outgroup node would only be ambiguous (see Maddison et al., 1984: 87, fig. 4 for a better understanding of the problem in question). This kind of polarization problem

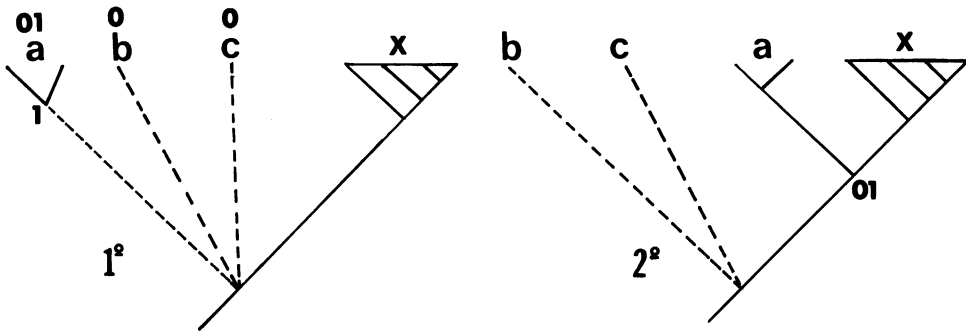


Fig. 2. Considering the topology of the tree in figure 1, for a given character that is polymorphic for the presence of the derived state in one (e.g., **a**) and only one of the outgroup taxa, **a**, **b**, and **c** (representing in any order Herpestidae, Hyaenidae, and Viverridae)—two assumptions are necessary for the **x** (exemplifying felids) outgroup node to become ambiguous: (1) the selected taxon **a** has its basal node unequivocal for the presence of the derived character state; and (2) this same taxon **a** is taken as the sister group of **x**. Hence, even considering the two assumptions, this case of character polarization would not meet the requirements to definitively place state 1 at the **x** outgroup node.

can also be provisionally solved by the criteria of relative abundance of character states suggested by Farris (1969), in which the plesiomorphic state, being more general in the outgroup, is likely to be more abundant; see schemes on figure 2 for further details.

In the text, *component* is used interchangeably with *clade*, according to the notion developed by Nelson and Platnick (1981). The word *tendency* is restrictively applied here in cases where a potential trace of the character is noted but no decisive evidence for the presence is observed.

#### CHARACTER TOPOGRAPHICAL CORRESPONDENCE AND POLARIZATION

Three regions of the felid skull are analyzed here, the masticatory apparatus (teeth and jaws), the basicranium (auditory region), and the facial region (including rostrum and frontal sinus). In this character analysis, topographical correspondence among bony structures is used as primary evidence of homology. Polarization based on outgroup or ontogeny or both criteria proceeded as a second step of analysis.

Only in the sections following the character analysis are congruence tests performed (as a result of a parsimony analysis) in order to support statements of monophyly defined by synapomorphies (Hennig, 1966; Patterson, 1982; Rieppel, 1988; de Pinna, 1991).

General cranial terminology follows Jayne (1898), Field and Taylor (1950), Novacek (1986), and specific regional terminology is referred to in each subsection below.

#### MASTICATORY APPARATUS

The masticatory apparatus of felids (and specifically the dentition and shape of the dentary) is highly specialized for vertebrate prey-killing and meat-shearing functions. Carnassial teeth are present in adults ( $P^4/M_1$ ) and also in juveniles ( $dP^3/dP_4$ ). The masticatory complex is characterized by a reduction in number of teeth. Generally there are three premolars and one molar at each side of the upper and lower jaws. Presence and degree of development of the second premolar are extremely variable among felids; this tooth is not considered in this study. Hence, for example, its loss is not considered a diagnostic character for lynxes.

Dental terminology follows that of Gaunt (1959), Van Valen (1966), Szalay (1969), and Flynn and Galiano (1982). See terminology scheme in figure 3.

Areas of the dentary where polymorphism is noted include the fossa of the angular process, which varies in depth (fig. 4), and in the position of its internal wall in relation to the inferior angular surface. The relevance of this specific case of polymorphism is that some species or even groups of species such as *Lynx* develop this fossa in late ontogenetic stages.

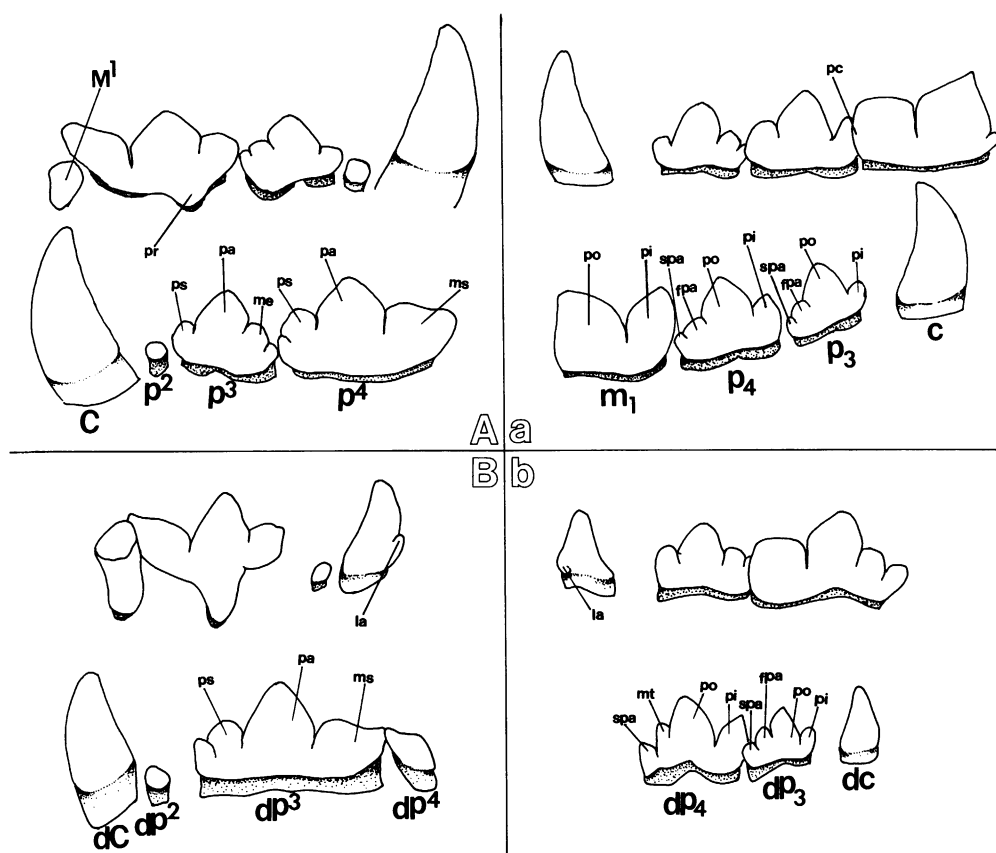


Fig. 3. A, upper permanent teeth; a, lower permanent teeth; B, upper deciduous teeth; b, lower deciduous teeth (see abbreviations on p. 5).

This situation in *Lynx* may easily be misinterpreted as a case of pedomorphosis, because the fossa is clearly plesiomorphic for cats. The coronoid process may also become relevant in terms of phylogenetic information, e.g., *Felis margarita* presents a distinctively elongate coronoid process, a condition that is shared by other members of the *Felis* clade. Better understanding of intraspecific variation is needed for formalization of such characters in this region. In general, further comparative anatomical work on the masticatory apparatus is required, primarily for aeluroids.

A research program on comparative functional morphology of the dentary in the carnivore lower jaw (with emphasis on some

aeluroids) has been initiated by Biknevičius (unpublished Ph.D. dissertation, 1990).

Characters of the masticatory apparatus are described and designated below.

**1. Anterior part of dentary** (fig. 5): The morphology of this region was considered by Pocock (1917b) and Herrington (1986). *Neofelis nebulosa* displays a marked anterodorsal curvature of the anterior part of the dentary. As Pocock stated, *N. nebulosa* has a nearly vertical symphyseal region. This cat also exhibits conspicuous changes in upper and lower canines. These two related changes have drastically transformed the anterior dentary ramus region to a character unique to the clouded leopard. A change in the opposite direction took place in *Acinonyx jubatus*.

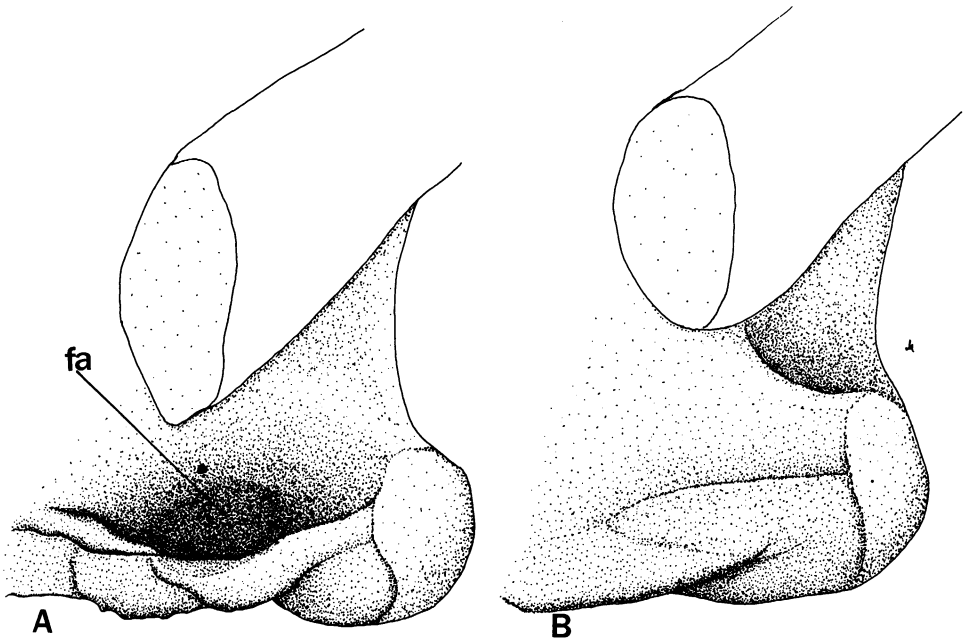


Fig. 4. Polymorphism for the degree of development of the fossa of the angular process: A, *Panthera onca* (AMNH 120998); B, *Panthera onca* (AMNH 147510). Lingual view, anterior to left.

Here, the anterior part of the dentary has nearly lost the upward curvature generally observed among felids, so that it stands almost at the same level of the middle portion

of the dentary. In order to formalize these character states in a cladistic analysis, I coded this character as nonadditive, the plesiomorphic state illustrated by the intermediate con-



Fig. 5. Anterior part of the dentary (character 1): state 2, *Neofelis nebulosa* (AMNH 35808); state 1, *Acinonyx jubatus* (AMNH 36426). Frontal view.

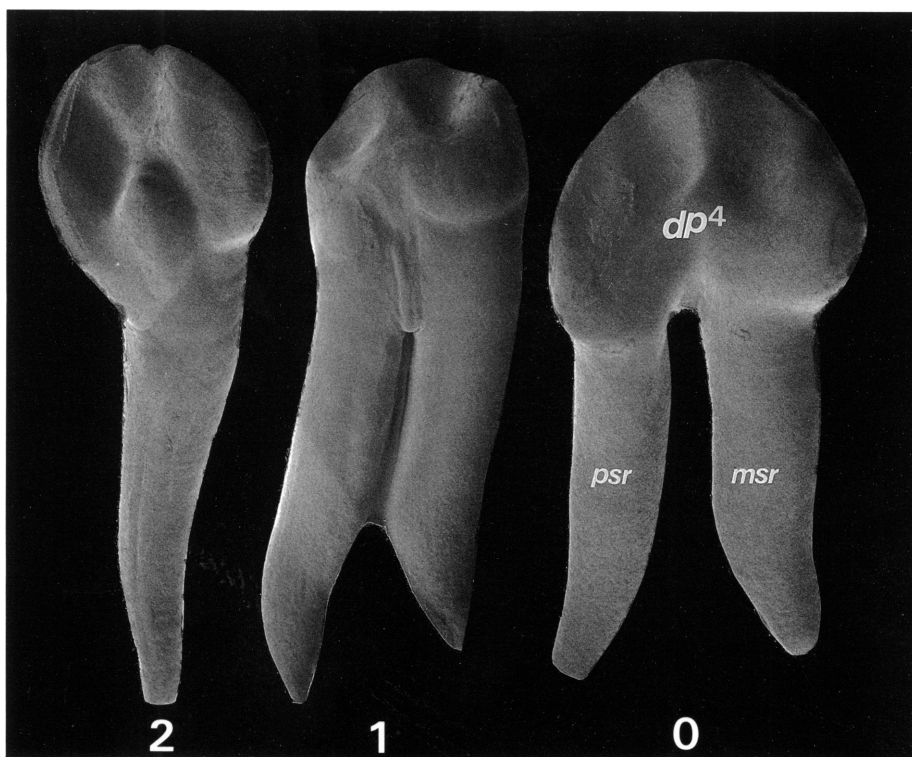


Fig. 6. Upper fourth deciduous premolar parastyle and metastyle roots (character 2): state 2, *Acinonyx jubatus* (AMNH 80618); state 1, *Panthera onca* (AMNH 37504); state 0, *Lynx rufus* (AMNH 1349). Labial view, anterior to left.

dition between the two unique states recorded for *N. nebulosa* (2) and *A. jubatus* (1) (see fig. 5).

### Teeth

The upper first molar, upper second premolar, and the incisors exhibited no clear pattern in my general search for detailed variation. It is still possible that further study of these teeth might yield phylogenetic information.

Deciduous teeth in felids and in most other mammals have not been used for systematic purposes. However, I have found them to be quite informative.

**2. Upper fourth deciduous premolar (dp<sup>4</sup>) parastyle and metastyle roots (fig. 6):** The crown of this tooth varies greatly in size and form. In contrast, the dp<sup>4</sup> para and metastyle roots exhibit three discrete character states (see fig. 6): bifurcate (0), partially fused (1),

and totally fused (2). These states were interpreted as additive. The bifurcate condition in all aeluroid outgroups (and at least in some Cynoidea) suggests that bifurcate is the plesiomorphic state. Nevertheless, a specimen of *Proteles cristatus* (AMNH 87697) was recorded as having these roots fused. This suggests ambiguity in hyaenas at the basal node, since a specimen of *Hyaena hyaena* (AMNH 187784) clearly has the roots bifurcate. Resolution at higher levels is needed for better assessment of polarity of this character. Until progress is made in aeluroid phylogenetics, polymorphism in hyaenas for this character does not rule out the possibility that the felid outgroup node might have been in state 1. However, the direction of state changes from 0 to 1 is here favored (see fig. 2 and text under Methods for discussion).

Future research should test if the basal node in the phylogeny of the Hyaenidae is unambiguous for this character, especially if

Hyaenidae turn out to be well supported as the sister taxon of Felidae, as Wozencraft (1989) advocated. Fused  $dP^4$  roots occur in *Acinonyx jubatus* (totally fused, state 2); *Puma concolor*, *Neofelis nebulosa*, *Panthera tigris*, *P. onca*, *P. leo*, *P. pardus* (all partially fused, state 1), and possibly *Uncia uncia* (coded as missing data). Other taxa for which I have no data for this character, and thereby also coded as missing data, are: *Profelis badia*, *Prionailurus viverrina*, *Felis cafra*, *F. silvestris*, *F. nigripes*, *F. bieti*, *Lynx pardina*, *L. canadensis*, *Leopardus jacobita*, and *L. colocolo*. An early juvenile specimen of *Leopardus tigrina* (AMNH 13924) has the roots apparently fused, but they are not clearly ossified and are very short. Under such conditions, I decided to code *L. tigrina* as missing data for this character, until new specimens become available for examination. A similar situation pertains to *Leopardus guigna*, where only one very young specimen was available (AMNH 33280). In this case if the roots are in fact partially fused, they at least have their inferior portion bifurcate. *Leopardus guigna* was considered to lack data also. A study of the early ontogeny of the roots can clarify this, testing if these roots are either bifurcate at their appearance or at some later stage of growth. In two adult specimens of *L. geoffroyi* (AMNH 41551 and AMNH 9433) roots are parallel and very close together, and they are here coded as missing data. Despite the uncertainty in determining this feature for some species of the supposedly monophyletic group *Leopardus* (Herrington, 1986), both *Leopardus pardalis* (AMNH 14858, 24642, 98608, 18947) and *L. wiedii* (AMNH 123395) are clearly plesiomorphic for this character.

**3. Upper third deciduous premolar ( $dP^3$ ), secondary parastyle cusp (fig. 7):** The crown of  $dP^3$  is generally uniform among Felidae. The parastyle cusp, seen from an occlusal view, commonly has a slight anterior projection, often presenting a shape more pointed than that of the secondary parastyle cusp. The parastyle cusp also varies in size in relation to the secondary parastyle cusp, being larger in some species and smaller in others. A  $dP^3$  secondary parastyle cusp was found in all aeluroid material examined. The only exception is *Nandinia binotata* (AMNH 167495 and 201413), which has neither the parastyle

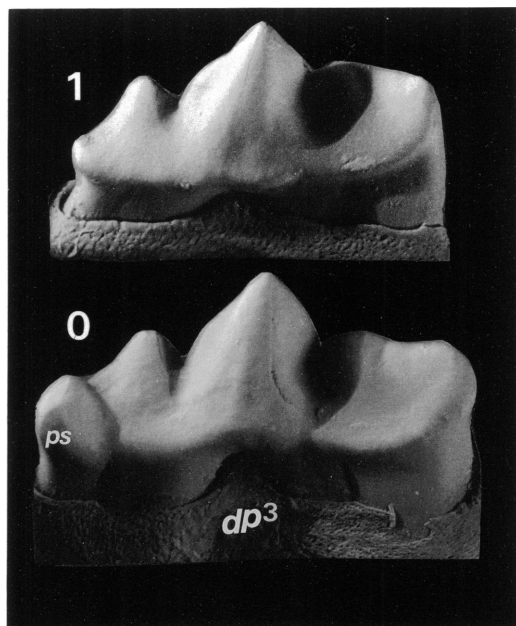


Fig. 7. Upper third deciduous premolar, secondary parastyle cusp (character 3): state 1, *Herpailurus yagouaroundi* (AMNH 150010); state 0, *Leopardus pardalis* (AMNH 71364). Lingual view, anterior to left.

nor the secondary parastyle cusp developed. The phylogenetic position of *Nandinia* is subject to an ongoing debate (Flynn et al., 1988), but no relationship postulated to date can affect this character polarization. Therefore the felid outgroup node was considered decisive for the presence of a well-developed  $dP^3$  secondary parastyle cusp. This position will not change if *Nandinia* is assumed to be the sister group of the rest of aeluroids (Hunt, 1987, 1989) or if *Nandinia* is considered a viverrid (Wozencraft, 1984), even if viverrids were to be accepted as the sister taxon of Felidae.

A parallel case of reduction of the secondary parastyle cusp (as noted for *Nandinia*, but not of the secondary parastyle cusp) occurs in the felid, *Herpailurus yagouaroundi* (see fig. 7). This feature was interpreted as an autapomorphy for the *yagouaroundi* cat. Among six juvenile specimens of *Puma concolor*, only one zoo specimen (AMNH 6295) has the same parastyle reduction. Therefore, until new data are available, the puma is considered to have missing data for this character. Other species

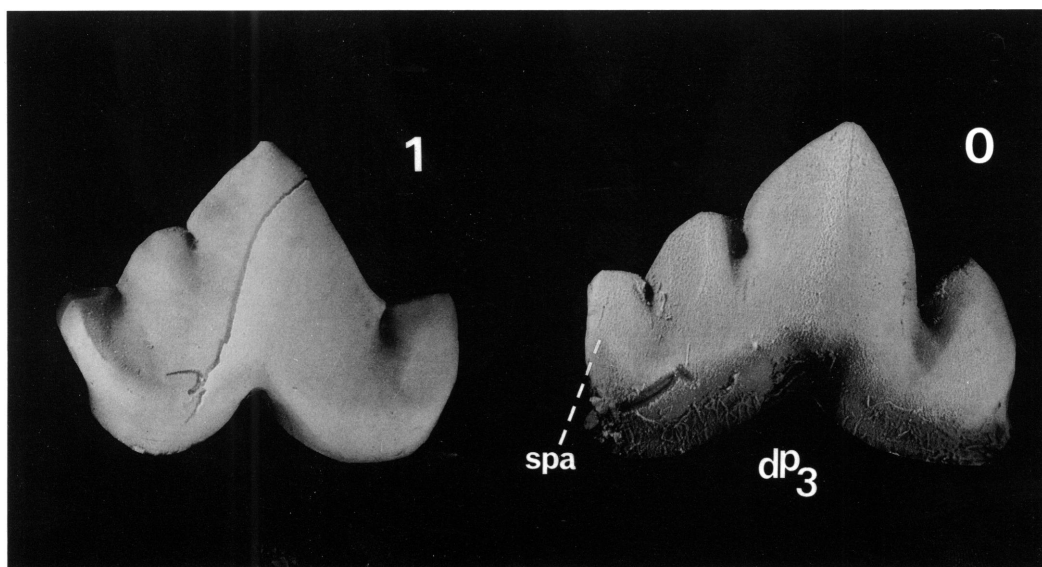


Fig. 8. Lower third deciduous premolar, second posterior accessory cusp (character 4): state 1, *Panthera pardus* (AMNH 81303); state 0, *Leopardus pardalis* (AMNH 71364). Labial view, anterior to right.

with missing data are *Felis bieti*, *Leopardus jacobita*, *Profelis badia*, *Lynx pardina*, and *Uncia uncia*. In the present analysis, the reduction of the secondary parastyle cusp is the only potentially unique feature that supports *H. yagouaroundi* as the sister group of *P. concolor*, a relationship advocated by a number of authors (Sonntag, 1923; Hemmer, 1978; Herrington, 1986). For further comments see Cranial Osteology, Internal Congruence and Historical Considerations.

**4. Lower third deciduous premolar ( $dp_3$ ), second posterior accessory cusp** (fig. 8): The paraconid, protoconid, and posterior accessory cusp of this tooth vary in size, form, and degree of development. The degree of development of the labial second posterior accessory cusp is also of interest. There is a distinct and characteristic pattern in the development of this cusp within Felidae. The most widespread pattern (state 0) of the posterior accessory cusp (observed from labial view) is a prominent cone, which is more or less uniformly cylindrical in shape, and generally pointed dorsally. In a second pattern (state 1), the accessory cusp is a reduced cone with a lateral quasi-flat surface (markedly projecting laterally), sometimes perpendicular to the external plane formed by the first pos-

terior accessory cusp (fig. 8). This determined derived  $dp_3$  pattern has been recorded in *Neofelis nebulosa*, *Panthera tigris*, *Panthera onca*, *Panthera leo*, and *Panthera pardus* (the latter species best illustrates this condition). The other character state is widespread among other Felidae, and is also present in other aeluroids. A specimen of *Cryptoprocta ferox* (AMNH 23090) among the outgroups examined best demonstrates the condition considered here the primitive state for felids. Some species are difficult to assign a character state because of reduction of the second posterior accessory cusp. Some specimens of *P. pardus* (AMNH 52001 and 52028), in which  $dp_3$  is not fully erupted, and thus with the posterior accessory cusps still in the mandibular cavity, unquestionably have the above-described second posterior accessory pattern (state 1). Thus, wear cannot explain it. Data on this character were not available for *Leopardus jacobita*, *Profelis badia*, *Felis cafra*, *F. silvestris*, *F. bieti*, *Lynx canadensis*, *L. pardina*, and *Uncia uncia*.

**5. Lower deciduous canine (dc), lateral accessory cusp** (fig. 9): This lateral accessory cusp, placed close to the anterointernal edge of the canine just above the third inferior incisor, is normally small and inconspicuous.





Fig. 9. Lower deciduous canine, lateral accessory cusp (character 5): state 1 (the black dots indicate edges of the two cusps), *Herpailurus yagouaroundi* (AMNH 98649); state 0, *Leopardus pardalis* (AMNH 14858). Lingual view, anterior to right.

In some cases the cusp is prominent (and variable in configuration), or even proportionally greatly enlarged as in *Acinonyx jubatus*. Cheetahs have a lateral accessory cusp of highly differentiated form that can be considered a uniquely derived feature. Aside from the variance in shape and size, this cusp displays two discrete character states among felids: unicuspid (0) and bicuspid (1) (see fig. 9). Presence of a single cusp, or near absence of this cusp, was coded as plesiomorphic (0). Curiously, in all other aeluroids examined, this cusp is highly reduced (and more often almost completely absent) in comparison to its clear presence in felids. This feature might be a felid synapomorphy. The bicuspid condition is another apomorphy in the deciduous dentition of *Herpailurus yagouaroundi*. No examined specimen of *Puma* had a bicuspid state. The only species considered to have an uncertain state was *Profelis aurata*.

Two specimens of this cat (AMNH 51996, and FMNH 99025) have a posterior lateral prominence coupled to the accessory cusp, connecting the major cusp to the lower part of the canine crown. It is questionable whether *P. aurata* should be coded as derived (1), and considered to have a derived character shared with *yagouaroundi*. There is further discussion of this character under Cranial Osteological, Internal Congruence. I have no data on this character for the following: *Leopardus jacobita*, *Profelis badia*, *Felis cafra*, *F. silvestris*, *F. nigripes*, *F. bieti*, *Lynx pardina*, *L. canadensis*, and *Uncia uncia*.

**6. Upper third premolar ( $P^3$ ), parastyle (fig. 10):** Despite the general uniformity of  $P^3$  among felids, a clear dichotomy occurs in the degree of development of the parastyle cusp. In extant felids this cusp is either extremely reduced (or almost absent) or greatly enlarged, and of swollen shape (fig. 10). The

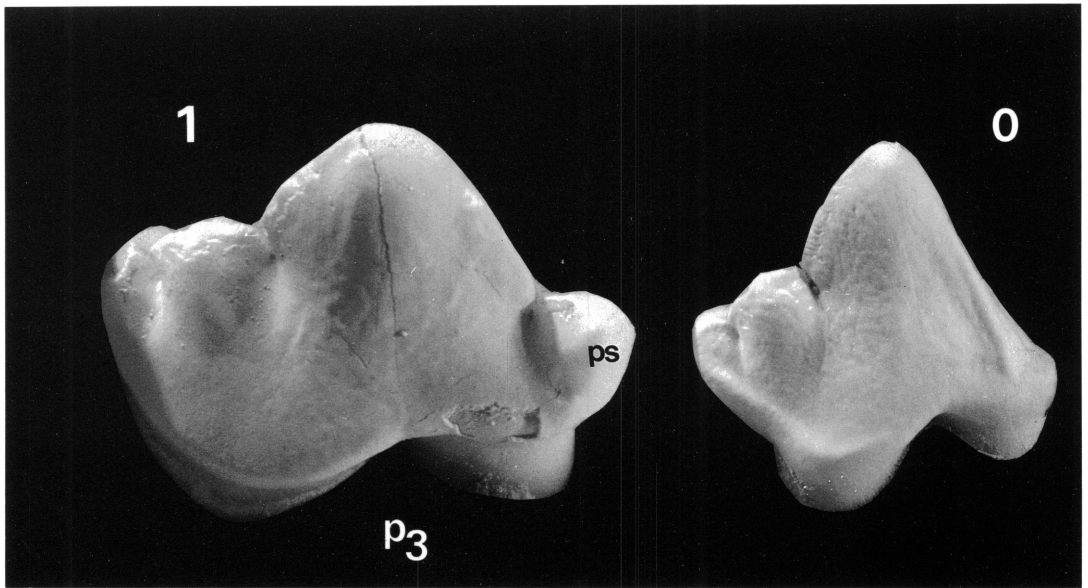


Fig. 10. Upper third premolar, parastyle (character 6): state 1, *Acinonyx jubatus* (AMNH 36426); state 0, *Lynx rufus* (AMNH 30884). Labial view, anterior to right.

felid outgroup node is unambiguous for this character; all other aeluroid families have the  $P^3$  parastyle reduced or nearly absent. *Acinonyx jubatus*, *Neofelis nebulosa*, *Panthera tigris*, *Panthera onca*, *Panthera leo*, and *Panthera pardus* share the derived condition,  $P^3$  parastyle enlarged. A tendency for enlargement of this cusp was also observed in *Profelis badia* (BM 95.5.7.3 and 88.8.13.1) and *Pardofelis marmorata* (AMNH 102844 and BM 55.1645). Those two species are coded as missing data for this feature until larger samples become available. *Uncia uncia* has an uncertain status for this character; therefore it is also coded as missing data. See next section for discussion of the phylogenetic status of these species in reference to this character, which might be interpreted as supporting the placement of *P. marmorata* as closely related to *N. nebulosa* and the *Panthera* clade, a relationship advocated by some authors (e.g., Herrington, 1986). The  $P^3$  paracone and metastyle do not show patterns of change worthy of record here, except for the marked reduction of the metastyle together with an elongate shape of the paracone observed in *Felis nigripes* and other small cats.

7. Upper fourth premolar ( $P^4$ ), protocone (fig. 11): As in most extant Carnivora,  $P^4$  and

the lower first molar form a permanent carnassial pair, at the posterior end of the tooth row in the maxilla and dentary. The  $P^4$  parastyle is slightly more variable than the metastyle and the paracone, but does not show any specific pattern. These cusps are in fact highly homogeneous across all extant felid taxa, indicating that they are states at a high hierarchical rank within the Felidae. In respect to the  $P^4$  protocone, three discrete states were observed. In the first state, the protocone varies from a greatly to a moderately or even poorly developed anterolateral projection in relation to the plane formed by the lingual paracone surface. The second state shows a marked reduction of the anterolateral projection of the protocone. The third state is a similar condition, but characterized by a greater protocone reduction, in which this cusp becomes almost totally suppressed. The third state is unique to *Acinonyx jubatus*. The second state is restricted to the following taxa: *Otocolobus manul*, *Felis nigripes*, *F. bieti*, *F. margarita*, *F. silvestris*, *Leptailurus serval*, *Lynx lynx*, *L. pardina*, *L. rufus*, and possibly *L. canadensis* and *Prionailurus bengalensis*. For the latter two cats I recorded only a tendency for reduction, which might be considered as extreme variants of the first

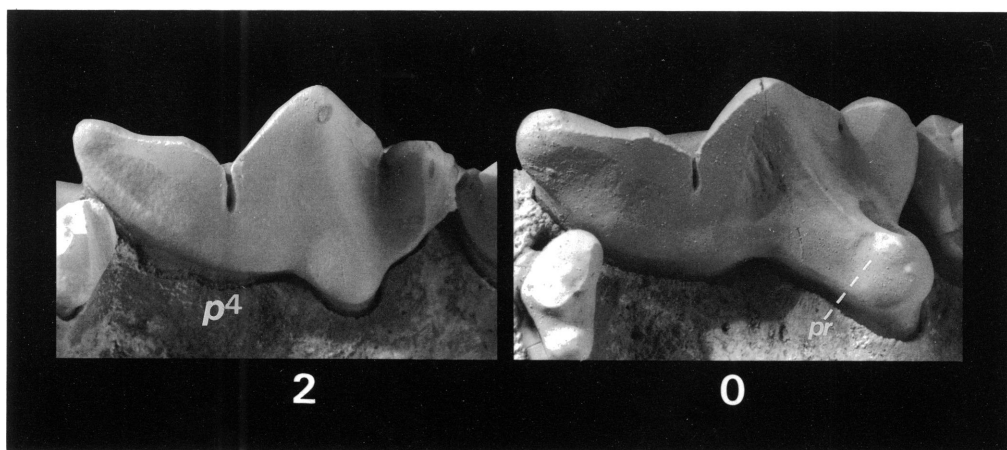


Fig. 11. Upper fourth premolar, protocone (character 7): state 2, *Acinonyx jubatus* (AMNH 36426); state 0, *Neofelis nebulosa* (AMNH 35808). Lingual view, anterior to right.

state considered above, the poorly developed protocone condition. Nevertheless, they were coded as derived (1), as were all the others listed. The absence of marked protocone reduction, or the evident presence of this cusp, is widespread among the other extant felids as well as in aeluroids. The presence of this cusp is evidently a homologous character at a higher level of generality than the one defining Felidae, as Herrington (1986) also noted. The few points where our views diverge are with respect to this character's distribution. She regarded it to occur in all species

in what was designated *Felis* (see Historical Considerations) and the yagouaroundi cat. Also, she did not report protocone reduction for lynxes, thus differing from the view of Pocock (1917b). She also recognized two instead of three character states. In contrast, I treat the character as an additive and multistate (see fig. 11): poorly or moderately to well developed (0), markedly reduced (1), and (2) almost totally suppressed.

**8. Upper third premolar ( $P^3$ ), metastyle (fig. 12):** The only useful character detected on the  $P^3$  crown was a size reduction of the meta-

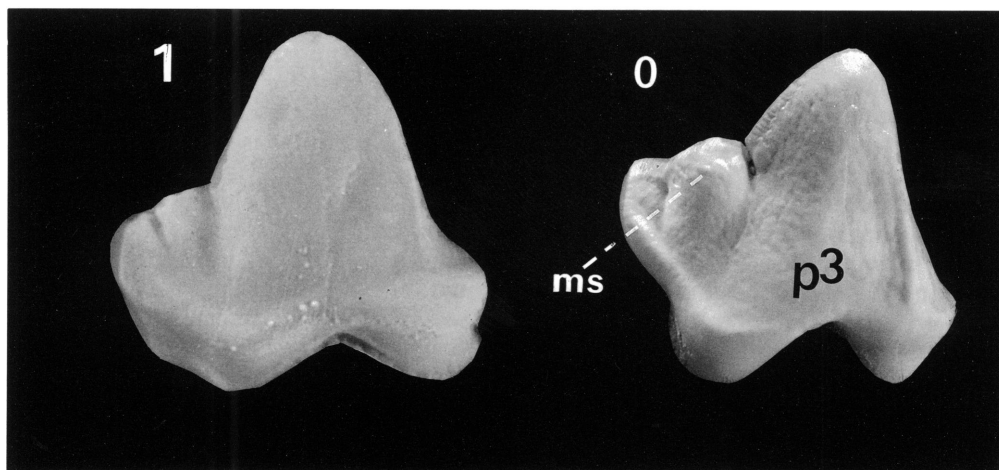


Fig. 12. Upper third premolar, metastyle (character 8): state 1, *Felis nigripes* (AMNH 21380); state 0, *Lynx rufus* (AMNH 30884). Labial view, anterior to right.

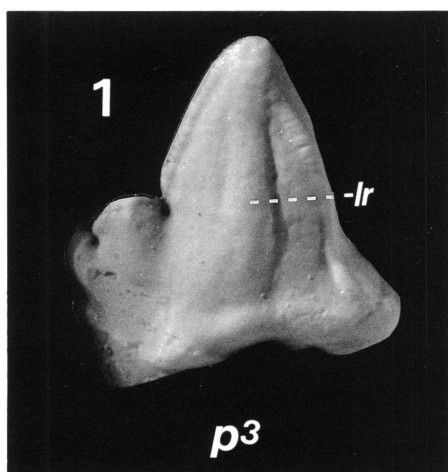


Fig. 13. Upper third premolar, lingual ridge (character 9): state 1, *Leopardus colocolo* (BMNH 42.57). Lingual view, anterior to right.

style. The greatest reduction occurs in *Felis nigripes*, where this cusp is extremely small in relation to paracone size. This conforms with the generally elongated teeth of the black-footed cat. A reduced condition (state 1; see fig. 12) was observed also in *Felis margarita*, *Prionailurus rubiginosa*, and *Leopardus geoffroyi*. The status of this feature in *Otocolobus manul* is unknown, and is coded as missing data. Absence of metastyle reduction is plesiomorphic among felids and other aeluroids.

**9. Upper third premolar (P<sup>3</sup>), lingual ridge** (fig. 13): A few species (*Felis margarita*, *F. silvestris*, *F. nigripes*, *Otocolobus manul*, and *Prionailurus planiceps*) tend to develop a lingual longitudinal paracone ridge on P<sup>3</sup>. However, all of these species cannot be diagnosed as having this ridge. Accordingly, they are coded as plesiomorphic for this character. One species, *Leopardus colocolo*, displays a distinct lingual longitudinal P<sup>3</sup> paracone ridge (fig. 13). An outgroup taxon tends to form the paracone ridge, the plesiomorphic paradoxurine *Arctogalidia trivirgata* (Wozencraft, 1984). This potential polymorphism within the Viverridae is similar to character 2. With the same procedure applied for character 2, it cannot have any effect on the decisive polarization of this character. The P<sup>3</sup> paracone ridge is considered to be an autapomorphy for the pampas cat.

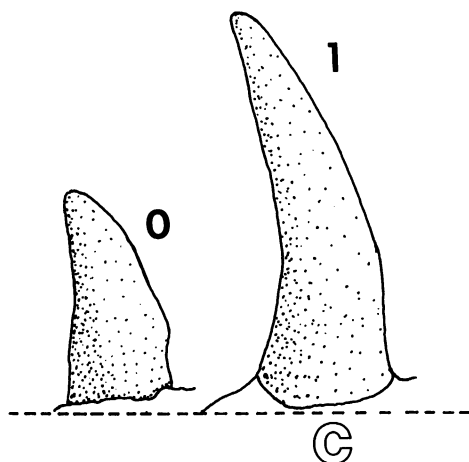


Fig. 14. Upper canine dorsoventral length (character 10): state 1, *Neofelis nebulosa* (AMNH 35808); state 0, *Acinonyx jubatus* (AMNH 36426). Lingual view, anterior to right.

**10. Upper canine dorsoventral length** (fig. 14): Upper canine length is positively correlated with skull size among felids. *Neofelis nebulosa* stands apart for having extremely elongated upper canines (state 1; fig. 14). Elongation is present also in the lower canines, which was noted earlier by Pocock (1917b) and later supported by Herrington (1986). This trait is interpreted as an autapomorphy for *N. nebulosa*.

**11. Upper canine lingual ridge** (fig. 15): This ridge is similar to that described for the P<sup>3</sup> of *Leopardus colocolo*. Based on available aeluroid outgroup information, a longitudinal lingual upper canine ridge is a derived character state for felids. Two derived character states are described (see fig. 15). In one state (2), the ridge is salient along the middle part of the lingual face, from the cingulum almost to the upper tip of the canine. In the other state (1), a weakly developed ridge is restricted to the upper middle part of the lingual face of the canine, well separated from the cingulum. Character state (1) occurs in *Neofelis nebulosa*, *Uncia uncia*, *Panthera tigris*, *P. leo*, and *P. pardus*. Curiously, the lingual ridge is absent in *Panthera onca*, although 2 of 12 specimens of jaguar examined (AMNH 149328 and 37503) have a trace of this ridge. For further discussion on the absence of this trait in the jaguar see Cranial

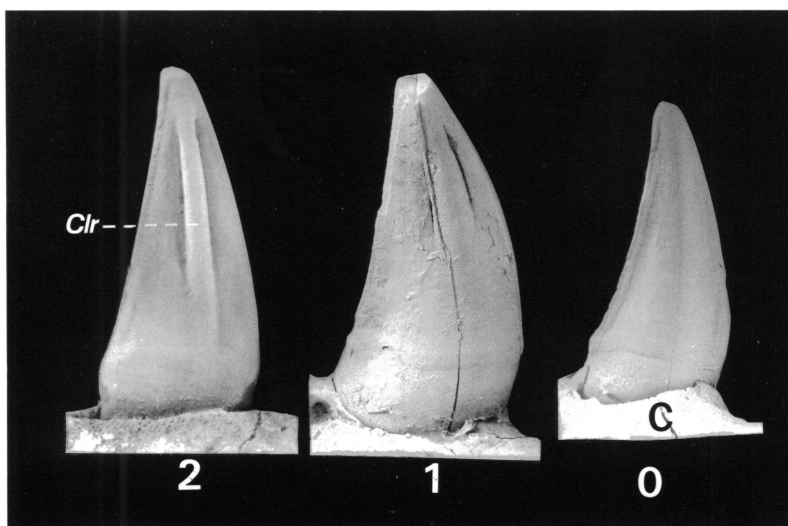


Fig. 15. Upper canine, lingual ridge (character 11): state 2, *Leopardus colocolo* (BMNH 42.57); state 1, *Panthera tigris* (AMNH 113744); state 0, *Prionailurus viverrina* (AMNH 102691). Lingual view, anterior to right.

**Osteology, Internal Congruence.** An intriguing assemblage of taxa is defined by the derived character state 2: *Leopardus colocolo*, *L. jacobita*, *Otocolobus manul*, *Felis margarita*, and *Prionailurus rubiginosa*.

The character states are assumed to be an ordered transformation series. Further comments on this character are found in the next sections. Absence of this lingual canine ridge is plesiomorphic for felids. In order to avoid topographical misinterpretation, the ridge must be distinguished from a crest at the anterior border of the upper canine.

**12. Lower canine lingual cavity (fig. 16):** Two discrete states of the lower canine lingual cavity were detected. A widespread condition among felids and also among aeluroid outgroups is the near absence of this cavity. In a second character state (1) a lower canine ridge is followed by a deep cavity along its anterior border (see fig. 16). State 1 occurs in the same group of species (*Leopardus colocolo*, *L. jacobita*, *Otocolobus manul*, *Felis margarita*, and *Prionailurus rubiginosa*) that have a salient lingual ridge on the upper canine, as well as in *Prionailurus planiceps*.

**13. Lower third premolar crown ( $P_3$ ) (fig. 17):**  $P_3$  is the tooth for which general elongation of teeth in *Felis nigripes* is most evi-

dent (fig. 17). Elongation of  $P_3$  (state 1) is regarded as an autapomorphy for the black-footed cat.

**14. Lower first molar ( $M_1$ ), paraconid crest (fig. 18):** This tooth, the lower carnassial, is

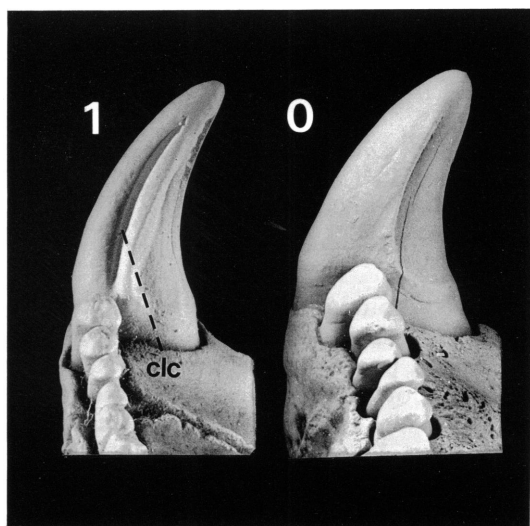


Fig. 16. Lower canine, lingual cavity (character 12): state 1, *Otocolobus manul* (AMNH 185371); state 0, *Panthera onca* (AMNH 75462). Lingual view, anterior to left.

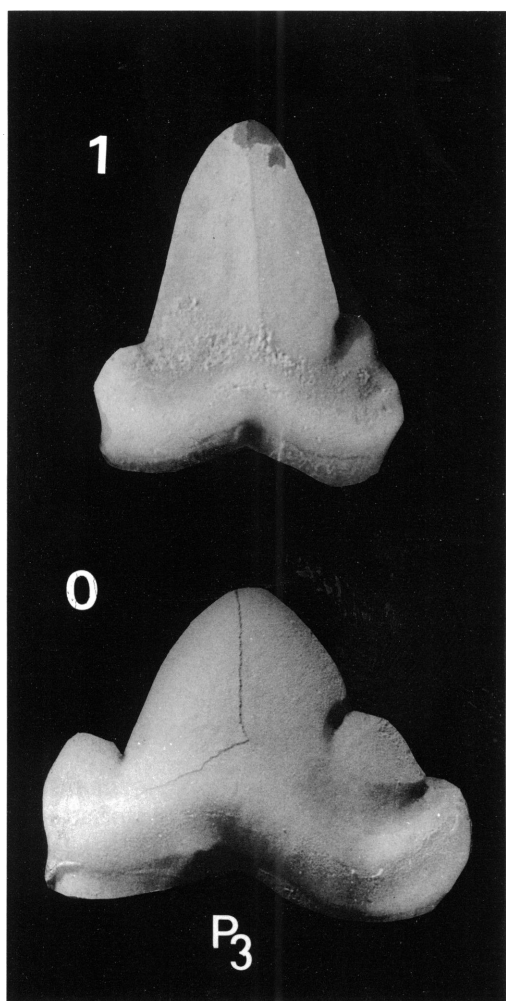


Fig. 17. Lower third premolar crown (character 13): state 1, *Felis nigripes* (AMNH 214380); state 0, *Leopardus pardalis* (AMNH 92835). Lingual view, anterior to left.

relatively homogeneous among Felidae. Besides some slight variation of the metaconid, the lateral paraconid edge displays a greater spectrum of shapes and sizes. A unique condition (state 1) in *Otocolobus manul* is a prominent longitudinal crest, greatly projecting outward along the external paraconid border (fig. 18). Some species, including *H. yagouaroundi* and *Leopardus pardalis*, have a similar development, but not to the degree found in pallas' cat. No aeluroid studied had the  $M_1$  longitudinal crest as described for the pallas cat, or even the state indicated to occur

in some other cats. Favoring discreteness, I have considered the distinct  $M_1$  paraconid crest of *O. manul* as a uniquely derived feature.

**15. Upper fourth and third premolars, relative positions on the maxilla (fig. 19):** The relative positions of these two teeth vary among cats. In *Otocolobus manul* and *Leopardus jacobita* the posterior part of  $P^3$  projects laterally well outward in relation to the alignment given by the orientation of the labial border of  $P^4$  on the maxilla (state 1; fig. 19). Based on information available, which for this case includes a photograph of a specimen of *L. jacobita* (MVZ 116317) (Scrocchi and Halloy, 1986), this condition is a derived character for the two species noted.

#### BASICRANIAL MORPHOLOGY

Since the work of Flower (1869) the basicranium in Carnivora has been considered an area of the skull rich in phylogenetic information. More recently the aeluroid basicranium (auditory region) has been studied by Hunt (1974, 1987, 1989), and a vast work on the basicranium of Nimravidae ("paleofelids") is included in the unpublished Ph.D. dissertation by Neff (1983). A critique of some of the proposals of homology advocated by Hunt can be found in Wozencraft (1989). An assemblage of characters in this region was proposed as a set of synapomorphies supporting the monophyly of Felidae (these characters are presented under Felidae Monophyly).

Terminology used for the basicranium (including the auditory region) is based on the above-cited work of Hunt, Cifelli (1982), Davis and Story (1943; for arteries and nerves), Jayne (1898), Macintyre (1972), MacPhee et al. (1988), Novacek (1986), and Wyss (1987). See figures 20 and 21.

**16. Relative position of foramen rotundum to basicranial plane (fig. 22):** The foramen rotundum is an opening in the alisphenoid bone, lying next to the sphenorbital fissure. Among felids the foramen rotundum occupies either of two positions. In the first and more general state, the foramen rotundum is definitely on the orbital wall (0), in the other, it is at the basicranium's plane (1) (see fig. 22). Quite a few cats display a slight displace-

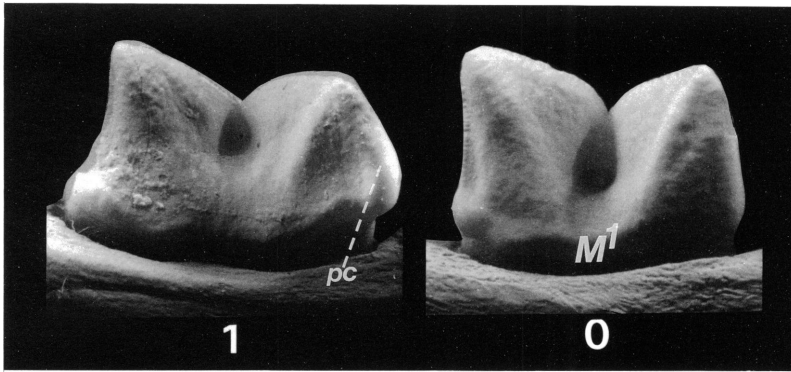


Fig. 18. Lower first molar, paraconid crest (character 14): state 1, *Otocolobus manul* (AMNH 185371); state 0, *Felis nigripes* (AMNH 214381). Lingual view, anterior to right.

ment toward the basicranium, but is is not feasible to define an intermediate character state. The felid outgroup node is unambiguously represented by the state 0. *Proteles cristatus* was the only examined outgroup taxon with a condition somewhat similar to that of the cats, noted as having a slight tendency for migration of the foramen rotundum onto the basicranium. *Prionailurus planiceps*, *P. viverrina*, and *P. bengalensis* were coded as state 1, these three species having

the foramen rotundum constantly present as a basicranial component. *Leopardus colocolo* and *L. wiedii* also display this state. However, these two are distinctly more polymorphic, some specimens having the foramen rotundum only slightly displaced onto the basicranium. This character, as analyzed by Herrington (1986) is not uniquely derived for the two neotropical cat species.

17. External pterygoid fossa (fig. 23): The pterygoid fossa serves as the surface of at-

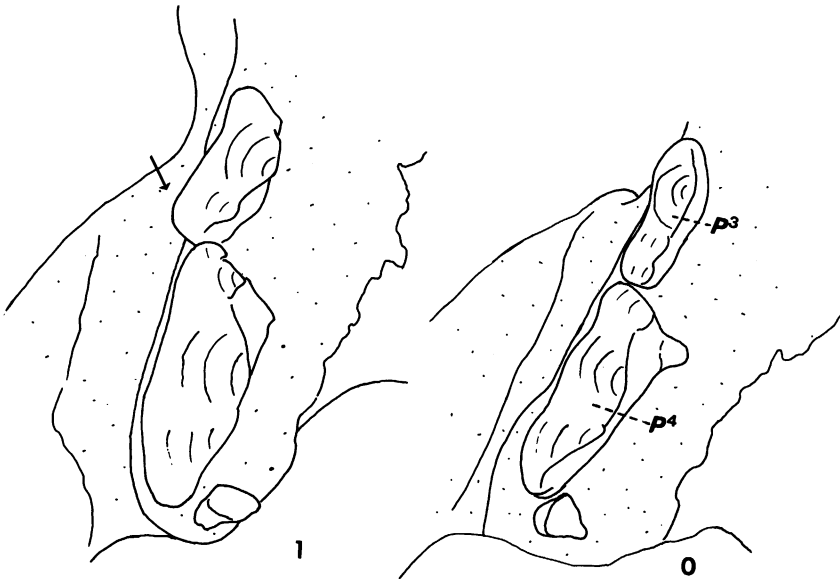


Fig. 19. Upper fourth and third premolar relative positions on the maxilla (character 15): state 1, *Otocolobus manul* (AMNH 185371); state 0, *Prionailurus planiceps* (AMNH 173515). Lingual view, anterior to right. Ventral view of crown, anterior toward top.



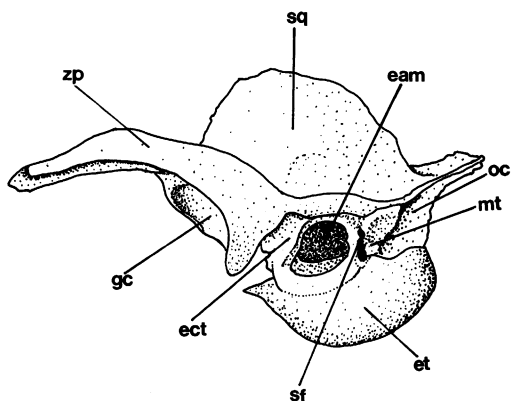


Fig. 20. Basicranial (auditory region) external morphology; lateral view (see terminology under Anatomical Abbreviations).

tachment for the internal pterygoid muscle. Lateral to this fossa lies the external pterygoid process, which projects outwardly. Different degrees of development of this fossa and process are distinguishable among felids. In the absence of more detailed (quantitative) information, a somewhat arbitrary division into two character states was adopted. According to outgroup referential knowledge, a poorly to moderately developed external pterygoid complex of fossa and process is considered plesiomorphic for felids. Among other families examined, viverrids are closer to the state generally found among felids. The derived (1) state has a more restricted distribution among felids; it is a conspicuous, well-developed (deep) pterygoid fossa with marked lateral pterygoid process ending laterally in a point (see fig. 23; state 1). Herrington (1986) discussed this character, but she did not record

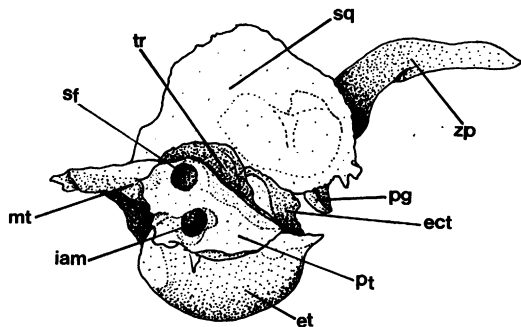


Fig. 21. Basicranial (auditory region) internal morphology; medial view.

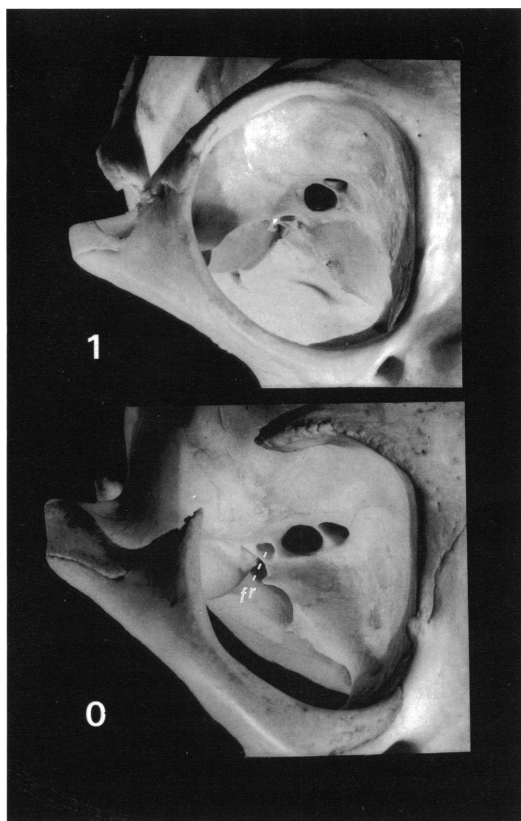


Fig. 22. Relative position of foramen rotundum to the basicranial plane (character 16): state 1, *Prionailurus planiceps* (USNM 185371); state 0, *Profelis aurata* (AMNH 51994). Frontolateral view.

it for *Profelis temmincki*, *P. badia*, and *Paradofelis marmorata* (this species displays a modified condition, not externally ending in a point, and is similar to the condition of *P. badia*). I agree that *Felis lybica*, *F. cafra*, *F. silvestris*, *F. nigripes*, *F. margarita*, *F. bieti*, *Caracal caracal*, and *Prionailurus rubiginosa* have this derived character state. *Felis chaus* is plesiomorphic for this character in contrast to other *Felis* species.

**18. Palatine bones (fig. 24):** Two extreme derived conditions of the posterolateral inflection of the palatines were observed. *Acinonyx jubatus* has a unique condition (state 2), where this inflection reaches a maximum breadth between the internal parallel borders of the palatine, of an extremely inflected choana (fig. 24). A highly discrete and opposite



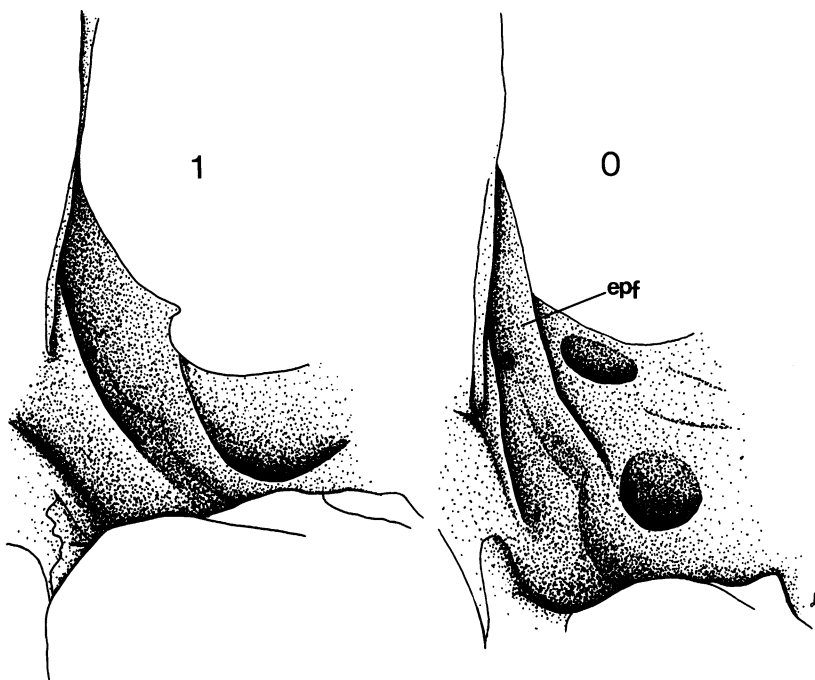


Fig. 23. External pterygoid fossa (character 17): state 1, *Felis nigripes* (AMNH 214380); state 0, *Lynx canadensis* (AMNH 29045). Ventral view, anterior toward top.

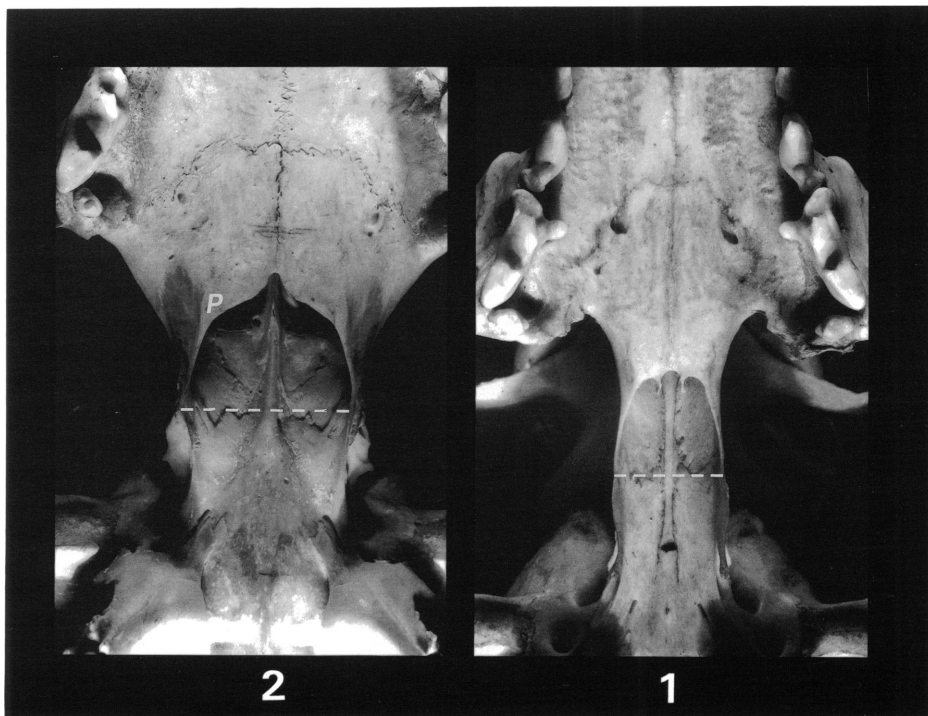


Fig. 24. Palatine bones (character 18): state 2, *Acinonyx jubatus* (AMNH 36426); state 1, *Prionailurus planiceps* (AMNH 35398). Ventral view of basicranium, anterior toward top.

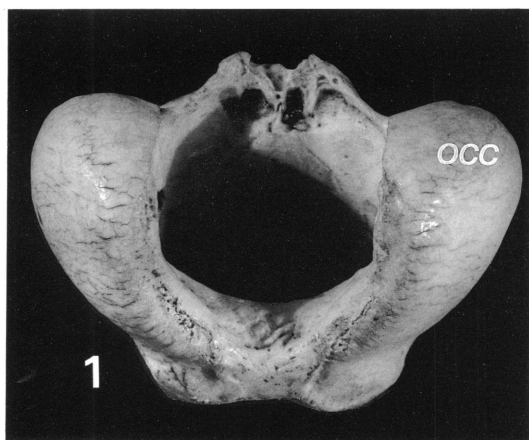


Fig. 25. Occipital condyles (character 19): state 1, *Panthera tigris* (AMNH 113744). Posteroventral view.

state (1) of inflection occurs in *Prionailurus planiceps*. These two conditions were coded as nonadditive for this feature. They were thus interpreted as two autapomorphies with all intermediate variants as plesiomorphic.

**19. Occipital condyles** (fig. 25): Despite attempts to formulate characters for variation perceived among extant felids in different parts of the occipital condyles, I could recognize only one distinctive configuration—a relative enlargement of these condyles in the tiger. This condition (state 1) is an autapomorphy for *Panthera tigris*. Herrington argued that *P. tigris* has a plesiomorphic shape of the anterior border of the condyles in relation to other *Panthera* species, *P. onca*, *P. leo*, and *P. pardus*, which are considered to be derived for this character. However, as noted above, no general pattern of these bones was detected for extant felids except the autapomorphy just postulated.

#### Auditory Region

As mentioned earlier, a series of homologies was proposed for this region in Aeluroidea, but this region has not been examined in detail among Felidae (extant taxa). Pocock (1916b) examined the felid auditory region, but that paper did not provide much phylogenetic information. Herrington (1986) suggested a few characters based on the morphology of the ear ossicles and gave an introductory character analysis of the auditory

region. Further investigations are needed, especially of the soft anatomy. The terminology is the same as that listed for basicranial morphology.

A reduction of the ventral promontorial process in felids is a feature revealed by Hunt (1989), however its distribution is still unclear; therefore it is not included in this character analysis.

No data were available for any feature of the internal auditory region for *Leopardus jacobita* or *Profelis badia*.

**20. Subarcuate fossa** (fig. 26): The subarcuate fossa is located at the posterior endocranial side of the petrosal, adjacent to internal surface of the tentorium. The fossa lodges the paraflocculus of the cerebellum. It is generally clearly marked in felids, being quite deep in some species. In fact, this condition was recorded for all juveniles examined, including those of species in which the adults do not conform. Hence, the direction of ontogenetic change suggests the presence of the fossa as the primitive condition. A closure of the subarcuate fossa characterizes two other proposed character states (see fig. 26). In state (1), the fossa is very poorly developed, its superior border (and in some cases its roof) having partial contact with the external surface of the tympanic roof process; it scarcely can be distinguished as a fossa. The further derived state (2) is characterized by a total disconfiguration of the subarcuate fossa, the whole superior wall becoming diffused into a residual depression, presumably vestigial evidence of former presence of a fossa. In the search for evidence of polarization in the outgroup taxa studied, herpestids and viverrids were observed to have a deep fossa (0), the exception being a specimen of *Civettictis civetta* (AMNH 116347) with a very poorly developed, but still present, fossa. A dramatically different condition was found in hyaenas, where a totally open cylindrical cavity marks the location of the subarcuate fossa. This state is definitely more like condition 2 in felids than any condition observed in other aeluroids. However, better understanding of the ontogeny of this fossa in hyaenas may be a requirement for such a topographical statement of sameness. It is very possible that the somewhat similar condition in Hyaenidae and Felidae was independently derived, and

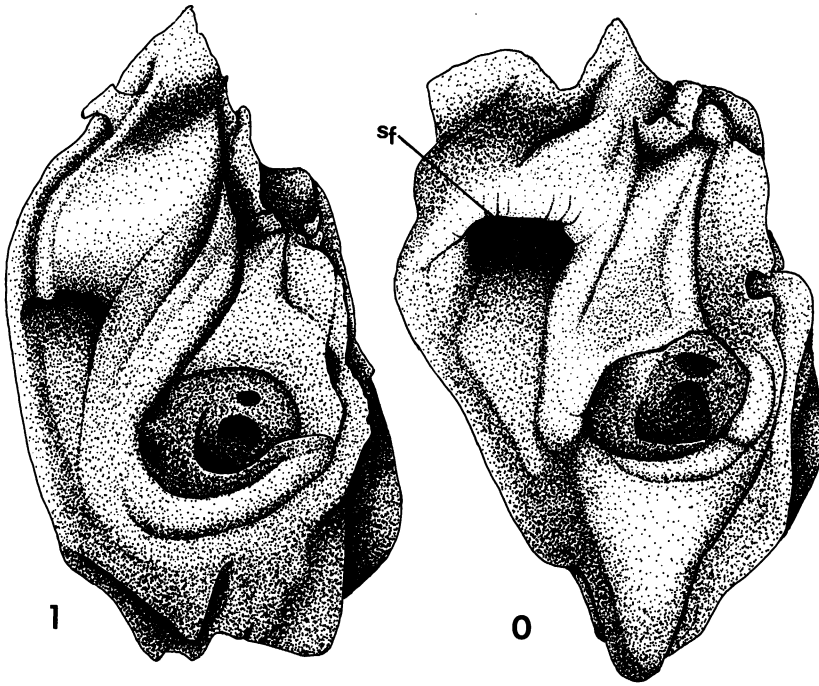


Fig. 26. Subarcuate fossa (character 20): state 1, *Leopardus pardalis* (AMNH 214743); state 0, *Herpailurus yagouaroundi* (AMNH 64111). Dorsal view, anterior toward bottom.

therefore does not constitute a potential synapomorphy. The felid outgroup node would be uncertain only if a decision is made favoring topographical correspondence between character state 2 and the condition observed for hyaenas, and if Hyaenidae is assumed to be the sister taxon of Felidae. At this stage of understanding of the subarcuate fossa in aeluroids, this character polarity is interpreted in concordance with its ontogeny in the Felidae.

Wyss (1987) dealt with similar problems when polarizing a parallel closure of the subarcuate fossa in pinnipeds (otariids and odobenids), because this condition is found also among various terrestrial arctoids.

Character state 1 of this additive character occurs in: *Leopardus tigrina*, *L. guigna*, *Profelis temmincki*, *P. badia*, *Prionailurus planiceps*, *P. viverrina* (it is possible that this species would be better coded as state 2), and *Pardofelis marmorata*. Character state 2 occurs in *Leopardus pardalis*, *L. wiedii*, *Caracal caracal*, *Lynx rufus*, *L. canadensis*, *Puma concolor*, *Acinonyx jubatus*, *Uncia uncia*,

*Neofelis nebulosa*, *Panthera tigris*, *P. onca*, *P. leo*, and *P. pardus*.

**21. Internal auditory meatus, marginal surface (fig. 27):** The internal auditory meatus is on the dorsal petrosal surface, and functions as a passage for the vestibular and facial nerves. The margin of the auditory meatus in felids is morphologically very stable. A few cats have a distinctive border that appears at a subadult stage, apparently emerging from the interior of the auditory cavity and moving onto the superior process of the tympanic roof, resulting in a salient border all around the auditory meatus. The superior segment of the border becomes, in ontogeny, laterally fused with the external surface of the posterior semicircular canal (fig. 27; 1). Cats with this condition are *Lynx lynx*, *L. pardina*, *L. rufus*, *L. canadensis*, *Caracal caracal*, and *Acinonyx jubatus*. The latter two are somewhat different. In *C. caracal* the border is not so salient, and in *A. jubatus* it has a distinct configuration. *Felis chaus* was difficult to classify and is coded as missing data for this feature, at least until better samples become

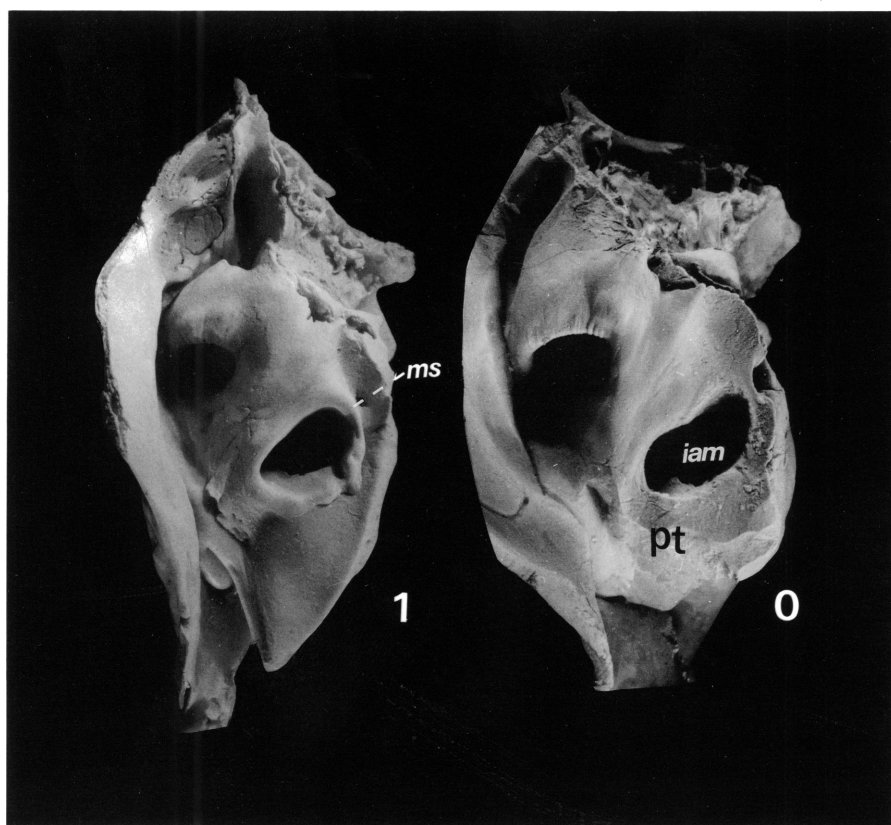


Fig. 27. Internal auditory meatus, marginal surface (character 21): state 1, *Lynx rufus* (AMNH 254478); state 0, *Profelis temmincki* (AMNH 113709). Ventral view, anterior toward bottom.

available. This character polarization is supported by ontogeny and also by comparisons with other aeluroid groups. Hyaenas display a prominent superior process of the tympanic roof that can sometimes be confused with the external border of the auditory meatus. This configuration in hyaenids is similar to that observed in *A. jubatus*. Even with a greater margin of error in the characterization for hyaenas, the polarization of this character would remain the same (see character 20 for an equivalent case).

**22. Longitudinal ridge of auditory meatus** (fig. 28): This ridge extends from a point just below the foramen singulare and follows the curvature of the near upper vestibulocochlear border. It forms the internal edge of a plane anterior to which the facial nerve penetrates the fallopian foramen. The ridge separates the foramen acousticum from the canal accommodating the facial nerve. The more

widespread, and presumably plesiomorphic, condition of the ridge is a nonprominent and homogeneously flat surface with the described plane of support for the facial nerve. In contrast, some felids exhibit a salient crest all along its length, forming an internal wall for the facial nerve (fig. 28). This process of the auditory meatus possibly functions as a ridge separating the two foramina mentioned. A further derived condition (state 2) of this same trait, assuming an ordered transformation series, was that recorded as an autapomorphy for *Acinonyx jubatus*.

No outgroup aeluroid examined has such a conspicuous ridge bordering the auditory meatus, a circumstance which further reinforces the assumed polarization. Polymorphism of this character within hyaenas is a matter for future research, because the only readily observable petrosal was from a specimen of *Crocota* (AMNH 55467), which was

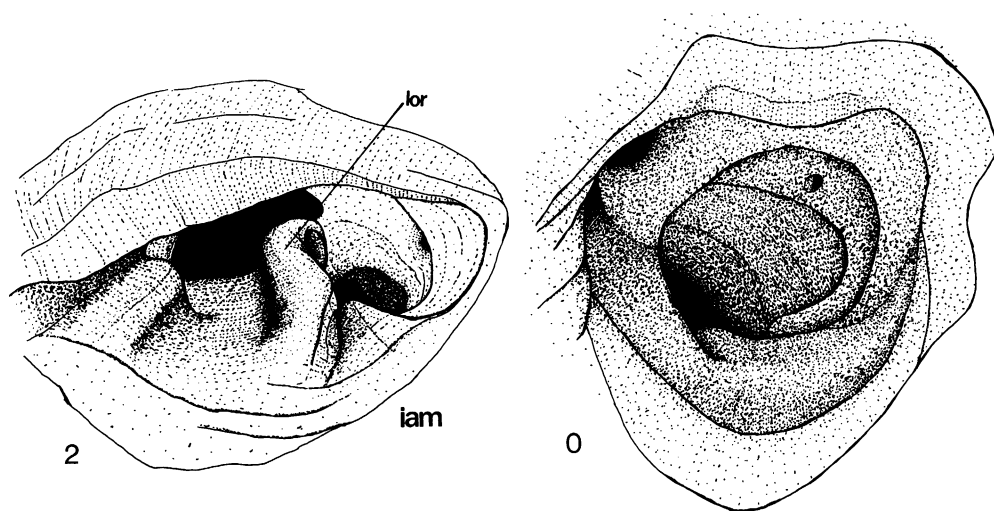


Fig. 28. Longitudinal ridge of the auditory meatus (character 22): state 2, *Acinonyx jubatus* (AMNH 80866); state 0, *Prionailurus bengalensis* (AMNH 87352). Dorsal view.

coded as displaying a plesiomorphic longitudinal ridge. Felid species grouped by this attribute (states 1 and 2) are *A. jubatus* (2), *Uncia uncia*, *Neofelis nebulosa* (questionable), *Panthera tigris*, *P. onca*, *P. leo*, *P. pardus*, and *Lynx pardina* and *L. canadensis* (1). The longitudinal ridge of the two *Lynx* species must be further examined for a better understanding of its topographical correspondence to the ridges of the other species mentioned. The two lynxes present only a residual, nonprominent longitudinal ridge. Nevertheless, they are here coded as derived. One specimen of *L. rufus* among many shows a condition similar to that found in other lynxes.

The possibility that this ridge might be correlated with deepness of the auditory meatus is at least partly refuted by the condition present in *Puma concolor*, which has a deep cavity and unquestionably lacks the ridge.

**23. Malleus, processus muscularis** (fig. 29): This process of the malleus is the base of attachment for the tendon of the tensor tympani muscle. Herrington (1986) proposed, among other characters for the morphology of ear ossicles, an enlarged processus muscularis as a synapomorphy for *P. leo*, *P. pardus*, and *Panthera onca* (due to a possible typographical error on page 322, she excluded *P. onca* from this group). Here this characterization is corroborated. Additionally, the

shape of this processus (in the three species referred to) when compared with that of *Panthera tigris*, is in some cases drastically different. *P. tigris* has the plesiomorphic condition in which this process has a large base that extends from the lower part of the malleus neck and gradually becomes pointed. The general aspect is thus of a short pointed processus muscularis. In contrast, other *Panthera* species mentioned show a more enlarged, elongated, cylindrical shape along the length of the malleus (state 1; see fig. 29). Polarity of this character is corroborated by herpestids, viverrids (*Galidictis grandidieri* was the only problematic case, because an elongated, somewhat similar condition of the processus muscularis was recorded for it), and hyaenids. Hyaenas are particularly similar to the tiger. A detailed comparative morphology of aeluroid ear ossicles is needed. With monophyly of *Panthera*, this attribute clearly supports the view of *P. tigris* as the basal extant taxon of this group.

**24. Malleus, processus brevis** (fig. 30): This is another process of the malleus, to which Herrington gave some attention. She proposed that an anteriorly oriented reflection of the processus brevis is a unique feature shared by *Acinonyx jubatus* and *Otocolobus manul*. At this point of my research I am not certain of the discreteness of this character state (fig. 30). Nevertheless, its distribution

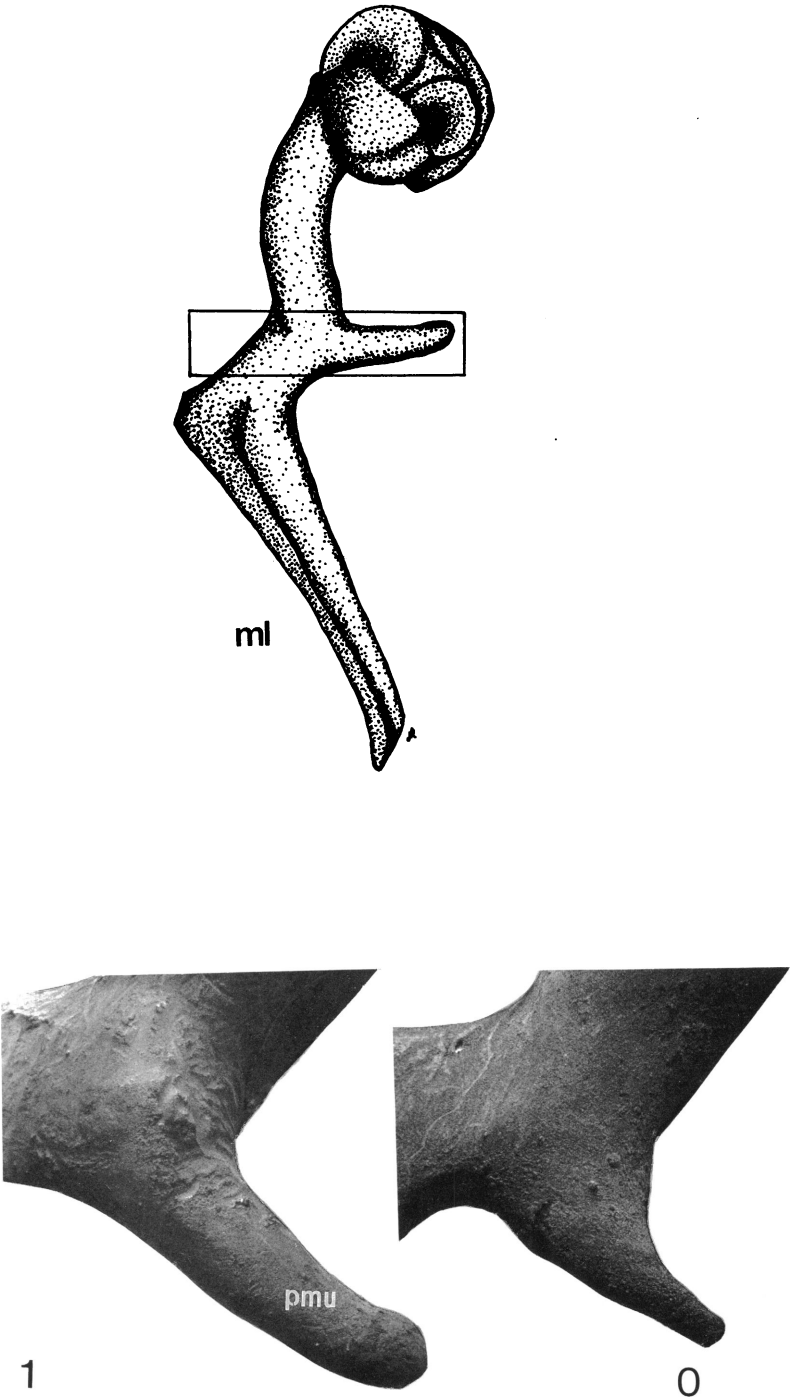


Fig. 29. Malleus, processus muscularis (character 23): state 1, *Panthera leo* (AMNH 83618); state 0, *Panthera tigris* (AMNH 54460). Lateral view, anterior toward bottom.

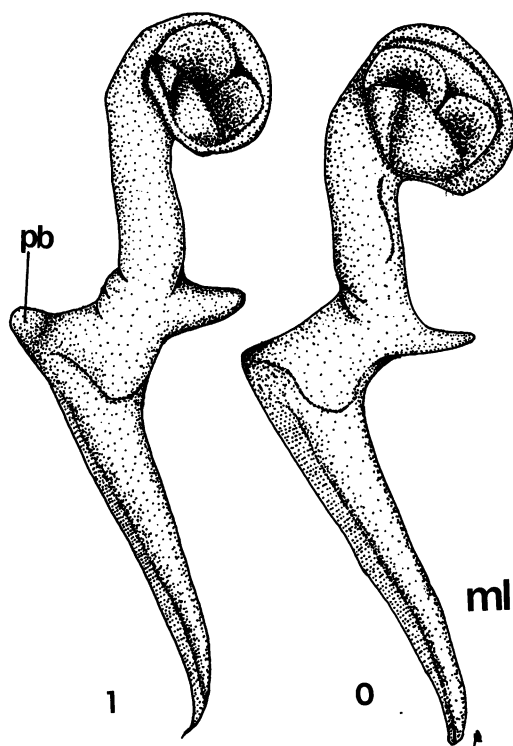


Fig. 30. Processus brevis (character 24): state 1, *Otocolobus manul* (AMNH 180268); state 0, *Panthera tigris* (AMNH 54460). Lateral view, anterior toward bottom.

is broader than Herrington thought. It is also present in *Lynx lynx*, *Leptailurus serval*, *Uncia uncia* (modified) and *Panthera onca*, and, not so clearly, in *Leopardus jacobita*, *Profelis temmincki*, *Felis silvestris*, *F. lybica*, *F. cafra*, *F. bieti*, *F. margarita*, *F. nigripes*, and *Caracal caracal*. These species were coded as derived. Since data are not sufficient to propose a multistate character, binary division was applied. No data were available for *Profelis aurata* and *P. badia*. Because of uncertainty *Leopardus geoffroyi*, *Prionailurus rubiginosa*, and *Pardofelis marmorata* were included in the group of taxa with missing data. None of the aeluroids examined had the processus brevis anteriorly reflected.

**25. Incus, inferior head with malleus** (fig. 31): The incus, a second ear ossicle, has its head articulated with the malleus and a stapedial lenticular process articulated with the stapes, the third ear ossicle. A distinct outward projection of the inferior head of the

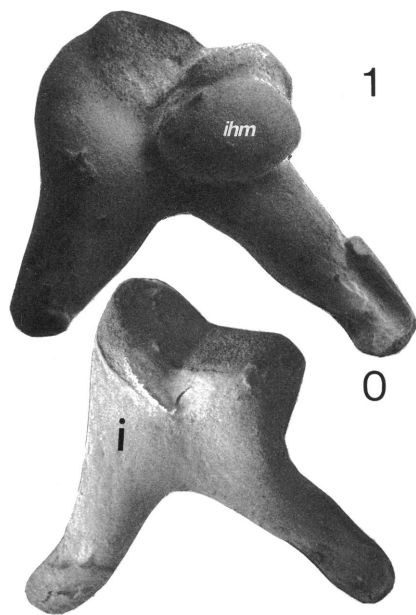


Fig. 31. Incus inferior head with malleus (character 25): state 1, *Otocolobus manul* (AMNH 18432); state 0, *Panthera leo* (AMNH 83618). Lateral view, anterior toward top.

incus with the malleus (state 1) occurs in some felids (fig. 31). In contrast, a smoother, less prominent projection is the plesiomorphic state (0) and is found among other extant felids. The discreteness of the two character states is not clear, since the categorization is difficult for a few cats. These problematic species were *Caracal caracal*, *Lynx canadensis*, *Felis chaus*, and *Uncia uncia*. Because at least one specimen in all these species was clearly defined by one of the two states, they were not coded as missing data. In the outgroup sample, polymorphism was observed in viverrids (Cryptoproctinae). They possess a prominent rounded inferior process of the incus, supposedly parallel with that of felids. All other aeluroids examined had the smooth nonprominent inferior head of the incus presumed to be plesiomorphic for Felidae. Even if it were assumed that the basal node of the Viverridae is ambiguous, and that Viverridae is the sister taxon of felids, this would not meet the requirements to definitively place state 1 at the felid outgroup node. This is another case similar to that in the previously discussed characters 2 and 9.

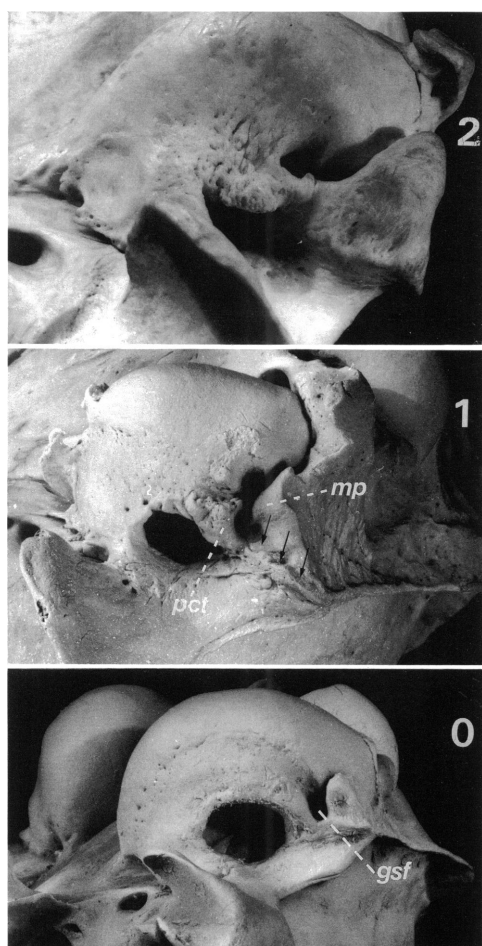


Fig. 32. Groove for stylomastoid foramen (character 26): state 2, *Panthera leo* (AMNH 81838); state 1, *Acinonyx jubatus* (AMNH 35998); state 0, *Felis bieti* (SMNH A585295). Lateral view, anterior toward left.

The derived character state occurs in the following taxa: *Otocolobus manul* (the species most clearly illustrating this condition), *Leopardus pardalis*, *L. wiedii*, *L. tigrina*, *L. guigna*, *L. geoffroyi*, *L. colocolo*, *Prionailurus bengalensis*, *P. viverrina*, *Herpailurus yagouaroundi*, *Acinonyx jubatus*, and *Uncia uncia*.

**26. Groove for stylomastoid foramen** (fig. 32): This foramen opens laterally on the posteroexternal part of the entotympanic. The foramen transmits the facial nerve and stylomastoid artery. Three discrete character states of this groove are described for extant

felids (see fig. 32). The most widespread state is a groove with small superior part of the posterior wall of the anterior crus of the ectotympanic fused with the squamosal, which blends posteriorly with the mastoid process and displays an inferior crest quasi-enclosing the groove. It is considered the plesiomorphic state. A modified groove condition (1) occurs in *Acinonyx jubatus* and *Uncia uncia*, which lack the circular aspect of the groove. Furthermore, the mastoid process does not have an anteroventral projection over the stylo-mastoid opening. A fissure separates the anterior crus of the ectotympanic from the complex formed by the mastoid process and the squamosal. On the outer side of this notch, a "flat" surface extends along the antero-inferior suture of the squamosal and the mastoid process. It may be characterized as an open passage, which gives a more posterior orientation to the facial nerve and stylomastoid artery in relation to the anterior groove condition described above.

A third character state, derived condition 2, is seen in *Neofelis nebulosa*, *Panthera tigris*, *P. onca*, *P. leo*, and *P. pardus*, all of which have the posterior wall of the anterior crus of the ectotympanic completely (or nearly so) fused with the squamosal and forming a continuous compact lateral surface with the mastoid process. The stylomastoid foramen reaches the outer side of the bulla and meets this compact wall. Then, as the groove for this foramen reaches the ventrolateral part of the mastoid, a passage along the external mastoid surface seems to be formed between its posterior crest and the caudal entotympanic surface. Although *Prionailurus viverrina* and *Caracal caracal* do not have the groove of the stylomastoid just described, they do have the anterior crus of ectotympanic almost fused with the complex squamosal mastoid process. These two taxa differ from *N. nebulosa* and the species of *Panthera* in having the complex lower portion making contact with the caudal entotympanic surface. The passage for the facial nerve and stylomastoid artery continues to lie laterally, as in most cats (plesiomorphic state). But in these felids the nerve and artery emerge over the wall formed by the fusion of bones. In other words, these two species do not have a marked groove for the stylomastoid foramen.



Nevertheless, they were coded as plesiomorphic for this attribute. The polarity of this character is difficult to assess, given its polymorphic nature among aeluroids. The shape of the groove seems to be affected by the degree of inflation of the bulla as well as the development of the mastoid process. In fact, this character was retained so as to maximize information.

The character states might be alternatively represented as presence and absence, each state as a separate character. Absence would simply mean nonexistence of the trait in question, rather than the plesiomorphic state, since no true polarization is performed (see Nelson and Platnick, 1981: 183–199). Condition (1), found in *A. jubatus* and *U. uncia*, was also recorded for *Crocota* and *Hyaena*. Most viverrid and herpestid genera display the groove widespread in felids. Considering the extinct genus *Pseudailurus* as a basal felid (Hunt, 1987, 1988), the laterally open semi-enclosed groove condition is corroborated as plesiomorphic for Felidae. In the face of this complex scenario—with a possibly uncertain outgroup node, and assuming Hyaenidae as the sister group of Felidae (for further discussion see Methods and characters 2, 9, and 25)—I coded this character as nonadditive. Its effect on the most parsimonious trees is discussed under Cranial Osteology, Internal Congruence.

#### FACIAL REGION

Terminology for the facial region, which includes the frontal sinus and rostrum, is listed in the general skull morphology referred to in the introduction of this section. Given the complexity of facial shapes, it is particularly difficult to detect morphological patterns of change in this region.

##### Frontal Sinus

The frontal sinus has been recently studied in Canidae by Berta (1988), whose analysis focused on the presence or absence of this cavity, and on its penetration to the postorbital process. Whether or not the sinus invades the postorbital process in felids is here considered to be influenced by the cavity's expansion, its position, and the form and degree of development of the postorbital pro-

cess. The functional significance of cranial pneumatization in Carnivora is still poorly understood.

**27. Frontal sinus, relative position on the skull (fig. 33):** The sinus in the frontal bone is a cavity that communicates via an opening with the nasoturbinal chambers. Three adult character states are recognized for the relative position of the sinus in the skull of felids. In the commonest state (1) of the frontal sinus among felids the sinus is centralized in the region of the postorbital processes, and ranges from spanning the posterodorsal part of the rostrum to the postorbital region. The two other states are in opposite positions (see fig. 33); the widespread state (1) is intermediate between the two.

In the first of these two other states, the frontal sinus is nearly or entirely restricted to the postorbital region (0). This condition was recorded for adult male specimens of *Panthera tigris*, *P. onca*, *P. leo*, and *P. pardus*. It was also recorded for all male and female adult specimens of all other nonfelid aeluroids examined. The presence of sexual dimorphism in the position of the sinus and the justification for the polarization of this character is addressed later (see Transformation Series). In ontogeny, the frontal sinus moves posteriorly (as it increases in volume) from the upper interorbital area to a postorbital position (state 0). What is suggested here is that this character transformation series involves a case of neoteny.

The second modified state of this neotenic trait is exhibited in two cats, *Felis nigripes* (the species which best illustrates this condition) and *F. silvestris*, in which the frontal sinus is anteriorly positioned and does not extend posteriorly to the line across the postorbital processes (2). The widespread intermediate condition is then interpreted as less extreme neoteny. This character was considered to be an additive (ordered) transformation series.

**28. Anterodorsal frontal sinus cavity (fig. 34):** An anterodorsal frontal sinus cavity was clearly homologized only among extant species of *Panthera*. It is connected with a main, rounded frontal sinus cavity in the posterior postorbital region as noted above. *Panthera leo* displays a striking enlargement of the anterodorsal cavity (state 1). Its anterolateral

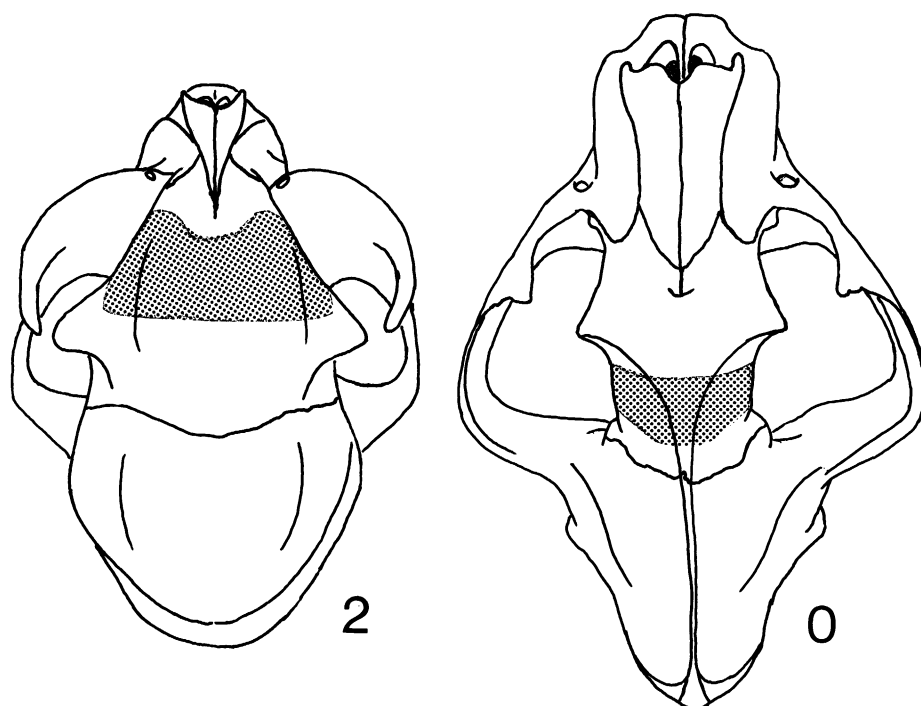


Fig. 33. Diagrammatic representation of the frontal sinus area (stippled) on the skull (character 27): state 2, *Felis nigripes* (AMNH 214380), state 0, *Panthera tigris* (AMNH 113744). Dorsal view, see lateral view in figure 35.

projection extends well beyond the position on the internal wall where the connection for the nasoturbinal chambers is situated, and reaches posteriorly to the posterior side of

the postorbital process (see fig. 34). Given the complexity of the ontogeny of the frontal sinus, the morphological relationships of this cavity with the sinus complex are still un-

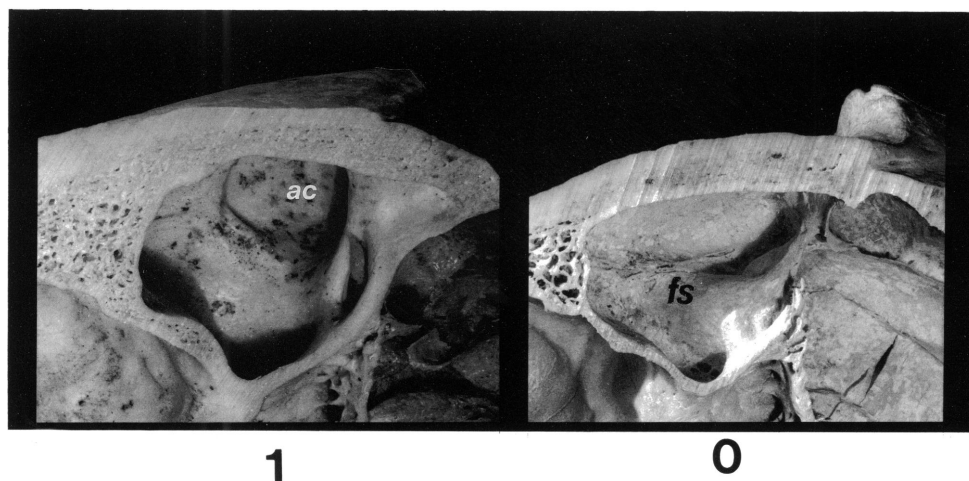


Fig. 34. Anterodorsal frontal sinus cavity (character 28): state 1, *Panthera leo* (AMNH 52076); state 0, *Panthera tigris* (AMNH 85404). Medial view, anterior toward right.

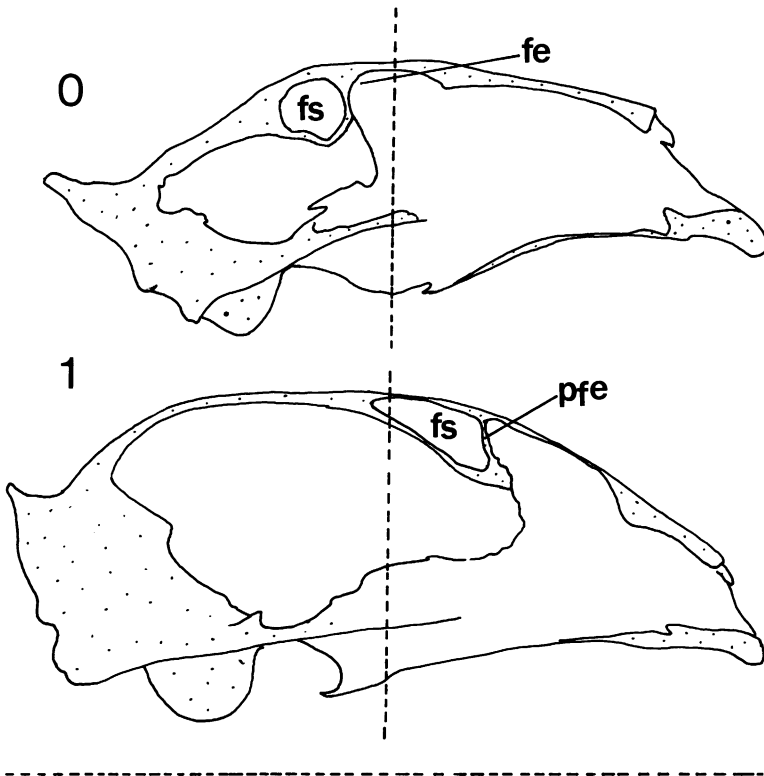


Fig. 35. Diagrammatic representation of the position of the posterior part of the first caudal ethmoturbinate scroll (character 29): state 1, *Prionailurus planiceps* (USNM 145593); state 0, *Panthera tigris* (AMNH 85404). Medial view, in sagittal section.

clear. Nevertheless, as homologized, this cavity stands as a unique derived character for *P. leo*.

**29. Position of posterior part of the first caudal ethmoturbinate scroll** (fig. 35): The posterior part of the first caudal ethmoturbinate meets the anterodorsal segment of the internal surface of the frontal bone, with which this nasal chamber connects through an opening to the frontal sinus. Although this character is related to the previous characters which involved the relative position of the frontal sinus in the skull, those characters are related to the position of the sinus and not the position of the connection between the sinus and nasal cavity. A somewhat different set of species was grouped by this feature. The binary coding for this attribute (see fig. 35) is as follows: internal frontal surface (constituting the posterior end of the first caudal ethmoturbinate scroll) is placed well before, or just before, a line across the postorbital

processes (1). The plesiomorphic state of this character (0), present in herpestids, viverrids, and hyaenas, has the frontal internal surface in a more posterior position, considerably posterior to the line across the postorbital processes. The taxa considered to be potentially plesiomorphic, and coded as such, were *Puma concolor*, *Neofelis nebulosa*, *Panthera tigris*, *P. onca*, *P. leo*, and *P. pardus*.

Other extant felids display state (1), in which the first caudal ethmoturbinate scroll does not extend posteriorly to the line across the postorbital process. This is apparently another case of neoteny, since this scroll migrates in ontogeny to the postorbital region. Some polymorphism was detected for *Lynx pardina*, but it is here coded as derived.

**30. Frontal sinus, volume** (fig. 36): *Acinonyx jubatus* has an extremely large frontal sinus (state 1, fig. 36). *Uncia uncia* possibly presents the next largest degree of enlargement, but quantitative data are needed to

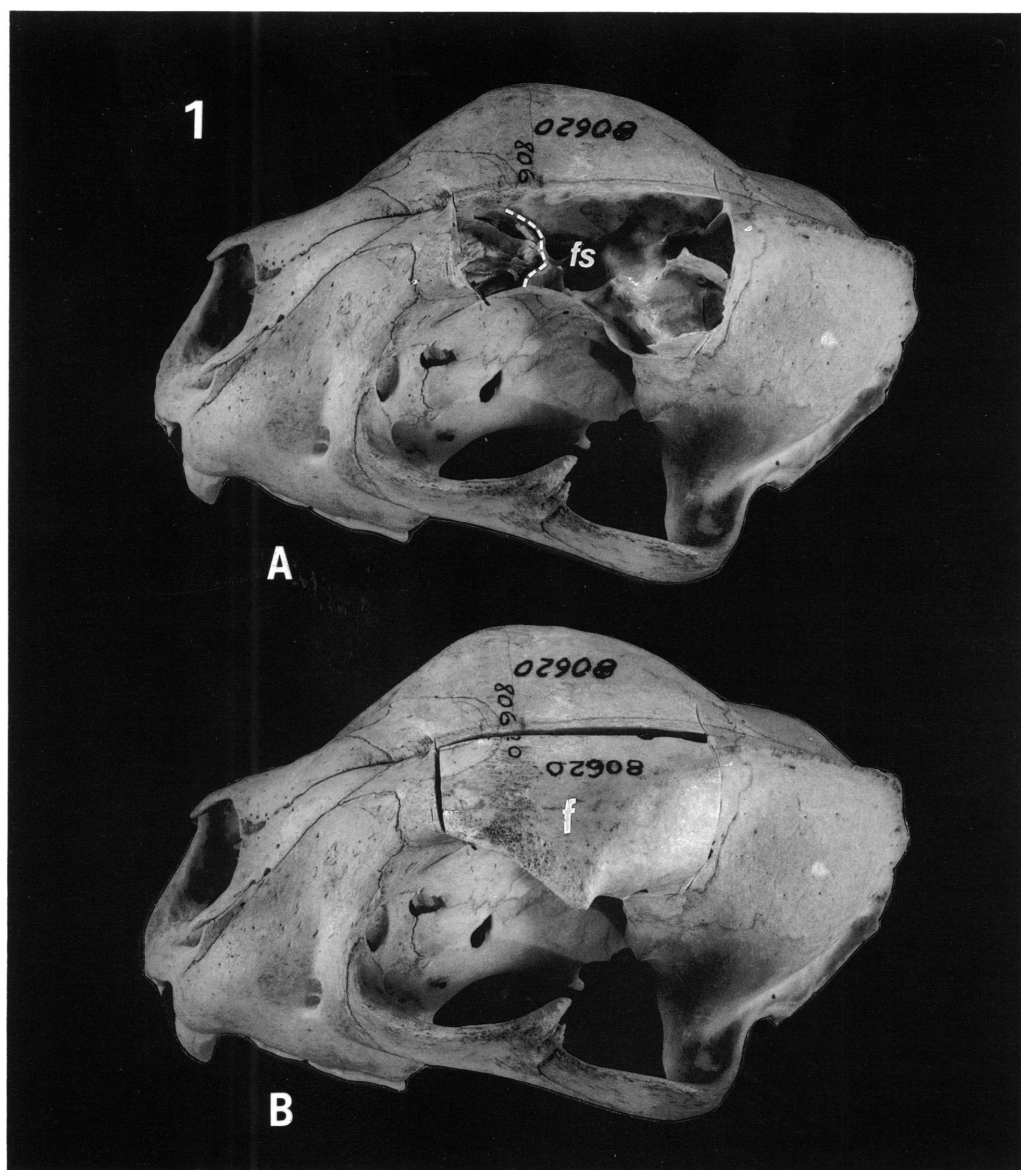


Fig. 36. Frontal sinus volume (character 30, state 1): A, *Acinonyx jubatus* (AMNH 80620); B, same specimen with part of the frontal removed to reveal the frontal sinus cavity (the dashed white line delimits the anterior end). Dorsolateral view, anterior to left.

verify this proposition. Hence it is here coded as 0. Examination of the frontal sinus in *Otocolobus manul* did not confirm Herrington's suggestion that this species shows a frontal sinus condition similar to that of cheetahs. Herrington proposed this character as a synapomorphy for these two species. The en-

larged superior surface of the frontal bone in the pallas cat gives the impression of a marked development of the cavity of the frontal sinus.

**31. Frontal bone, outer surface depression** (fig. 37): A marked depression symmetrically divided by the frontal suture, occupies most

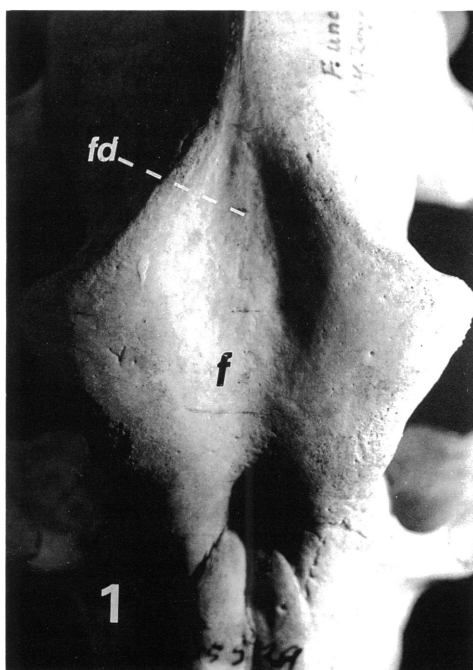


Fig. 37. Frontal outer surface depression (character 31): state 1, *Uncia uncia* (AMNH 35529). Dorsal view, anterior to bottom.

of the upper frontal region of the snow leopard, *Uncia uncia* (state 1; fig. 37). This is a unique derived feature for this species.

**32. Frontal bone, lateral expansion (fig. 38):** Expansion of the lateral surface of the frontal reaches its greatest breadth across the post-orbital processes. This feature is not a necessary function of the size of the frontal sinus, greater frontal expansion is not always accompanied by a markedly developed frontal sinus cavity. The incorrect assumption of correlation resulted in the synapomorphy suggested for *Acinonyx jubatus* and *Otocolobus manul* by Herrington (1986). In fact, as will be noted, these two species share a derived condition related to frontal breadth with a group of other species.

Expansion of frontal breadth characterizes a large group of cats. Two additive derived states have been proposed to formalize this character. The more general derived condition is that of marked but not great increase in width of the frontal (1). In the extreme development of this trait, the frontal breadth

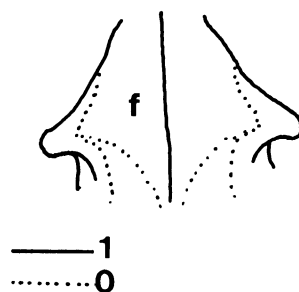


Fig. 38. Diagrammatic representation of the frontal lateral expansion (character 32): state 1 (continuous line), *Felis nigripes* (AMNH 214380); state 0 (dashed line), *Neofelis nebulosa* (AMNH 35808). Dorsal view, anterior to top.

measures more than half the condylobasal length (state 1; fig. 38). The plesiomorphic state is a relatively narrow frontal and occurs in *Neofelis nebulosa*, all *Panthera* species, *Uncia uncia* (has a close condition to state 1), *Prionailurus planiceps*, *P. viverrina*, *Leopardus geoffroyi*, *Profelis aurata*, and possibly *Caracal caracal*. This narrow condition also occurs in other aeluroids. Cats which display state 2 are: *Felis lybica*, *F. cafra*, *F. silvestris*, *F. nigripes*, *F. margarita*, *F. chaus*, *F. bieti*, *Otocolobus manul*, *Profelis badia*, *Prionailurus rubiginosa*, *Pardofelis marmorata*, and *Acinonyx jubatus*. The latter shows the most extreme development of frontal breadth. Other felids exhibit state 1 (see data matrix).

### Rostrum

Extant felids display significant variation in the rostrum, which includes the premaxilla, maxilla, and nasal. Arrangements are greatly affected by position and degree of development of the frontal sinus and nasoturbinal cavities. This is undoubtedly one of the most difficult regions of the felid skull in which to discover clear patterns of change, or useful phylogenetic characters, as can be seen in descriptions of this region's morphology (e.g., by Pocock, 1917b; Hattenorth, 1937).

Three related characters are described here for the rostrum, rostral constriction, nasal curvature, and frontonasal planes of curvature.

**33. Frontonasal region, dorsal profile (fig. 39):** The plesiomorphic rostral configuration

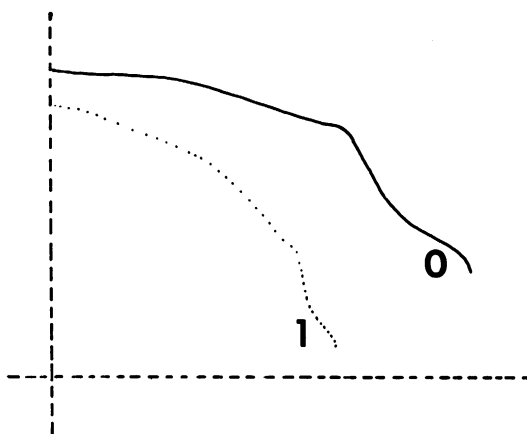
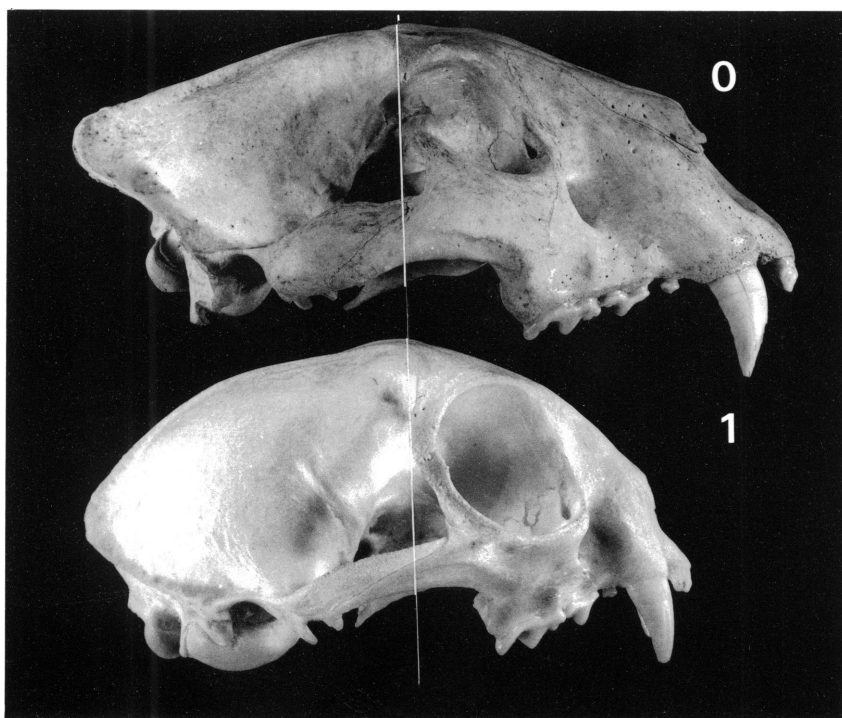


Fig. 39. Diagrammatic representation of a profile of the frontonasal region (character 33): state 1 (dotted line), *Pardofelis marmorata* (USNM 239326); state 0 (continuous line), *Panthera tigris* (AMNH 113744). Lateral view.

for felids shows no major change in the dorsal profile, the angle being less than  $25^\circ$  between the anterodorsal frontal and nasal parts. This condition distinctly occurs in *Prionailurus planiceps*, *P. viverrina*, *Neofelis nebulosa*, *Panthera tigris*, *P. onca*, *P. leo*, and *P. pardus*.

In other species there is a marked increase in the angle formed by the nasal and frontal parts of the profile, which reaches values of about  $45^\circ$  or higher (state 1; fig. 39), and there is generally a concave nasal profile. These species are *Acinonyx jubatus*, *Pardofelis mar-*

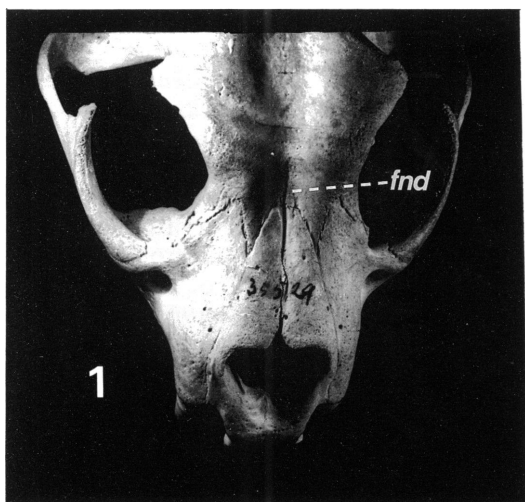


Fig. 40. Frontonasal region compressed (character 34): state 1, *Uncia uncia* (AMNH 35529). Frontal view.

*morata*, *Leptailurus serval*, *Caracal caracal*, *Lynx rufus*, *L. lynx*, *L. canadensis*, *L. pardina*, *Felis lybica*, *F. cafra*, *F. silvestris*, *F. nigripes*, *F. margarita*, *F. bieti*, and *Otocolobus manul* (the species that best illustrates this condition).

**34–36. Frontonasal region, shape** (figs. 40–42): Three species have unique modifications of this region. *Uncia uncia* has a distinctly dorsoventrally compressed frontonasal region, characterized by absence of upper nasoturbinal chamber expansion (state 1). Expansion is general among felids (fig. 40; state 0, character 34). The second unique condition occurs in *Herpailurus yagouaroundi*,

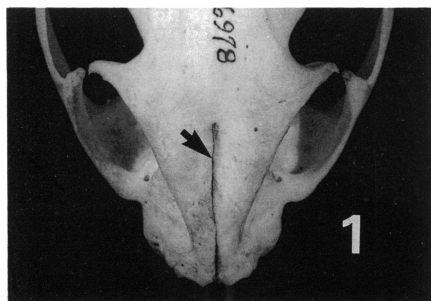


Fig. 41. Distinct fossa along the posterior internasal and anterior interfrontal sagittal sutures (character 35): state 1, *Herpailurus yagouaroundi* (AMNH 126978). Dorsal view.



Fig. 42. Salient ridge (shown by black arrows) along the upper orbital border extending onto the anterodorsal frontonasal region (character 36): state 1, *Pardofelis marmorata* (USNM 239326). Dorsofrontal view.

which has a deep and distinct fossa along the posterior internasal and anterior interfrontal sagittal sutures (fig. 41; state 1, character 35), a feature used by Pocock (1917b) as diagnostic for *Herpailurus*. The third unique rostral configuration, found in *Pardofelis marmorata*, is a salient ridge along the upper orbital border that extends onto the postero-dorsal frontonasal region (fig. 42; state 1, character 36).

**37. Rostral constriction** (fig. 43): Some felids exhibit a rostral constriction accompanied by enlargement of the upper part of the maxilla, best estimated by the length of a "horizontal" dorsal margin of the maxilla at the dorsolateral part of this region. This constriction is greatest between the dorsal maxillary margins of each side of the skull at the anterodorsal edge of the frontals. Maxillary enlargement seems related to the expansion of the nasoturbinal upper chambers, resulting in an extension of the frontonasal part of the dorsal profile. Two derived character states are proposed to represent the degree of rostral constriction. In state (1) the constriction is



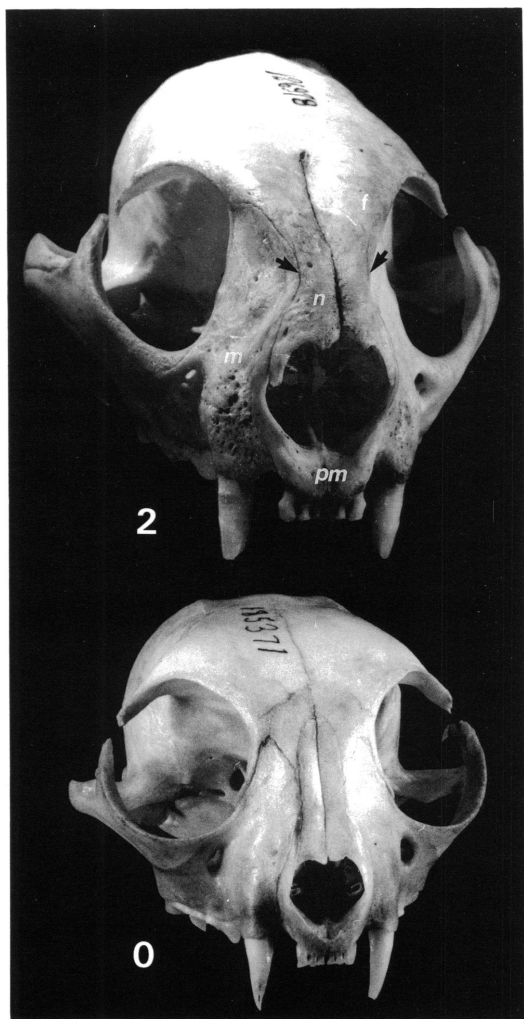


Fig. 43. Rostral constriction (character 37): state 2 (black arrows show anterior end of constriction), *Herpailurus yagouaroundi* (AMNH 126978); state 0, *Odocoileus columbianus* (AMNH 185371). Laterofrontal view.

limited to the posterior frontonasal region; this state is present in *Profelis aurata*, *P. badia*, *Prionailurus viverrina*, *Felis chaus*, *F. lybica*, *Caracal caracal*, *Leptailurus serval*, *Lynx rufus*, and *Puma concolor*. In state (2), the rostral constriction distinctly reaches the area between the anterior frontal and posterior premaxilla tips (fig. 43). This further rostral constriction was recorded for *Herpailurus yagouaroundi*, *Leopardus tigrina*, *L. guigna*, *L. geoffroyi*, *L. colocolo*, *L. wiedii*, *L. pardalis* (not as clearly as in the other *Leopardus* spe-

cies), *Profelis temminckii*, *Prionailurus bengalensis*, and *P. rubiginosa*. The plesiomorphic condition is the absence of rostral constriction. This polarization is unequivocally supported by outgroup comparisons.

**38. Nasal curvature** (fig. 44): Nasal curvature is related to rostral constriction. Felids generally have a concave curvature of the nasal near the junction of the frontal and the premaxilla. Some species of *Leopardus* display a convex anteroposterior nasal surface. Some felids, as well as other aeluroids, differ in having the nasal surface nearly constituting a single flat plane. This feature is complex, and only the condition characterized by a well-marked concave curvature (1) at the region noted (fig. 44) is here singled out. Taxa displaying this derived condition are *Felis silvestris*, *F. nigripes*, *F. margarita*, *F. bieti*, and *Odocoileus columbianus*.

**39. Interorbital breadth** (fig. 45): This breadth is variable in felids. An extremely narrow interorbital breadth occurs in *Prionailurus viverrina* and *P. planiceps* (state 1; fig. 45).

**40. Infraorbital foramen** (fig. 46): This infraorbital foramen is extremely variable in shape and diameter among felids. Herrington (1986) suggested that *Acinonyx jubatus* has a considerable reduction of this foramen (state 1; fig. 46), and I have confirmed this. Hence, this feature was added to the set of autapomorphies for cheetahs.

**41. Maxilla expansion over infraorbital foramen** (fig. 47): The degree of maxillary expansion above and below the infraorbital foramen is highly variable. Rarely among felids are these maxillary expansions fused at the upper infraorbital surface; the jugal generally extends to contact the lacrimal. In *Uncia uncia* this fused maxillary area is uniquely enlarged and the jugal is nearly excluded as an element of the superior infraorbital surface (state 1; fig. 47). A tendency for this condition was recorded for *Profelis aurata*, however this species was not considered as having the derived state for this character.

**42. Jugal and frontal postorbital processes** (fig. 48): In a few extant felids the jugal and frontal postorbital processes tend to fuse, forming a continuous postorbital bar encircling the orbit. Two derived additive states are proposed for this character. The more





Fig. 44. Nasal curvature (character 38): state 1 (white arrow points to nasal concave depression), *Felis bieti* (SMNH A585295); state 0, *Neofelis nebulosa* (AMNH 35808). Laterofrontal view.

general state (1) has a tendency for encircling the orbit, and the other, less inclusive state (2) has the well-developed postorbital processes totally fused (fig. 48). The complete postorbital bar condition (2) is present only in *Pardofelis marmorata* and *Prionailurus planiceps*. The more general derived condition (1) occurs in *Prionailurus viverrina*, *P. bengalensis*, *P. rubiginosa*, *Profelis badia*, and *Otocolobus manul*. This trait was not found among other aeluroids; therefore its polarization is considered to be well corroborated by outgroup criteria.

**43. Jugal anterior process** (fig. 49): Comparative morphology of the zygomatic arch failed to reveal major discrete patterns of variation. Nevertheless, an anterolateral projection of the jugal over the infraorbital foramen (state 1; fig. 49) was considered to be a derived condition. *Panthera tigris*, *P. onca*, *P. leo*, *P. pardus*, *Acinonyx jubatus*, *Uncia uncia*, *Lynx lynx*, *L. pardina*, and *L. canadensis* lack this derived trait. *Otocolobus manul* and *F. margarita* are of questionable status and, because the jugal is extremely

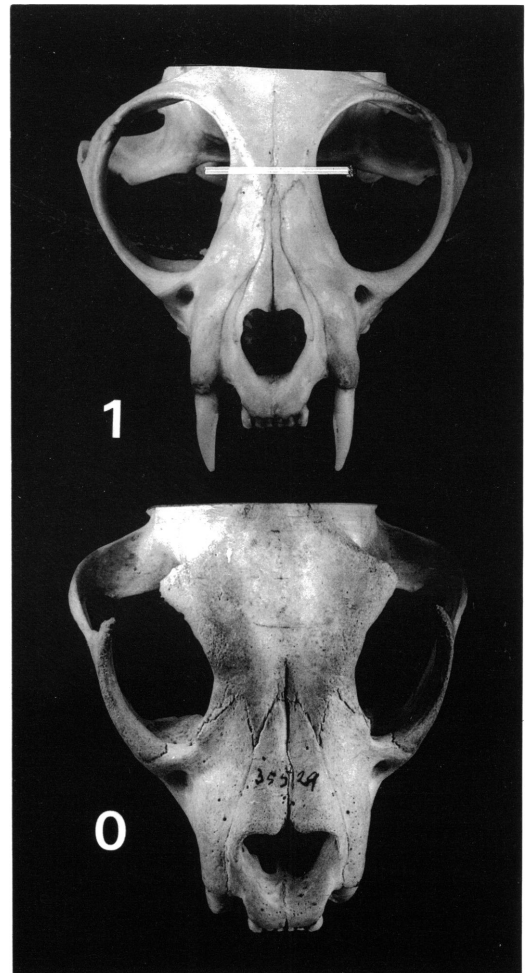


Fig. 45. Interorbital breadth (character 39): state 1 (white bar, proportional to skull size, represents plesiomorphic condition of interorbital breadth); state 1, *Prionailurus planiceps* (USNM 49973); state 0, *Uncia uncia* (AMNH 35529). Dorsal view.



Fig. 46. Infraorbital foramen (character 40): state 1, *Acinonyx jubatus* (AMNH 36426); state 0, *Uncia uncia* (AMNH 35529). Laterodorsal view, anterior toward left.

modified in these two species, were coded as missing data. All other felids possess the derived condition (1). Mazak (1968) proposed this character as diagnostic for extant species of *Panthera* plus *Uncia uncia*. The anterior

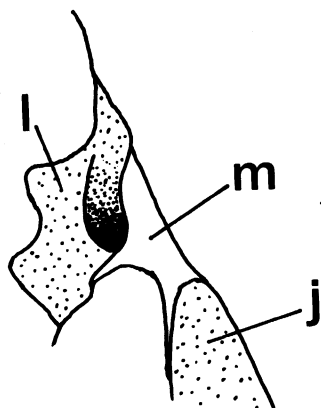


Fig. 47. Maxilla expansion over the infraorbital foramen (character 41): state 1, *Uncia uncia* (AMNH 35529). Dorsal view, anterior toward top.

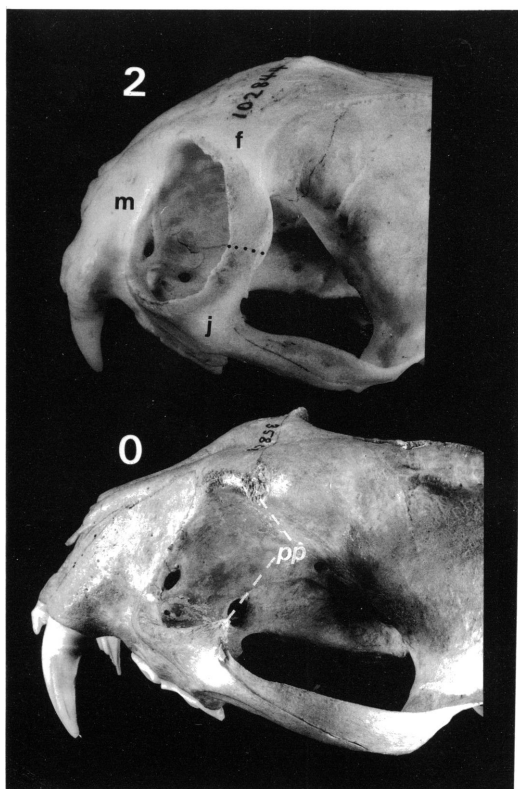


Fig. 48. Postorbital processes (character 42): state 2, *Pardofelis marmorata* (AMNH 102844); state 0, *Neofelis nebulosa* (AMNH 35808). Lateral view, anterior to left.

projection might be a synapomorphy for Felidae, later lost in some species, or alternatively a synapomorphy of a felid subclade. Similar alternative paths of character state change were described for the position of the frontal sinus and posterior part of the first caudal ethmoturbinate scroll.

**44. Lower rim of the orbit (fig. 50):** All extant species of the genus *Felis* (except *F. chaus*) and *Otocolobus manul* exhibit a modified flat, enlarged, and medially inflected lower rim surface (state 1). In *F. nigripes*, *F. margarita*, *F. bieti*, and *O. manul* the lower rim of the orbit further displays a distinct anterior projection in an open angle (fig. 50; state 2). These two related features are interpreted as unambiguously derived for these taxa.

Overall, a total of 21 autapomorphies and 33 shared derived character states of the felid skull emerge as basic phylogenetic evidence.

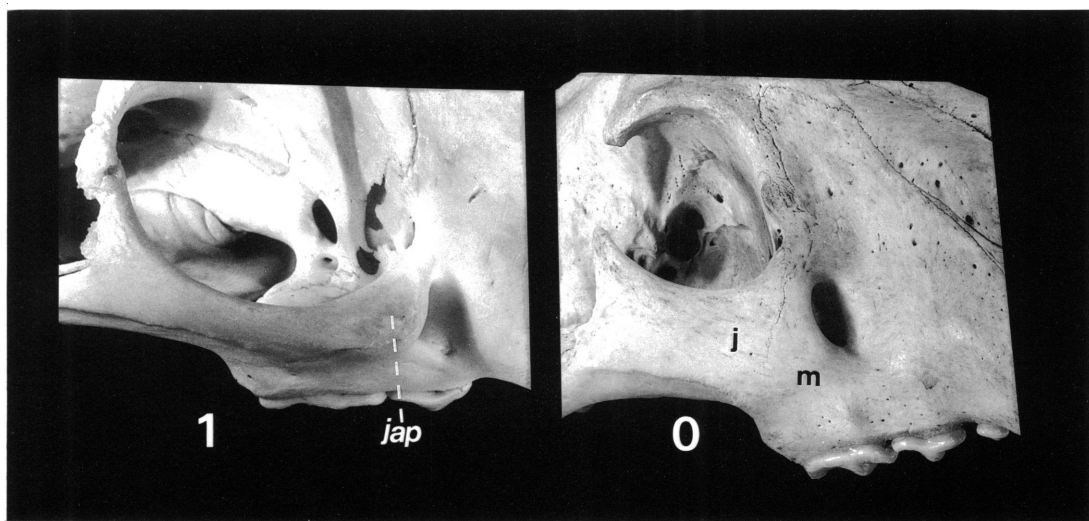


Fig. 49. Jugal anterior process (character 43): state 1, *Prionailurus viverrina* (AMNH 102691); state 0, *Panthera leo* (AMNH 81838). Laterodorsal view, anterior toward right.

#### CRANIAL OSTEOLOGY, INTERNAL CONGRUENCE

In this section I discuss results from a parsimony analysis of cranial characters de-

scribed in the previous section. A set of non-cranial features (characters 45 to 57) are later added to the cranial matrix, which considerably affects results based on cranial data alone. As mentioned under Methods, two

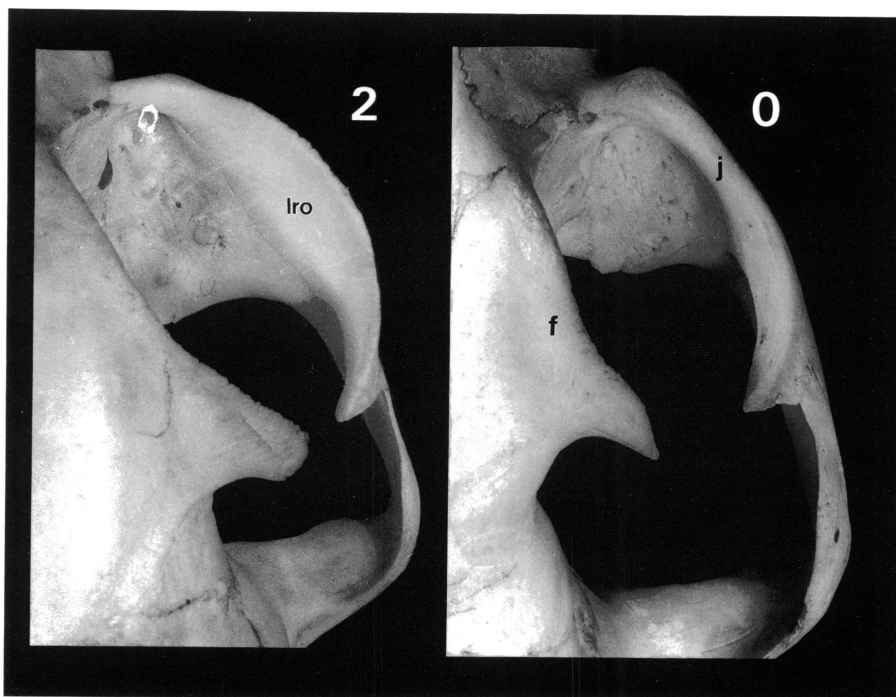


Fig. 50. Lower rim of the orbit (character 44): state 2, *Felis nigripes* (AMNH 214380); state 0, *Caracal caracal* (AMNH 116512). Dorsal view, anterior toward top.



branch-swapping algorithms (mhennig\* and bb\*) from the Hennig86 program (Farris, 1988) were applied for all data examined in this study. The bb\* command differs from mhennig\* for generating all possible trees allowed by its logic structure. The combination mhennig\* bb\* has been considered by Farris (1988) as a reasonable option when dealing with large data matrices.

After use of the combination mhennig\* bb\* on the data matrix composed of the 44 cranial characters (see table 1, features 1 to 44) of the 38 recent felids studied, with three characters left unordered (1, 18, and 26), 1348 equally parsimonious trees with length of 124 and a consistency index of 0.45 were calculated. The Nelson consensus of these 1348 trees (appendix 1) presented only three clades rooted at the basal node, and 24 species directly branching off from the basal node. This tree is discussed later.

The successive weighting option (a procedure that fundamentally weights characters according to their consistency index, thus maximizing overall congruence; Farris, 1969; and Carpenter, 1988) was then applied, and 229 trees with length 431 and consistency index of 0.80 followed as the new outcome. Note that the point made by Carpenter (1988) about the necessity of recoding multistate characters to binary, when using the successive weighting option, is not applicable to the Hennig86 program (Farris, personal commun.). The Nelson consensus of these 229 trees resulted in a tree topology with three major components, and nine species (*Leopardus pardalis*, *L. tigrina*, *L. geoffroyi*, *L. guigna*, *Profelis aurata*, *P. temmincki*, *Felis chaus*, *Puma concolor*, and *Herpailurus yagouaroundi*) comprising an area of the tree with no phylogenetic information. These nine species and the three major components formed a polytomy at the base of the cladogram.

Examining the data in light of these results, I discovered that the lack of resolution at the base of the cladogram was due to the lack of sufficient character types to "fully resolve" the tree, rather than any major character incongruence. With 38 taxa and 44 characters, a well-resolved most parsimonious tree seems unlikely. Nevertheless, the largest clade of the three recognized above is composed of 22

terminal taxa and displays only one trichotomy at the top of the clade.

In order to better reveal the phylogenetic information in the set of cranial attributes, the same procedure described above was used with a data matrix of 33 taxa. *Herpailurus yagouaroundi*, *Puma concolor*, *Profelis aurata*, *Leopardus guigna*, and *Felis chaus* were excluded from this analysis. The 229 most parsimonious trees were reduced to eight (with a length of 413 and consistency index of 0.80, the latter unchanged). A modified Nelson consensus (analogous to "general cladograms" of Nelson, 1979, and biogeographic consensus of Nelson and Platnick, 1981) of these eight trees are represented in figure 51. Components 2 and 4 were not part of the Nelson consensus. What differentiates these two cases from the other conflicting hypotheses seen here is that the absence of these two components involves only a decrease in the resolution of the consensus. Attempting to reveal the maximum potential phylogenetic information present in the 44 cranial attributes studied, I considered it acceptable to preserve these two components until new evidence suggests otherwise (see Mickevich and Platnick, 1989, for discussion).

Three competing hypotheses relate to the trichotomy at the base of this consensus cladogram (fig. 51). One places component 1 as the sister group of 3, and a second places component 3 as the sister taxon of 8. The first hypothesis ([1, 3] 8) is supported by the marked rostral constriction (character 37, state 2) at the node (1, 3), and the presence of rostral constriction (1) as a synapomorphy of the whole family Felidae. Following the second hypothesis (1 [3, 8]), state 1 of character 37 is the evidence for the relationship between component 3 and 8. According to the third hypothesis, the rostral constriction does not support either of the first two; it is characterized by a trichotomy at the base of the cladogram, and the presence of the rostral constriction is qualified again as a synapomorphy for the family. The transformation series of rostral constriction character states is complex, requiring nine steps under the most parsimonious weighted arrangement, and after the second weighting its consistency index was 0.65.

The three basal taxa of component 3,

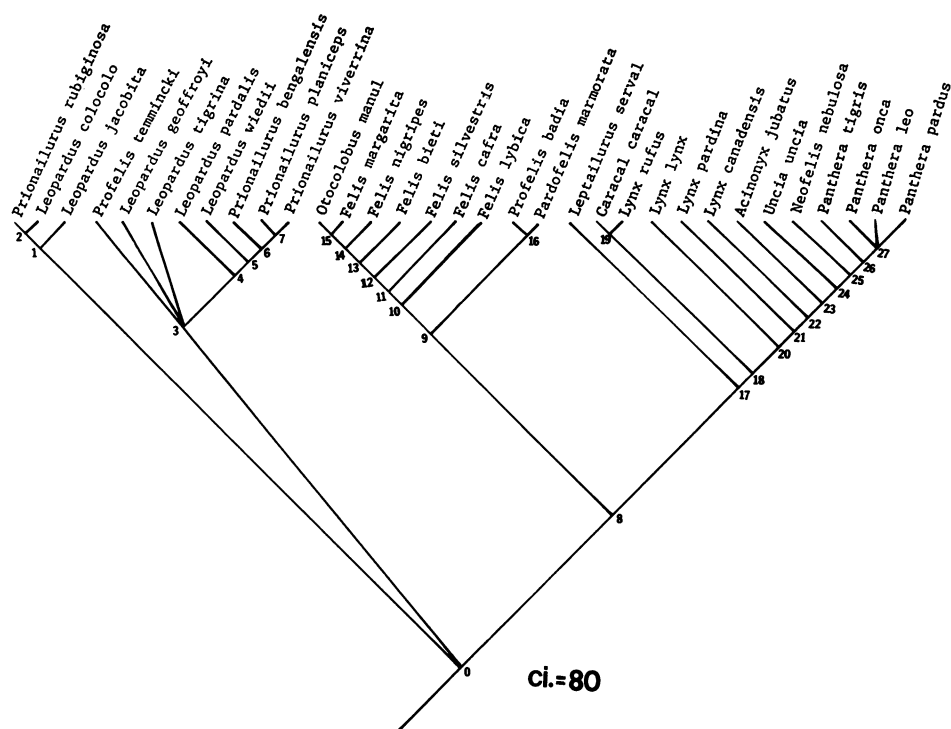


Fig. 51. Consensus of eight equally parsimonious trees resulting from the cranial congruence analysis based on 44 characters for 33 of 38 taxa.

namely *Profelis temminckii*, *Leopardus geoffroyi*, and *L. tigrina*, comprise another problematic area of this cladogram. None of the eight most parsimonious trees places any of these three species at any other position within component 3. As mentioned earlier, *Leopardus pardalis* was part of this area in some of the most parsimonious trees, where the few basal taxa are placed at the node of the clade. Nodes 4 and 5 are represented by the ambiguous presence of two derived states proposed for the closure of the subarcuate fossa (character 20). *Leopardus pardalis* and *L. wiedii* display the further derived state 2 in contrast to the other members of component 3, which exhibit state 1, although *Leopardus geoffroyi* is plesiomorphic for this character. This ambiguity is related to two alternative paths of minimum "evolutionary" change for character state 2. It could be interpreted as a synapomorphy of component number 4, subsequently lost by the *Prionailurus* group (node 6), or as two independent appearances in *L. pardalis* and *L. wiedii*. A similar situation

occurs with component 2, comprising *Leopardus jacobita*, *Leopardus colocolo*, and *Prionailurus rubiginosa* and the presence of the rostral constriction, which is only present in the last two species.

All other areas of the cladogram illustrated in figure 51 are identical among the eight most parsimonious trees. As an outcome of this consensus, five major groupings are distinguished (only features unambiguously tied to their defining nodes are listed in the diagnoses of these components, which follow):

Component 1: This defines the monophyly of an intriguing composite of species (*Leopardus jacobita*, *L. colocolo*, and *Prionailurus rubiginosa*). This grouping is supported by the derived condition of the upper canine lingual ridge (character 11, state 2) and the presence of the lower canine lingual crest followed by a deep cavity along its anterior edge.

Component 3: This clade includes eight taxa, as was shown earlier, *Profelis temminckii*, *Leopardus geoffroyi*, *L. tigrina*, and component 5, which can be transcribed in

parametric notation as (*L. pardalis*, *L. wiedii* (*Prionailurus bengalensis* (*P. viverrina* (*P. planiceps*))). This clade is supported by the derived inferior head of the incus with mal-leus condition (character 25), which is characterized by a distinct outward projection.

Component 8: This is the largest grouping in the consensus tree, composed of two major inclusive clades, 9 and 17, discussed separately below. The character supporting the monophyly of group 8 is the abrupt change on the plane of curvature of the dorsal frontonasal surface (character 33). This condition was lost in component 25.

Component 9: This includes two major sister taxa. The first, component 10, consists of all species of the *Felis* group considered in this analysis plus *Otocolobus manul*, placed at the very top of this hierarchical branching as the sister taxon of *F. margarita*. The other group, component 16, consists of *Profelis badia* and *Pardofelis marmorata*. A parenthetical representation of these relationships is: ((*Profelis badia*, *Pardofelis marmorata*) (*Felis lybica* (*F. cafra* (*F. silvestris* (*F. bieti* (*F. nigripes* (*F. margarita*, *Otocolobus manul*))))). The monophyly of component 10 is based on the presence of a well-developed (deep) external pterygoid fossa (character 17), and character 32, state 2, for the enlargement of the frontal breadth.

Component 17: This component has the peculiarity of including all large extant felids considered, plus all lynxes, the caracal, and the serval. *Leptailurus serval* is the basal branch of component 17. No cranial feature supported the monophyly of lynxes. Curiously enough, *Caracal caracal* came out as the sister group of *Lynx rufus*; this clade was the second most plesiomorphic taxon of component 17. This paraphyletic area constituted by the lynxes and the caracal is limited between nodes 17 and 23. Within this scheme of synapomorphies for component 17, the best-supported relationships are represented by the following sequence: (*Acinonyx jubatus* (*Uncia uncia* (*Neofelis nebulosa* (*Panthera tigris* (*P. onca*, *P. leo*, *P. pardus*))), which have a hypothetical common ancestor represented as component 23. This clade is based on the fusion of the para- and metastyle roots of the upper fourth deciduous premolar (character 2). The monophyly of component

17 is supported by the marked reduction of the fourth premolar protocone (character 7).

The relation between the number of components and the number of terminal taxa minus one ( $c/t - 1$ ) is here taken as a measure of the overall character congruence (resolution) obtained. The examined tree, displaying 27 components and 33 terminal taxa has this relation represented by a value approximately 0.85. This value can serve as a general index of the internal cranial osteological congruence acquired for the 33 extant felids considered. Given the preliminary nature of this data set, it can be interpreted as a very reasonable result. None of the components of the first, unweighted consensus tree (appendix 1) are incongruent with the components of the cranial tree (fig. 51). The identical components between these two trees, weighted (fig. 51) and unweighted (appendix 1), are: 1 = 46; 26 = 47 (all inclusive components of both clades are also identical); 10 = 48. The last two pairs have all their inclusive components identical.

## OTHER MORPHOLOGICAL FEATURES

A brief description of noncranial felid features is presented here. These statements are summarized from pertinent literature (only gross morphology is considered in this cladistic character review) and enumerated below:

45. The hyoid apparatus was described by Pocock (1916a) who suggested that an imperfectly ossified suspensorio hyoid, with a cartilaginous ligament connecting the styloid process to the ceratohyal is a condition (1) unique to *Panthera tigris*, *P. onca*, *P. leo*, *P. pardus*, and *Uncia uncia*. This condition contrasts with a more general condition in which the hyoid elements are fully ossified, without a cartilaginous ligament.

46. The head of the fibula with a greater development of an anteriorly projecting flange (state 1) was suggested by Herrington (1986) as a derived feature shared by *Acinonyx jubatus*, *Puma concolor*, and *Herpailurus yagouaroundi*.

47. Tendon for extensor digitorum longus originating on the lateral epicondyle of the femur, passing through a notch on the head



of the tibia, and under a flange (1). This was said by Herrington (1986) to occur only in *Acinonyx jubatus*, *Puma concolor*, and *Herpailurus yagouaroundi*.

48. Olecranon of the ulna, showing emphasis of the medial side as a site for muscle attachment (1), is another character studied by Herrington (1986), and polarized as derived for *Acinonyx jubatus* and *Otocolobus manul*.

49. A reduction of caudal vertebrae, accompanying a very short tail, is a diagnostic attribute (state 1) for *Lynx lynx*, *L. pardina*, *L. rufus*, and *L. canadensis* (Pocock, 1917b).

50. Pocock (1917a) discussed external felid morphology and reported that *Felis chaus*, *F. lybica*, *F. cafra*, *F. silvestris*, *F. bieti*, *F. margarita*, *F. nigripes*, *Caracal caracal*, *Lynx lynx*, *L. pardina*, *L. rufus*, and *L. canadensis* display a distinctly angular and pointed shape at the tip of the ear (1). I consider *Leptailurus serval* to be of questionable designation in this regard.

51. Pocock (1917a) proposed two character states for the presence of a pencil of hair at the tip of the ears. In the first, the tip is provided with a long well-developed pencil (state 2), a condition unique to *Lynx lynx*, *L. pardina*, *L. rufus*, *L. canadensis*, and *Caracal caracal*. The second state (1) is a short, rudimentary developed pencil, which occurs only in *Felis chaus* and *F. lybica*.

52. Rhinarium reduced (1) is unique to *Felis chaus*, *F. lybica*, *F. cafra*, *F. silvestris*, *F. bieti*, *F. margarita*, and *F. nigripes* (Pocock, 1917a). *Otocolobus manul* is coded as missing data.

53. Interdigital webs of hind foot are distinctly reduced (1) in *Acinonyx jubatus* and *Caracal caracal* (Pocock, 1917a).

54. Digit tips (fore and hind feet), with at least a single cutaneous lobe protecting the retracted claw on the inner side of digits 2 and 3 and on the outer side 4 and 5 (state 1) is a complex suggested by Pocock (1917b) as diagnostic of a large group of felids, excluding only *Acinonyx jubatus*, *Uncia uncia*, and the *Panthera* group.

55. Reversed neck fur, growing forward instead of backward (1) is a condition present only in *Leopardus pardalis*, *L. wiedii*, *Profelis aurata*, *Panthera tigris*, *P. leo*, *P. onca*, and *P. pardus* (Pocock, 1917b); *Profelis badia* is considered indeterminate.

56. Nawa (1967) studied the pupils and noted that a round pupil (1) occurs in *Herpailurus yagouaroundi*, *Puma concolor*, *Acinonyx jubatus*, *Uncia uncia*, *Panthera tigris*, *P. onca*, *P. leo*, and *P. pardus*. This was first considered to be derived for felids by Herrington (1986), but for a reason not specified (because data used were also based on Nawa's work) she excluded *U. uncia* and *Panthera* from this grouping. For a number of taxa, data were not available; see missing data in table 1.

57. The felid tongue was studied by Sonntag (1923). Among various statements presented, I was able to polarize (based on text and figures) only the following character: spinous patch beginning close to the apex of the tongue (1) which is unique to *Herpailurus yagouaroundi*, *Puma concolor*, *Panthera tigris*, *P. onca*, *P. pardus*, and *P. leo*. For a number of taxa, data were not available, see missing data in table 1.

## FELID MONOPHYLY

As previously discussed, relationships within aeluroids are controversial. No resolution was reached at the level of the felid sister-group relationship (see for discussion Flynn et al., 1988). Synapomorphies that confine felids in the idealized aeluroid type structure are the following (character numbering follows that previously used):

58. Ectotympanic chambered (Hunt, 1987).

59. Caudal entotympanic expanded and inflected (Hunt, 1987).

60. Margin of caudal entotympanic inflected to form true septum bullae (Hunt, 1987).

61. Ventral promontorial process applied to the lateral edge of the basioccipital (Hunt, 1989).

62. Hypoglossal foramen closely adjacent to, or confluent with, posterior lacerate foramen (Wozencraft, 1989).

63. Paroccipital process cupped around posterior edge of entotympanic (Wozencraft, 1989).

64. Cowper's (bulbourethral) gland present and well developed (Wozencraft, 1989).

65. Prostate large bilobed ampulla (Wozencraft, 1989).



66. P<sup>4</sup>, parastyle present (Flynn et al., 1988).

These characters are assumed to be non-controversial evidence for monophyly of Felidae.

Basing their views on basicranial morphology, Flynn and Galiano (1982), Neff (1983), and Hunt (1987) rejected the hypothesis of Nimravidae (paleofelids) as sister group of Felidae.

**Cranial attributes interpreted here as synapomorphies for Felidae are:**

27. Frontal sinus centralized in region of the postorbital processes, ranging from the posterodorsal part of the rostrum to the postorbital region (indicated above as a case of neoteny).

29. Posterior wall of the first caudal ethmoturbinate scroll placed well anterior to or just anterior to a line across the postorbital process.

37. Presence of a marked rostral constriction.

43. Jugal anterior process projected anteriorly over the infraorbital foramen.

**Other morphological characters providing evidence for the monophyly of Felidae are:**

54. Digit tips with at least a single cutaneous lobe protecting the retracted claw on the inner side of digits 2 and 3 and on the outer side of 4 and 5 (Pocock, 1917b).

67. Carotid canal absent (Wozencraft, 1989).

68. Course of the internal carotid exterior to entotympanic (Wozencraft, 1989)

69. Caudal entotympanic intervenes between ectotympanic and rostral entotympanic (Hunt, 1987).

70. Modified rhinarium (Hunt, 1987).

71. Loss of interramal facial tuft (Hunt, 1987).

To conclude, nine characters were suggested to be defining for Aeluroidae, and 10 morphological synapomorphies were postulated for Felidae. Felid soft anatomy is still an open area for basic discoveries.

#### PHYLOGENETIC RELATIONSHIPS OF FELIDAE

Results of a parsimony analysis of 57 morphological characters studied (data matrix in table 1) for 38 extant felids are considered here. After use of the mhennig\* and bb\* com-

mands of the Hennig86 program, leaving unordered those characters cited as such in the cranial analysis plus character 51, 409 trees with a length of 157 and a consistency index of 0.45 resulted. The Nelson consensus of these 409 trees (appendix 2) has five clades rooted at the basal node and seven species branching off from this same basal node. This consensus tree is discussed under Concluding Remarks. Given the notorious difficulty in analyzing felid morphology, it is plausible to expect it to be expressed here as part of the "noise" present in the data. Therefore, successive weighting is applied in order to differentially weight characters according to their consistency index. Successive weighting reduced 409 most parsimonious to 18 trees (see Salles, 1991) with a length of 503 and a consistency index of 0.77. A Nelson consensus of these 18 is illustrated in figure 52; this is, in fact, a modified Nelson consensus tree in reference to one node, node 2. The justification for such a measure is analogous to that presented earlier. A lack of resolution was detected only in some of the 18 trees in which node 2 was absent. The decision here was again made in order to maximize consistent character information.

This consensus tree has two distinct areas, the first formed by the paraphyletic branching interval limited by the components 0 and 3. This basal area is composed of four terminal taxa: ((*Prionailurus planiceps*, *P. viverrina*) (*Profelis aurata* (*Leopardus geoffroyi*, component 4))). The second area is represented by component 4; it is placed above under parenthetical notations as the sister group of *Leopardus geoffroyi*. This component presents a polytomy at the basal node (4); this is due to such a number of conflicting hypotheses of interrelationships among five components (5, 6, 7, 8, and 15) and two terminal taxa (*Leopardus tigrina* and *Leopardus guigna*), that detailed discussion is not worthwhile given the myriad arrangements figured. One of the 18 trees has a branching pattern displaying a clade that includes the major components 8 and 16 (from the consensus tree) plus *Leopardus tigrina*-*L. guigna* and *L. pardalis*-*L. wiedii* (as sequential sister groups). Two other trees that deserve comment, as they are the most informative trees with respect to their greater number of components, 32 components for 38 taxa.

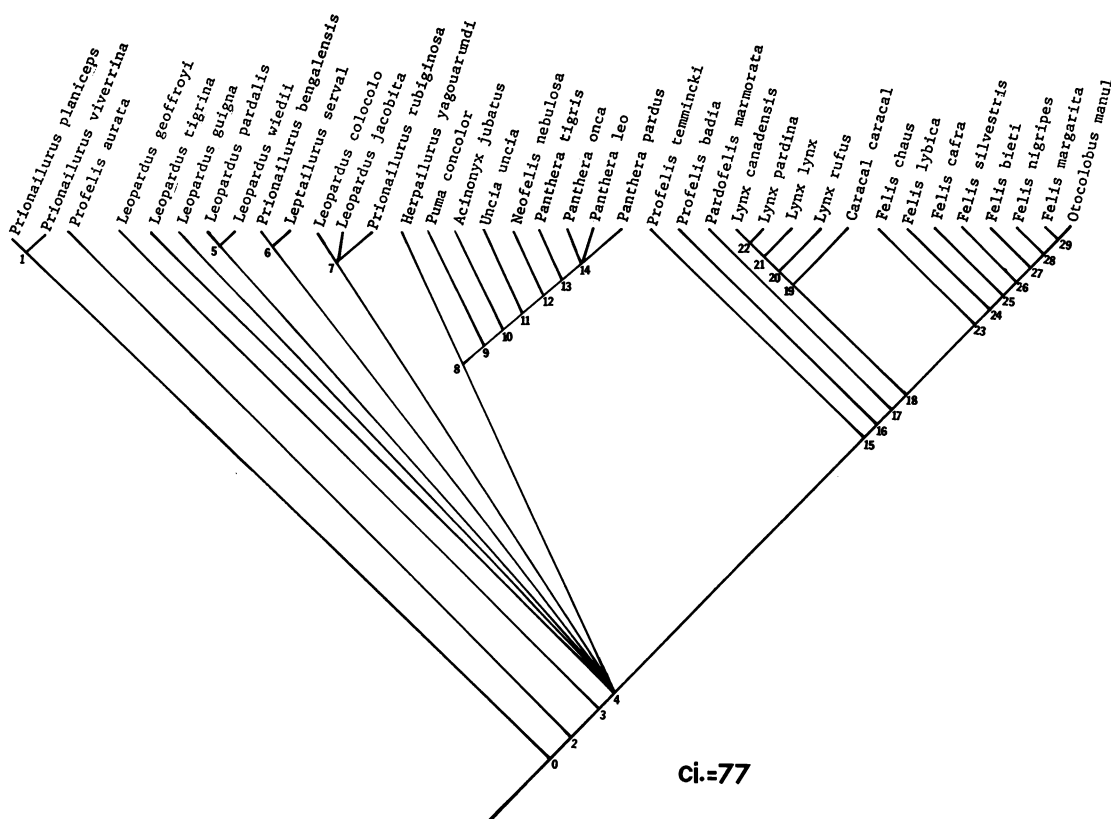


Fig. 52. Consensus of 18 equally parsimonious trees resulting from the morphological character analysis of 57 characters for 38 taxa.

#### BASAL TAXA

A basal area of the consensus cladogram is restricted to the paraphyletic branching limited by nodes 0 and 3. Before I discuss the characters of the basal components, it is relevant to note that this area is not present on the cranial summary of synapomorphies, and that it results only after the use of successive approximation weighting.

What first appears curious is the placement of *Prionailurus planiceps* and *P. viverrina* (component 1) as the most plesiomorphic extant felids. Notice that *Prionailurus bengalensis* is not part of this grouping, but is instead a member of component 4. This arrangement therefore indicates an element of paraphyly at the *Prionailurus* rank. Nevertheless, the cranial data alone do support the monophyly of *Prionailurus* (if *P. rubiginosa* is excluded as Herrington suggested in

1986), with *P. bengalensis* as the sister taxon of the group formed by the two other species. The marked interorbital constriction (character 39, with a consistency index of 1.00), foramen rotundum on the basicranium (character 16), subarcuate fossa poorly developed (character 20, state 1), well-developed post-orbital process (character 42, state 1) are the four pieces of evidence for the monophyly of component 1.

*Profelis aurata* is the second most plesiomorphic taxon in this consensus tree, rooted at node 2 as sister taxon of clade 3. This relationship established a break of identity of *Profelis* as a monophyletic group, since the other two species (*P. temminckii* and *P. badia*) of this "group" constitute a paraphyletic area limited by nodes 15 and 16. As previously noted, component 2 is not present in all 18 trees. Presence of rostral constriction (character 37, state 1) is ambiguously present at

nodes 1 and 0, which renders questionable the rostral constriction as a synapomorphy for clade 2 (this condition is apparently absent in *Prionailurus planiceps*).

*Leopardus geoffroyi* is placed within the basal area as the sister group of the clade 4. This is an intriguing result, the first evidence of the morpho-based cladogram against the monophyly of *Leopardus*, with *L. geoffroyi* emerging from node 3. Clade 3 has as synapomorphies the distinct outward projection of the inferior head of the incus with malleus (character 25) and the rostral constriction distinctly reaching the area between the anterior frontal and posterior premaxilla tips (character 37, state 2).

#### AFFINITIES IN CLADE 4

This clade has five major components and two terminal taxa forming a basal polytomy. Note that *Leopardus* species, except *L. geoffroyi* (which is not a member of this clade), composed a paraphyletic area which includes *L. tigrina*, *L. guigna*, and components 5 and 7. *Leopardus pardalis* and *L. wiedii* (component 5) are supported as sister taxa by the synapomorphy of reversed neck fur. No cranial evidence supports the grouping of these two species. A presumably independent development of reversal of the neck fur also supports the monophyly of *Panthera*. Clade 4 has character 32, the frontal lateral expansion, as an unambiguous synapomorphy.

Component 7, *Leopardus colocolo*, *L. jacobita*, and *Prionailurus rubiginosa*, is identical to component 1 of the cranial cladogram presented in figure 51, which differs only in the presence of an inclusive component 2 (*L. colocolo* and *P. rubiginosa*) that is absent in component 7 of figure 52. Component 7 has its monophyly supported by the presence of a well-developed upper canine lingual ridge (character 11) and the cavity along the anterior border of the lower canine lingual ridge (character 12). These two character states are also placed at node 29.

*Prionailurus bengalensis* and *Leptailurus serval* constitute the terminal taxa of component 6. The feature revealing this grouping is the reduction (state 1) of the protocone of the upper fourth premolar (character 7). This character displays five steps in all 18 most

parsimonious trees and a final consistency index of 0.72. This relationship came as an unexpected result, given the position assumed by both of these species in the tree based on cranial characters alone. In the cranial cladogram, *Prionailurus bengalensis* is placed as the sister taxon of *P. viverrina* and *P. planiceps*, and *L. serval* is the sister group to a separate larger clade (based at node 17 in fig. 51). That larger clade includes *Caracal*, *Lynx*, and component 22 which is identical to component 10 of figure 52. Clade 6 of figure 52 should be carefully considered; none of the 18 trees presents further resolution regarding this clade's affinities.

Component 8 and component 15 are discussed in the next section.

#### TRANSFORMATION SERIES

Given the complexity of the topographical scenario of the 18 equally parsimonious trees of the successive weighting analysis of the expanded data set (fig. 52), the examined transformation series are restricted to two clades. Based on these 18 trees, transformation series were postulated for characters chiefly involved in relationships within clade 8 and separately within clade 15.

#### CLADE 8

Among the 22 characters considered synapomorphies within clade 8, 4 of those 16 that were originally binary remained so; 3 others are only potentially binary, since at one or more node they are ambiguous; 8 displayed only reversals; and 1 became only homoplastic (lost its identity, as proposed in the section on character topographical correspondence). Of 6 multistate characters, 2 showed no reversals or homoplasy, 2 presented reversals, and 2 became homoplastic (reversal is a distinct case of homoplasy).

Character 2: Fusion of the upper fourth deciduous premolar para- and metastyle roots (1) is a synapomorphy for clade 9, which comprises *Puma concolor*, *Acinonyx jubatus*, *Uncia uncia*, *Neofelis nebulosa*, and *Panthera*. Character state 1 appears at this node in all 18 most parsimonious trees. As discussed earlier, the more advanced condition of these roots' fusion (character state 2) is an

autapomorphy for *A. jubatus*, and under the scenario described character state 2 was derived from an hypothetical common ancestor (of clade 10) displaying the less inclusive state 1.

Character 4: The derived, lateral quasi-flat surface of the second posterior accessory cusp of the lower third deciduous premolar is unambiguously present at nodes 14, 13, and 12; however, this is not true at node 11, since *Uncia uncia* was coded as missing data for this feature. Therefore, it is uncertain if this character is a synapomorphy for clade 11 or 12 (*N. nebulosa* and *Panthera*).

Character 6: The plesiomorphic condition of this character, reduced or almost absent secondary parastyle cusp of the upper deciduous third premolar, is retained in *Herpailurus yagouaroundi* and *Puma concolor*, and it also occurs in all other terminal taxa placed outside clade 8. A distinctly enlarged and swollen secondary parastyle cusp is a synapomorphy for clade 10 (*A. jubatus*, *U. uncia*, *N. nebulosa*, and *Panthera*).

Character 11: A weakly developed ridge restricted to the upper middle part of the lingual face of the canine (character state 1) is a synapomorphy for clade 11 (*U. uncia*, *N. nebulosa*, and *Panthera*). This ridge is subsequently lost in *Panthera onca*.

Character 20: Transformation series within this character are complex, given the myriad arrangements found in the 18 trees among components 5, 6, 7, 8, and 15. Node 8 is ambiguously represented by each of the three states described for this character, depending on the arrangement of the components mentioned. Nevertheless, nodes 9 to 14 are unambiguously represented by character state 2, total disconfiguration of the subarcuate fossa. Therefore, character state 2 stands here as a potential synapomorphy for clade 9, but if so, it is at least homoplastic with respect to other clades. In contrast, two trees of the 18 most parsimonious trees display an extra component, in which clade 5 (*Leopardus pardalis* and *L. wiedii*) is the sister group of clade 8; under such conditions this extra component is ambiguously supported by states 1 and 2.

Character 22: Presence of a distinguishable salient crest along the longitudinal ridge of the auditory meatus (1) is (from the parsimony analysis performed)

a synapomorphy for clade 10 (*A. jubatus*, *U. uncia*, *N. nebulosa*, and *Panthera*). *Acinonyx jubatus* displays a further derived condition of this trait (2), thus constituting an autapomorphy for this species. Character state 1 is in fact homoplastic, due to its appearance also at node 22.

Character 23: The enlarged, elongated processus muscularis of the malleus is a synapomorphy for *P. onca*, *P. leo*, and *P. pardus* (clade 14). *Panthera tigris* is hypothesized to be the most basal extant species of clade 13.

Character 24: This is another feature of the malleus distributed in clade 8. The three terminal taxa of this clade that display the derived anteriorly oriented reflection of the processus brevis are *A. jubatus*, *U. uncia*, and *P. onca*. This character state is then ambiguously present at nodes 10 and 11, since it can be interpreted equally parsimoniously as a synapomorphy of clade 10 that subsequently reverts to the plesiomorphic condition at clade 12, or as two independent appearances in *A. jubatus* and *U. uncia*. This feature stands also as an autapomorphy for *P. onca*. It is relevant to note that this character state is also present ambiguously in some of the most parsimonious trees at the base of clade 15 (the transformation series within clade 15 is later addressed).

Character 25: As discussed earlier, the derived state of this character is postulated as a synapomorphy for clade 3. The distinct outward projection of the inferior head of the incus with malleus is subsequently lost in clade 12 (*N. nebulosa* and *Panthera*). The loss of this character thus corroborates the monophyly of clade 12.

Character 26: The two most basal taxa of clade 8, *H. yagouaroundi* and *P. concolor*, display the primitive condition (0) for this feature, as do extant felids outside this clade. The modified character state 1 (lacking a circular groove and having a suture separating the anterior crus of the ectotympanic from the complex formed by the mastoid process and squamosal) appears in all 18 trees at node 10. Thus, together with character 6, it constitutes another synapomorphy for clade 10. Subsequently, the placement of character state 2 (the formation of a passage along the external mastoid surface between the mastoid

posterior crest and the caudal entotympanic) at node 12 characterizes this transformation series changing first from state 0 to 1 and then from 1 to state 2 ( $0 \rightarrow 1 \rightarrow 2$ ). Hence, character state 2 is considered to be a synapomorphy at a lower hierarchical level, namely clade 12.

Character 27: This character is discussed under Felid Monophyly, because state 1 (frontal sinus cavity centralized at the post-orbital processes) is evidence for monophyly of the Felidae. A secondary loss of this condition is a synapomorphy for clade 13, hence supporting the monophyly of *Panthera*.

Character 29: The case here is slightly different from that just described for character 27 in that character state 1, internal frontal surface placed well before a line across the postorbital process, is lost in clade 12. The secondary loss of this derived condition, a defining character of the Felidae, corroborates the hypothesis that *N. nebulosa* and *Panthera* are sister taxa. A presumably parallel loss also occurred in *Puma concolor* and in *Lynx pardina*.

Character 32: This is again a case of loss, now at a higher level, clade 11, than in previous cases. The loss here is of the frontal lateral expansion, considered as character state 1. *Uncia uncia* was difficult to assign to a state since the values obtained for frontal breadth of specimens examined were close to the ones considered derived within Aeluroidea.

Character 37: This is another case of reversal to the plesiomorphic condition. The derived state is lost in clade 10. However, the situation here is more complex; first, state 1, presence of rostral constriction, is considered to be a synapomorphy for extant felids (clade 0); then the further derived state 2 of this constriction is a synapomorphy of clade 3. State 2 is retained by *H. yagouaroundi*, which determines that node 8 is represented by this same state. *Puma concolor* has lost state 2 and displays state 1. Finally, the hypothetical common ancestor of clade 10 lost condition 1. The transformation series here can be schematized as follows:  $0 \rightarrow 1 \rightarrow 2 \rightarrow 1 \rightarrow 0$ .

Character 43: The transformation series for the anterior jugal process corroborates the monophyly of clade 10 based on secondary loss of the anterior projection of the jugal over the infraorbital. This projection is evi-

dence for monophyly of the Felidae (see Felid Monophyly for additional comments).

Character 45: Presence of a cartilaginous ligament connecting the styloid process to the ceratohyal is either a synapomorphy for clade 11 that was secondarily lost in *N. nebulosa*, or an autapomorphy for *U. uncia* with homoplastic appearance in clade 13 (thereby supporting the monophyly of *Panthera*). These two hypotheses are equally parsimonious, both requiring two steps.

Character 46: The head of the fibula with greater development of an anteriorly projecting flange (1) is considered unique to the three most basal branches of clade 8, *H. yagouaroundi*, *P. concolor*, and *A. jubatus*. For clade 8, this character is a synapomorphy that subsequently was lost by the hypothetical common ancestor of clade 11.

Character 47: The derived appearance of a tendon for extensor digitorum longus originating on the lateral epicondyle of the femur, passing through a notch on the head of the tibia and under a flange (1), has a distribution identical to that of the character 46. The transformation series here requires two steps, appearance at node 8 and subsequent reversal or loss at node 11. Characters 46 and 47 thus support the monophyly of the same group.

Character 54: This is another character proposed as a synapomorphy for extant felids (node 0) that was secondarily lost in clade 8. Cutaneous lobes at the tips of digits are lost in clade 10.

Character 55: The derived character state is homoplastic, occurring both at node 13, where it is a synapomorphy for *Panthera*, and at node 5. This feature is the reversal of the generally backward direction of neck fur growth.

Character 56: This feature is the derived round pupil (1) uniquely present in the members of component 8, except for *Neofelis nebulosa*. Therefore, it constitutes a robust synapomorphy supporting this clade's monophyly, with a reversal to the plesiomorphic condition in *N. nebulosa*.

Character 57: This feature is the spinous patch beginning close to the anterior border of the tongue (1) earlier suggested as occurring only in *H. yagouaroundi*, *P. concolor*, and *Panthera* (among taxa coded as missing data was *U. uncia*). The transformation series

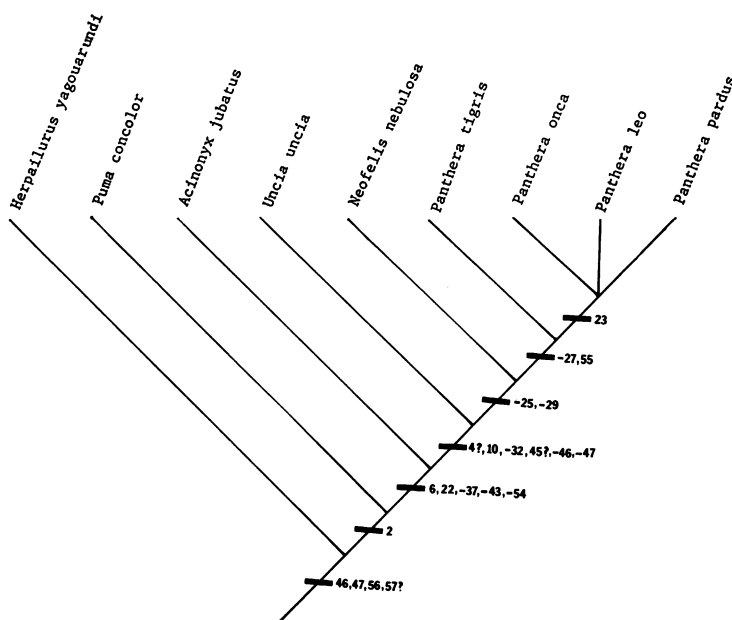


Fig. 53. Clade 8 (from fig. 52) and characters which have their distribution not affected by the topologies of the 18 most parsimonious trees of the general morphological analysis.

here are complex, requiring reversals or independent origins of this feature. Nodes 8 to 12 are ambiguous with regard to the presence of this character. Equally parsimonious hypotheses are as follows: the first is that for clade 8 this character is a synapomorphy, which was subsequently and independently lost by *A. jubatus* and *N. nebulosa*—requiring three steps. A second hypothesis is that the derived character state has its first appearance at node 8 and subsequently reverts to the plesiomorphic state at node 10, and finally reoccurs at node 13—requiring the same number of steps, three, as the first hypothesis.

It is relevant to note that clade 8 exhibits a high ratio of reversals to the condition at the outgroup node. Interestingly, most cases of reversal within clade 8 clearly represent losses of neotenic traits, which seems to characterize the felid general morphology (Fagen and Wiley, 1978; Herrington, 1986). Therefore, these cases of reversals could be reinterpreted as further derived (*sensu stricto*) secondary return to aeluroid states.

Figure 53 includes only the characters whose distributions within clade 8 are not affected by the topologies of the 18 most parsimonious trees.

#### CLADE 15

Nineteen characters were selected for discussion of transformation series within clade 15. Of the 13 that were binary, 3 required one appearance, 1 exhibited only a reversal, 5 became homoplastic, and 4 displayed reversals and required independent origins. Of the 6 multistate characters, only character 43 did not display reversals or independent appearances, 3 displayed both, 1 displayed only a reversal, and another an independent appearance in clade 7.

Character 7: The protocone cusp of the upper fourth premolar independently became reduced (1) four times in felids. State 2 of this feature, protocone almost totally suppressed, is derived directly from an ancestral condition 0, and is interpreted as an autapomorphy for *Acinonyx jubatus*. Another reduction occurred in clade 6 (*Prionailurus bengalensis* and *Leptailurus serval*). Reductions also took place within clade 15, in clade 20 (supporting the monophyly of *Lynx*), and in clade 26, which is composed of *Felis silvestris*, *F. bieti*, *F. nigripes*, *F. margarita*, and *Otocolobus manul*.

Character 8: This feature is the extreme

reduction of the metastyle of the upper third premolar (1). This reduction is a synapomorphy for clade 28 (*Felis nigripes*, *F. margarita*, and *Otocolobus manul*). This character state is homoplastic as autapomorphic in *Prionailurus rubiginosa* and in *Leopardus geoffroyi*.

Character 11: State 1 discussed above in the subsection Clade 8, is uniquely present in clade 11. The well-developed lingual ridge of the upper canine, character state 2, is a synapomorphy for clade 28 (*F. margarita* and *O. manul*) and has an independent appearance at node 7.

Character 12: This feature has a distribution similar to that of state 2 of character 10, and in fact only one species is added (*Prionailurus planiceps*). Therefore, the homoplastic occurrences of the derived deep cavity along the lower canine lingual ridge (1) outside clade 15 are in clade 7 and in *P. planiceps*. This character is additional evidence for the sister-group relationship between *F. margarita* and *O. manul*.

Character 17: The well-developed external pterygoid fossa with a marked lateral pterygoid process (1) is a synapomorphy that supports monophyly of clade 15. However a reversal to the plesiomorphic condition occurred in *Lynx* (clade 20).

Character 20: Homoplasy outside clade 15 in the closure of the subarcuate fossa is not addressed here, because it was discussed under Basal Taxa and Clade 8. Character state 2, total disconfiguration of the subarcuate fossa, is ambiguously present at nodes 22, 21, 20, and 19. Placing state 2 as a synapomorphy for clade 19 (*Caracal caracal* and *Lynx*) requires a reversal to the plesiomorphic condition in *Lynx lynx* and in *L. pardina*, or a loss in clade 21 with a reversal to state 2 in *L. pardina*. An equally parsimonious interpretation would be to consider three independent appearances of state 2 in *C. caracal*, *L. rufus*, and *L. canadensis*.

Character 21: The salient well-developed border of the auditory meatus (1) is a synapomorphy for clade 19, but is homoplastic in *Acinonyx jubatus*. As discussed earlier (under Character Topographical Correspondence and Polarization), this border in *A. jubatus* was considered different from that observed in *Lynx*.

Character 22: This feature of the auditory meatus, the distinct development of the longitudinal ridge (1), displays an independent origin in clade 10. It is also a synapomorphy for clade 22, *Lynx pardina* and *Lynx canadensis*.

Character 24: This feature is ambiguous at nodes 15 to 21, at 22 it reverses to the plesiomorphic condition, and at node 23 it is ambiguous. The anteriorly oriented reflection of the processus brevis (1) becomes unambiguous in clade 24. This feature seems to indicate a close relationship between clades 8 and 15. It is suggested that this character might well be a synapomorphy for clade 15 or, at a higher hierarchical level, which would include clade 8.

Character 32: As discussed earlier, the derived frontal lateral expansion (state 1) is a synapomorphy for clade 4, and within clade 15 two transformations occurred. First, a change to the further derived state 2 occurred in the hypothetical common ancestor of clade 16 (*Profelis badia*, *Pardofelis marmorata*, *Caracal caracal*, *Lynx*, *Felis*, and *Otocolobus manul*), and subsequently a reversal to state 1 occurred in clade 19, thus supporting the monophyly of the *Caracal caracal* and *Lynx* grouping. Note however that *C. caracal* lost this derived condition 1.

Character 33: The dorsal profile of the frontonasal surface assuming angular values of about 45° (1) is a synapomorphy for clade 17; it is secondarily lost in *Felis chaus*. Two homoplastic appearances of this character were detected, one in *Acinonyx jubatus* and the other in *Leptailurus serval*.

Character 37: Transformation series for character 37, rostrum constriction, were discussed earlier; only changes in clade 15 are addressed here. The first change recorded is a reversal from state 2 to 1 in clade 16, then two parallel reversals to the plesiomorphic condition, one in clade 21 (*Lynx lynx*, *L. pardina*, *L. canadensis*) and the other in clade 24 (all *Felis*, except *F. chaus*, plus *O. manul*).

Character 38: Presence of a well-marked concave curvature of the outer surface of the nasal bones (1) is a synapomorphy for clade 26 (*Felis silvestris*, *F. bieti*, *F. nigripes*, *F. margarita*, and *Otocolobus manul*).

Character 42: The jugal and postorbital processes meeting and encircling the orbit

(state 1) is ambiguously present at nodes 16 and 17. Two minimum paths of "evolutionary" change for this character are the encircling of the orbit as a synapomorphy for clade 16 that is subsequently lost by the hypothetical common ancestor of clade 18, or as parallelism with independent appearances in *Profelis badia* and in *Pardofelis marmorata*. In fact, the latter species displays this character further derived (state 2—well-developed postorbital processes totally fused). Character states 1 and 2 are both homoplastic due to their appearances in other branching areas (component 1, autapomorphy for *Prionailurus rubiginosa*). State 1 is considered part of the *Otocolobus manul* mosaic, as an autapomorphy for it.

Character 43: The anterolateral projection of the jugal over the infraorbital foramen is here interpreted as synapomorphy for Felidae. This condition reverts to the plesiomorphic state in clade 21 (*Lynx lynx*, *L. pardina*, and *L. canadensis*).

Character 44: The modified flat, enlarged lower rim surface of the orbit (1) is a synapomorphy for clade 24, *Felis lybica*, *F. cafra*, *F. silvestris*, *F. bieti*, *F. nigripes*, *F. margarita*, and *Otocolobus manul*. The related anterior projection of the lower rim of the orbit (character state 2) is a synapomorphy for clade 27, subsequently lost in *O. manul*.

Character 49: Caudal vertebrae reduction, characterized by a very short tail (1), is a synapomorphy for *Lynx*, clade 20. This character has a consistency index of 1.0.

Character 50: Ears displaying a more angular shape and pointed tip (1) is evidence for the monophyly of clade 18 (*Felis*, *Otocolobus manul*, *Caracal caracal*, and *Lynx*); however it exhibits a reversal to the plesiomorphic condition in *O. manul*.

Character 51: This character has an uncertain transformation series within clade 15. The more general state 1, with the tip of the ear provided with a pencil, is first ambiguously present at node 18. In fact, at this node the three states described for this character, 0, 1, and 2, are each present in some resolutions. If character state 1 is considered a synapomorphy for clade 18, a reversal occurs at node 25, and a transformation to state 2 (elongation of the pencil) occurs in clade 19, hence supporting the sister-group relation-

ships between *Caracal caracal* and *Lynx*. This is one of the possible alternatives among the various equally parsimonious resolutions, depending on the state considered for node 10.

Character 52: The reduced rhinarium (1) is a synapomorphy for clade 23. It is questionable whether this state is modified in *Otocolobus manul* because no clear information was available; this cat was coded as missing data.

On figure 54 are placed only those characters that have their distribution within clade 15 unaffected by any of the topologies of the 18 most parsimonious trees.

#### HISTORICAL CONSIDERATIONS: A COMPONENT CONGRUENCE ANALYSIS

Since the early 19th century, schemes postulating the naturalness ("monophyly") of Felidae were specifically present in the work of G. Fischer (1817) and J. E. Gray (1821). Relationships within extant felids were first formalized by S. W. Jardine (1834), M. N. Severtzon (1857–58), J. E. Gray (1867), and others.

In this historical reappraisal of extant felid systematics, the cladogram hypothesized here based on general morphology (see fig. 52) is compared against other schemes of relationship suggested by authors of this century. A common problem encountered was inconsistency in taxonomic approach within a single publication. Usually, these inconsistencies between authors' views are presented in text (not necessarily based on explicit empirical evidence), classification schemes, diagnostic keys, and character information contained in text. None of the species names used in this historical analysis differs from the ones applied here (see table 1). This study begins with an examination of the work of Pocock (1917b).

#### CONGRUENCES WITH POCKOCK, 1917

Pocock's 1917b article illustrates the problem mentioned. His classification divides the felids into three major groups, but it offers no further information aside from generic ranks postulated. Therefore, I decided to



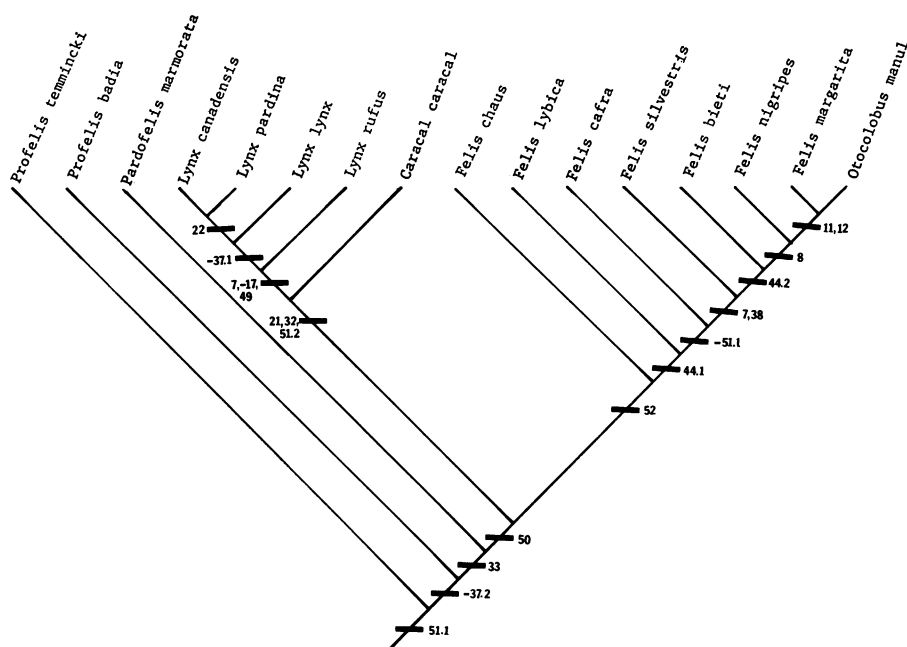


Fig. 54. Clade 15 and related characters which have their distributions not affected by the topologies of the 18 equally parsimonious trees of the morphological analysis.

summarize the character information presented in that publication (as part of a larger cladistic character review being developed for felids and aeluroids). Figure 55 is the branching diagram derived from this character information survey. The list of the characters considered, combined by type distribution, can be found in appendix 3; these characters were selected almost exclusively on the basis of avoiding redundancy, i.e., I am not necessarily corroborating all the homologous relations postulated by Pocock.

The branching diagram (fig. 55) constructed from Pocock's characters has a major component 3 which excludes *Acinonyx jubatus* and Pantherinae and embraces the genera *Panthera* and *Uncia*. Almost all inclusive clades of component 3 branch from node 3, forming a large polytomy. Pocock's characters support the monophyly of clade 13 of *Felis* (component 15), and *Lynx* (component 13; incorporating *Lynx* (= *Caracal*) *caracal*). They also support a sister-group relationship between *Trichaelurus* (= *Otocolobus*) *manul* and *Dendrailurus* (= *Leopardus*) *colocolo* (component 12), as well as between *Ictailurus* (= *Prionailurus*) *planiceps* and *Zibethailurus* (= *Prionailurus*) *viverrina* (component 11).

*Profelis aurata* and *P. temminckii* (node 10), and *Pardofelis marmorata* and *P. badia* (node 9) are resolved as each other's sister taxa, and both genera formed a group (component 8). *Leopardus pardalis* and *L. wiedii* form their own genus, *Leopardus* (node 7), which is the sister group of *Leptailurus serval*. Under *Herpailurus* (= *Leopardus*) (node 5) are grouped *H. yagouaroundi*, *H. geoffroyi*, *H. tigrina*, and *H. guigna*; and *Prionailurus* (node 4) only embraces *P. bengalensis* and *P. rubiginosa*. Finally, *Puma concolor* and *Neofelis nebulosa* are monotypic genera directly linked to node 3.

Fourteen components are suggested in this diagram (fig. 55), about 50 percent of the components of the morphological tree of this study (fig. 52). There are four identical components (the components as determined in Pocock's diagram are on the right): 1 = 11, 5 = 7, 14 = 2, and 19 = 13. Four others from figure 52—13, 20, 21, and 22—are not incongruent; and five more would not be incongruent if *O. manul* were disregarded as a member of component 23. They are components 24, 25, 26, 27, and 28 (fig. 52). There are also two similar areas that deserve comment. The first is component 11 (fig. 52),

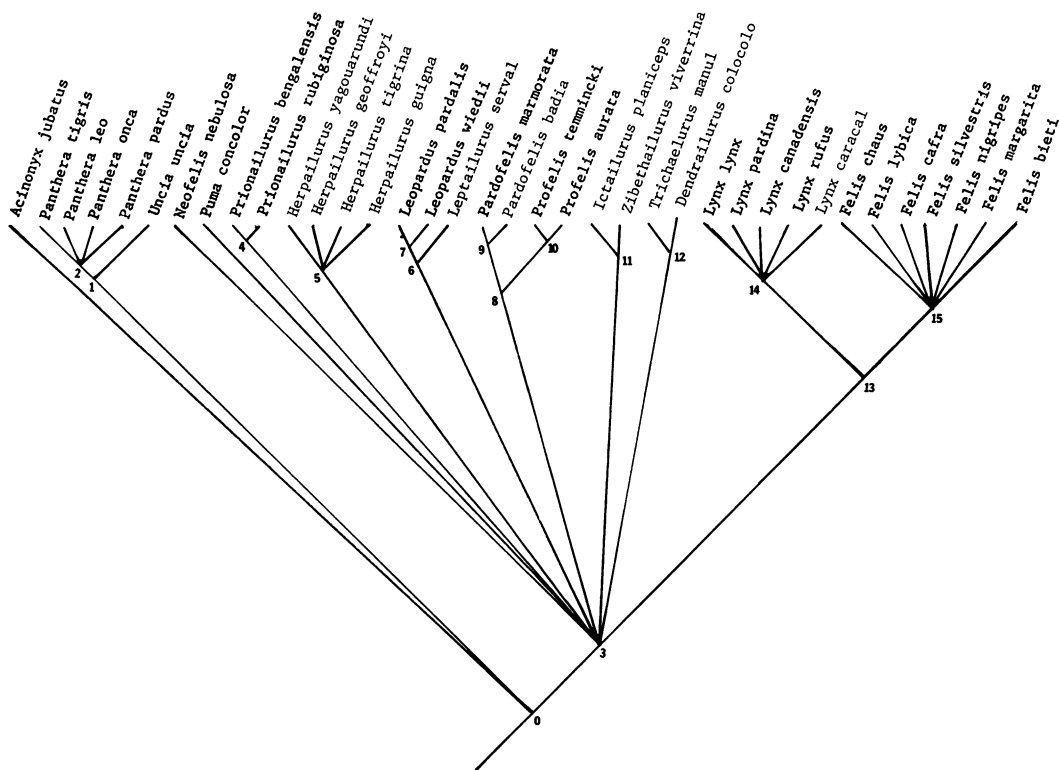


Fig. 55. Branching diagram derived from the character survey of Pocock (1917b), using his generic names. To facilitate comparisons, a few minor changes were made in species recognized by Pocock (when appropriate, species were synonymized). For example, since the species under *Felis* were not fully described, it is assumed that *F. cafra*, *F. bieti*, and *F. margarita* are members of that genus.

which supports close relationship between *Uncia uncia*, *Neofelis nebulosa*, *Panthera tigris*, *P. onca*, *P. leo*, and *P. pardus*; the only difference from Pocock is that *Neofelis nebulosa* is not a member of Pocock's component 1. The second similarity is the sequential branching area delimited by nodes 15 and 17 of figure 52, indicating similar close relationships to those present in component 8 of Pocock's diagram, although *Profelis aurata* is not part of this branching area in figure 52.

A reasonable amount of congruence exists between these two branching diagrams, although further studies are needed for a better understanding of the overall character information present in Pocock's publications related to felids.

#### CONGRUENCES WITH WEIGEL, 1956

Based on skin morphology and color patterns, Weigel (1956) suggested a scheme of

relationships for felids. A branching diagram (fig. 56) is derived directly from this scheme. When this diagram is compared with the one proposed here based on general morphology (fig. 52), six identical components (Weigel's components on the right), 19 = 5, 10 = 13, 2 = 18, 5 = 19, 6 = 20, 3 = 23, are verified. Two others are not inconsistent, component 1 (fig. 52) with Weigel (fig. 56) component 15, 21; and 22 (fig. 52) with component 6 (fig. 56). Five others would be not inconsistent if *Otocolobus manul* is disregarded as a member of component 23 (fig. 52); these are components 24, 25, 26, 27, and 28. Similar areas are also verified, component 9 (fig. 52) would be identical to the potential grouping that could be formed by the terminal taxa between *Puma concolor* and *Uncia uncia* in the polytomy of node 7 of figure 56. The sequential branching area delimited by nodes 15 and 17 (fig. 52) is similar to the relationships established in component 10 (fig. 56), *Profelis au-*

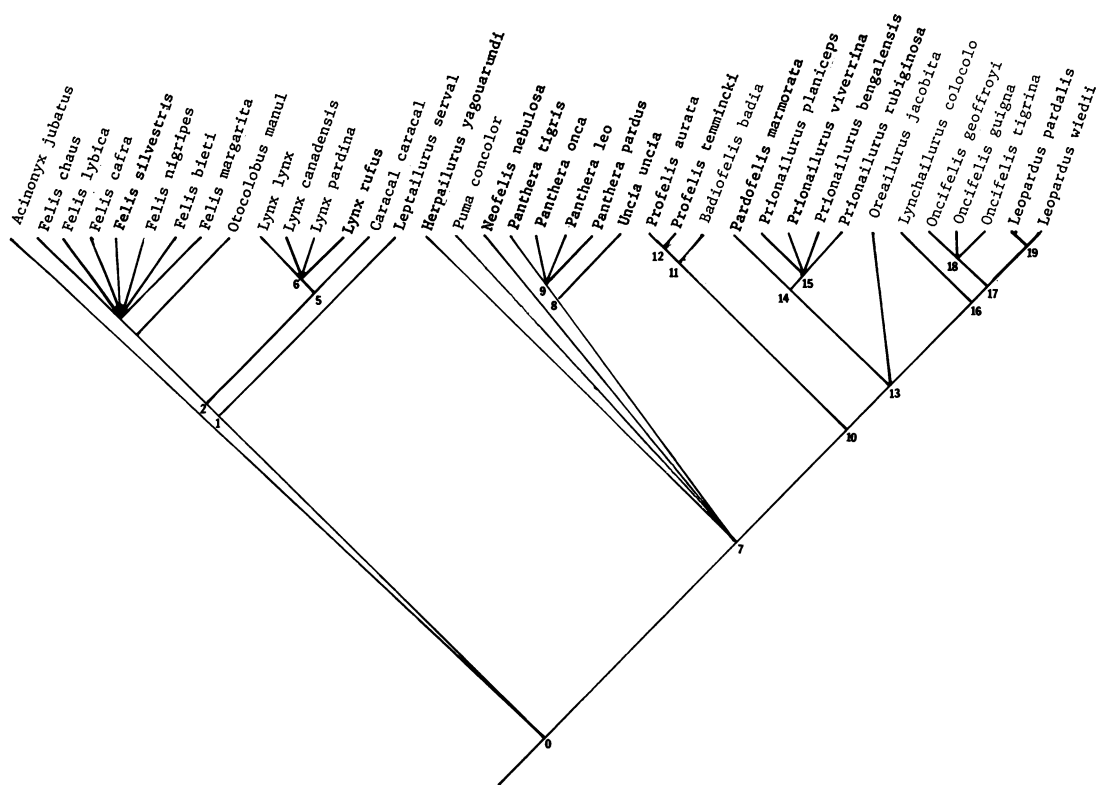


Fig. 56. Branching diagram derived from the schemes suggested by Weigel (1956).

*rata* being the only taxon not present in the area mentioned in figure 52.

Given that Weigel's diagram has 19 potentially conflicting components, the congruence observed is substantial.

#### CONGRUENCES WITH HEMMER, 1978

In 1978, Hemmer reviewed the literature on extant felids, providing comments on disputed relationships, and proposed a scheme of relationships based on successive geographical radiations. P. Müller (1973) was cited as a reference for the geographical method used. Hemmer's scheme (1978) seems to be a combination of his views of what he considered to be well supported relationships and the geographical method advocated. Figure 57 is a redrawing of his diagram. Of 19 components in this branching diagram, a total of 5 identical components are verified (components in fig. 52 on the right): 5 = 8, 11 = 5, 14 = 7, 20 = 14, 21 = 15.

There are also two other partially identical

components. If *Leptailurus serval* is disregarded as a member of component 18 in figure 52, this component would be identical to Hemmer's component 13. Component 23 (fig. 52) is a similar case, in that if *O. manul* is not considered as a member of this component, it would be identical to 16 (fig. 57). Component 13 (fig. 52) is not inconsistent with component 6 (fig. 57); and 22 (fig. 52) is not with 15 (fig. 57). Component 7 (fig. 52) is not inconsistent with 9 (fig. 57) if *Prionailurus rubiginosa* is not considered. Component 1 (fig. 52) shares similarities with 11 (fig. 57) to the extent that they both indicate close relationships between *P. planiceps* and *P. viverrina*.

The amount of congruence is similar to that noted with Weigel.

#### CONGRUENCES WITH HERRINGTON, 1986

Herrington (1986), in her unpublished Ph.D. dissertation, proposed a cladogram for extant felids (fig. 58). Since no data matrix

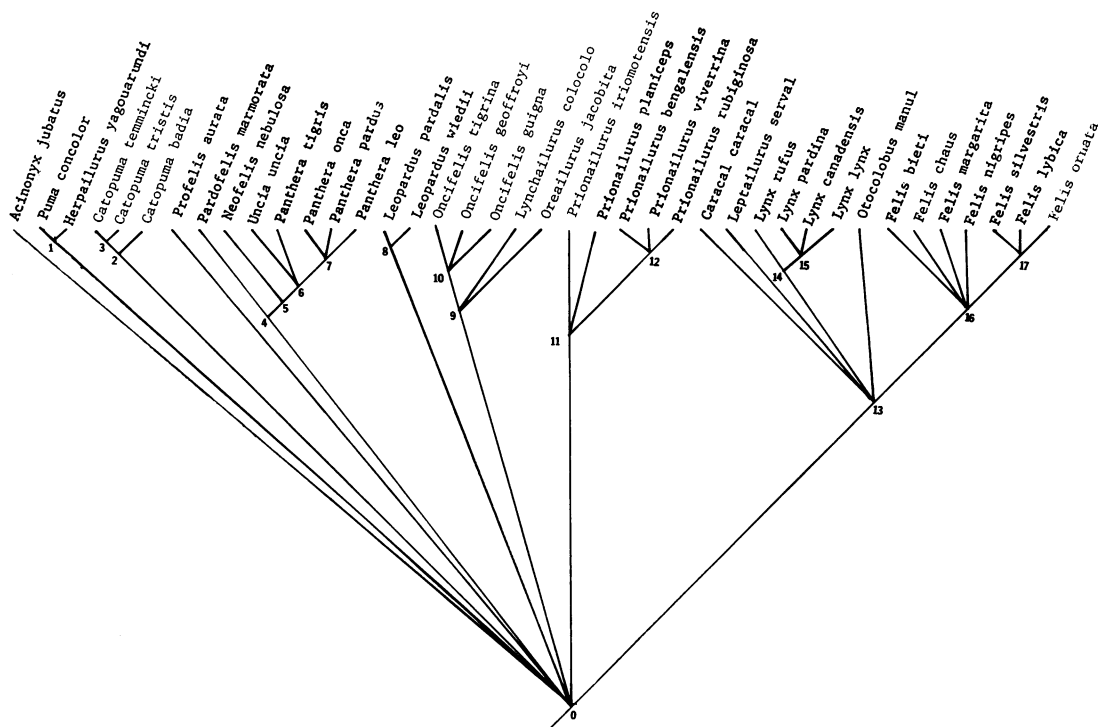


Fig. 57. Branching diagram derived from the phylogenetic tree proposed by Hemmer (1978).

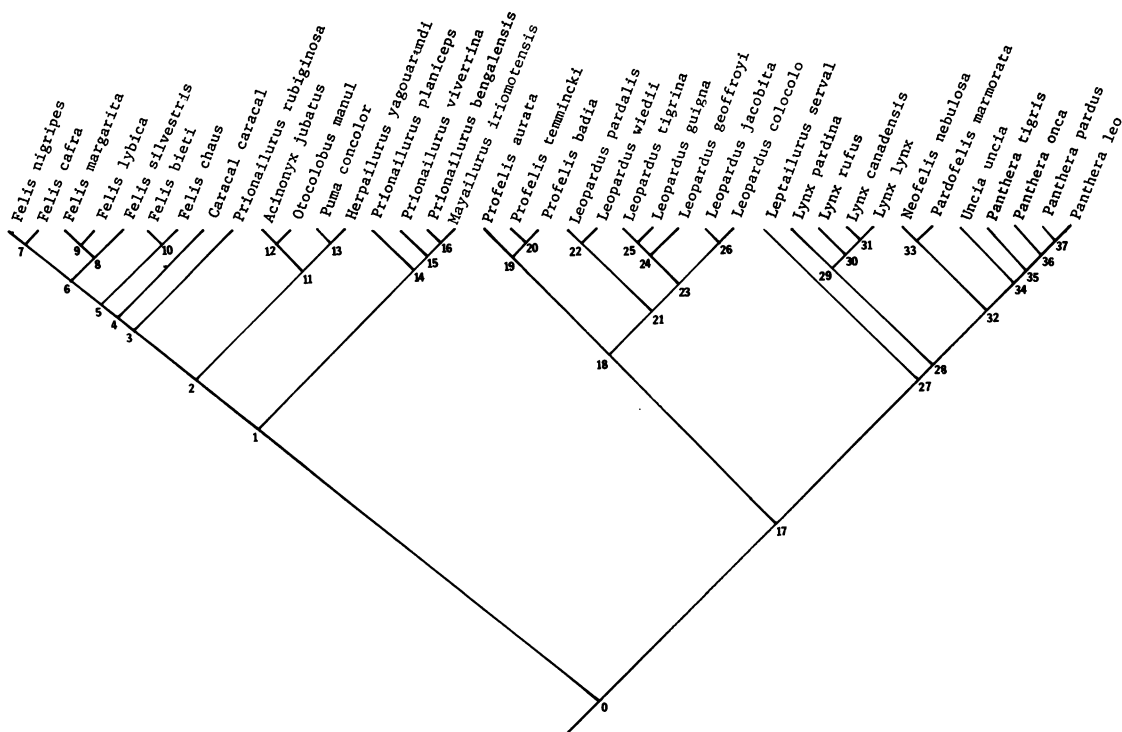


Fig. 58. Branching diagram redrawn from the cladogram for extant felids proposed by Herrington (1986).

was offered, I constructed one based on the character information contained in the text. After applying the *mhennig\** and *bb\** commands of the Hennig86 program to these data, nine equally parsimonious cladograms resulted. The Nelson consensus tree of these nine cladograms displayed a total of 23 components for 39 taxa (see appendix 4). Herrington's (1986) cladogram is fully resolved, having 38 components for 39 taxa. The inconsistencies are in the components themselves; for example, major component 60 of the consensus tree (appendix 4) is highly inconsistent with her cladogram (fig. 58).

Four identical components are verified between the summary of synapomorphies (based on the whole morphology) for extant felids hypothesized here (fig. 52) and Herrington's cladogram (fig. 58; Herrington's components on the left), 22 = 5, 35 = 13, 36 = 14, and 29 = 20. Two are partially identical: the first is a result of the incongruence between the monophyly of *Felis* including *O. manul*, component 23 (fig. 52), and Herrington's component 5 (fig. 58), of which *O. manul* is not part; and in the second, component 11 (fig. 52) would be identical to 32 (fig. 58) if *Pardofelis marmorata* were not considered. Components 1 (fig. 52) and 14 (fig. 58) indicate a close relationship between *Prionailurus planiceps* and *P. viverrina*. Component 7 (fig. 52) and 26 (fig. 58) suggest close affinities between *Leopardus colocolo* and *L. jacobita*. The sequential branching area delimited by nodes 15 and 16 (fig. 52) shares similarities with component 19 (fig. 58).

Comparisons of the above four authors' schemes reveals many repeated congruences and similarities. This indicates that at least some phylogenetic relationships have been corroborated since the work of Pocock (1917b).

#### CRANIAL VERSUS WHOLE MORPHOLOGY

Here, I compare the morphological (fig. 52) and cranial (fig. 51) cladograms proposed in this study. A total of 13 identical components are identified, that is, about half of the mean number of components present in the two trees. Components 1, 8, and 9 of the morphologically based cladogram (fig. 52) are consistent with the cranially based cladogram (fig. 51). Component 5 (fig. 52) shares simi-

larities with the paraphyletic branching area demarcated by nodes 4 and 5 (fig. 51). Component 16 (fig. 52) differs from 9 (fig. 51) in the exclusion of *Lynx* and *Caracal caracal*. The close relationship between these felids is supported by the monophyletic group 19 (fig. 52) and the paraphyletic area delimited by nodes 18 and 22 (fig. 52). *Lynx* monophyly is not supported by the cranially based phylogeny (fig. 51). In contrast to the morphologically based phylogeny (fig. 52), it is indicated to be a paraphyletic branching area delimited by nodes 18 and 22. The cranially based cladogram, in fact, suggests *Lynx* species as closely related to "large cats," represented in figure 51 by component 23, unlike *Felis* as indicated by component 18 of figure 52.

One of the major differences between these two branching diagrams is that component 3 of the cranial diagram is not present in the morphological one.

#### MORPHOLOGY VERSUS MOLECULAR (IMMUNOLOGICAL) EVIDENCE

Collier and O'Brien (1985) published a phenogram for extant felids based on albumin immunological distance (fig. 59). Despite similarities between this phenogram (fig. 59) and the tree proposed here based on morphology (fig. 52), only two identical components were verified (Collier and O'Brien's components on the right), 23 = 6 (although the relationships within this group are not in concordance) and 20 is consistent 20 (the inclusive 21 and 22 of fig. 52 are not inconsistent with component 20 of fig. 59). Components 8 (fig. 52) and 18 (fig. 59) share similarities; disregarding *Puma concolor* of component 8, and other *Lynx* plus *Pardofelis marmorata* of 18, these two components would be identical. Component 11 of the morphological tree (fig. 52) would also be identical to 21 (fig. 59) if *Neofelis nebulosa* were included in this last component. The paraphyletic area delimited by nodes 15 and 16 (fig. 52) has similarities with component 13 (fig. 59).

Finally, the placement of *Leptailurus serval* on the cranial scheme of synapomorphies (fig. 51) is partially corroborated by Collier and O'Brien's diagram (fig. 59), since both place *L. serval* similarly within felids. This adds to

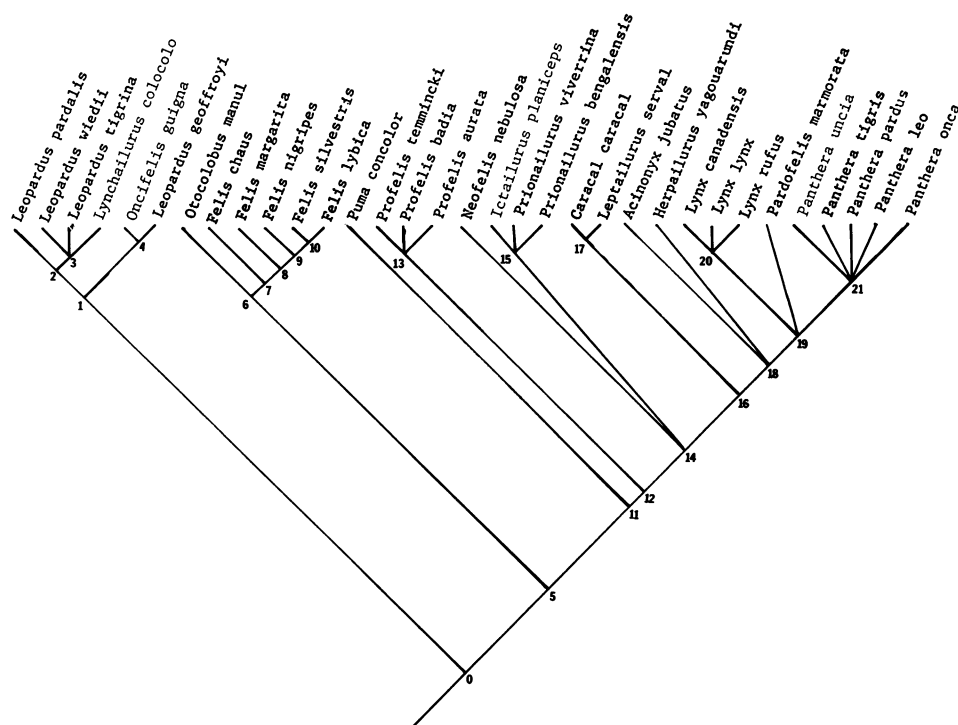


Fig. 59. Branching diagram redrawn from Collier and O'Brien's (1985) tree (of fig. 1) for extant felids based on albumin immunological distance.

the previously suspected problem regarding the alternative placement of this species in the morphologically based tree.

Some congruence was observed between these two kinds of data. I appraise with special interest the partial concordance between component 8 (of the morphological tree; fig. 52) and component 18 (fig. 59). One must bear in mind that a phenetic hierarchical diagram and a morphological summary of synapomorphies based on parsimony are compared here. Therefore, the mismatch (or similarities) may be largely due to differences in methodology. New investigations on molecular character information are needed (e.g., an analysis of parsimony exploring DNA base sequence).

### CONCLUDING REMARKS

First, the morphologically based tree of figure 52 is considered here the best scheme of relationships. Not only because it includes the 38 felids examined and involves a broader diversity of characters, but also because its

consistency index does not significantly differ from that of the cranial tree (which has an index only 3% higher). However, some considerations should be made of the few inconsistencies in the unweighted morphological tree (appendix 2). Nearly all components of these two trees are identical; congruence between them is described as following (components of fig. 52 are on the left side): 5 = 57; 1 = 59; 7 = 58; 10 = 61; 13 = 56; 14 = 52; 15 is nearly identical to 60, but 15 lacks *Leptailurus serval* as a member; the branching area limited by nodes 15 and 17 is somewhat corroborated by the monophyletic group 54; component 18 differs from 55 only for the presence of *Leptailurus serval*, which is placed as the sister taxon of *Felis* plus *Otocolobus manul*. The unweighted tree (appendix 2) has 23 components and the weighted (fig. 52) 29. Component 53 of the unweighted tree is consistent with component 7 (fig. 52), but relationships described by component 53 are not explicit in component 7.

Monophyly of *Prionailurus* clearly is problematic. Although *P. planiceps*, *P. viverrina*,

and *P. bengalensis* emerge as a monophyletic group in the cranial analysis, *P. rubiginosa* is not a member of this group, and the final morphological analysis supports only the sister-group relationship between *P. planiceps* and *P. viverrina*. Herrington (1986) suggested that *P. rubiginosa* is a basal taxon of *Felis* (which included *Caracal caracal*), and constitutes a monotypic new genus. This relationship is not supported here. According to my summary of character information in Pocock (1917b), there is evidence suggesting sister-group relationships for *P. bengalensis* and *P. rubiginosa*, and for *P. planiceps* and *P. viverrina*, but not monophyly for *Prionailurus*.

In both cranial and morphological summaries of synapomorphies, *Leopardus* was not supported as a monophyletic group, and most of its members contribute to the decrease in resolution in both summaries. In other words, morphology of these cats has not become a good source of character information. Nevertheless, the results of this study clearly indicate that *L. pardalis* and *L. wiedii*, if not sister taxa, are relatively closely related compared to the other species of this "group," and the same is true for *L. colocolo* and *L. jacobita*. Several previous studies also support these relationships. I failed in my attempt to detect the square appearance of the malleus suggested by Herrington as a share derived character state for *Leopardus*. Collier and O'Brien's (1985) albumin data supported *Leopardus* as monophyletic, and positioned it as the basal felid.

*Profelis* is another grouping for which morphological evidence of monophyly was not discovered. In the morphological branching diagram (fig. 52), *Profelis aurata* is suggested to be a basal cat, and *P. temmincki* and *P. badia* form a paraphyletic group delimited by nodes 15 and 16. These two species (as members of component 15) are suggested to be closely related to *Pardofelis marmorata*, *Lynx* plus *Caracal caracal*, and *Felis* plus *Otocolobus manul*. These relationships are discordant with those in the cranial diagram. However, the unweighted tree (appendix 2) also supports close relationship of these species, as indicated above. The only significant difference is that the unweighted tree has the following three species related in this manner

(under parenthetical notation): (*Profelis temmincki* (*P. badia* and *Pardofelis marmorata*)). Hemmer (1978) also suggested that *P. temmincki* and *P. badia* form a group of which *P. aurata* is not a member. In fact, he considered them as part of another genus, *Catopuma* Severtzon, 1858. Herrington (1986) instead supported monophyly of *Profelis* and considered it as the sister group of *Leopardus*. Collier and O'Brien (1985) also favored the integrity of *Profelis*.

Relationships within *Felis* were proposed in the works of Herrington (1986) and Collier and O'Brien (1985); a review of subspecific relationships within *Felis* was presented in Haltenorth (1953). The only real agreement on relationships within *Felis* is the basal position of *Felis chaus*. Collier and O'Brien's (1985) data indicate a close relationship between *Felis* and *Otocolobus manul*, specifically that *O. manul* is the sister taxon of a monophyletic *Felis*. This view is contrary to that advocated here (figs. 51, 52), in which *O. manul* is placed as the sister group to *Felis margarita* within a *Felis* clade. In fact, this relationship between *Felis* and *O. manul* was proposed much earlier by Pocock (1917b; in the text) and later restated in his 1951 publication.

As noted earlier, parallelism occurs between *O. manul* and *F. margarita* (component 29 of morphological tree, fig. 52) and component 7 (fig. 52), composed of *Leopardus colocolo*, *L. jacobita*, and *Prionailurus rubiginosa* (note that Pocock's diagram, fig. 55, supports *O. manul* and *L. colocolo* as sister groups). This might indicate a case of reticulation among these cats, but further examination is necessary to sustain such a position.

Monophyly of *Lynx* is relatively stable, but relationships within extant lynxes are disputed. In fact, the cranially based phylogeny does not support the monophyly of *Lynx*. The phylogeny suggested by Werdelin (1981) has one component with respect to extant lynxes, *L. lynx* and *L. canadensis*. This relationship is not supported here, although Herrington (1986) suggested the same. A consensus between Herrington's component 29 (fig. 58) and 20 of the morphological tree (fig. 52) would result in lack of resolution for interrelationships within *Lynx*. The phylogenetic status of *Caracal caracal* is debatable;

this felid has traditionally been considered a member of *Lynx*, but Herrington suggested that it is instead a member of *Felis*. The position of *C. caracal* as sister taxon of a monophyletic *Lynx* (forming component 19, fig. 51), and the fact that this group is supported as sister taxon of clade 23 (*Felis*, plus *Otocolobus manul*, fig. 52) agree with Herrington's views, particularly because she suggested *C. caracal* to be a basal *Felis*. However, the cranial cladogram (fig. 51) suggests *Lynx* species and *Caracal caracal* (as sister taxon of *Lynx rufus*) to be more closely related to component 23 (*Acinonyx jubatus* (*Uncia uncia* (*Neofelis nebulosa*, *Panthera*))), of this cladogram. This relationship is supported by component 16 of Collier and O'Brien's phenogram (fig. 59); see discussion below.

As discussed above, component 18 of the morphological tree indicates a sister-group relationship between *Lynx* (plus *C. caracal*) and *Felis* (plus *O. manul*). This component agrees with the view of Pocock (1917b), but it is not reflected in the diagram (fig. 55) derived from his paper, and it is partially congruent with Hemmer's component 15 (see fig. 57). Peters (1987) discussed the phylogenetic status of *Lynx*, and indicated the sister-group relationship between *Lynx* and *Felis* based on pattern of vocalization. This relationship is also supported by Werdelin (1983).

As pointed out, component 18 of the cranial branching diagram (fig. 51) determines lynxes as a paraphyletic group closely related to component 23 (*Panthera* and relatives). This component is very similar to component 28 (fig. 58) of Herrington (1986) and to component 17 (fig. 59) of Collier and O'Brien (1985). Nevertheless, *Lynx* is not a member of component 8 of the morphological tree (fig. 52). This component strikes me as especially curious, since it has *Herpailurus yagouaroundi* as the first taxon branching off of a completely asymmetrical clade. Also, *Puma concolor*, which has been considered by different felid specialists to be most closely related to *H. yagouaroundi*, is the second most basal taxon. The whole component 8 (fig. 52) reads in parenthetical notation as (*Herpailurus yagouaroundi* (*Puma concolor* (*Acinonyx jubatus* (*Uncia uncia* (*Neofelis nebulosa* (*Panthera*)))))). Component 9 (fig. 52) is fully

congruent with the relationships suggested by Haltenorth (1937), and 11 (fig. 52) is identical to the basal component of the branching diagram hypothesized by Hemmer (1981) (fig. 57); the latter is based on behavioral patterns. The suggestion of *Panthera tigris* as the basal *Panthera* species is also congruent with Hemmer's (1981) data, and Herrington (1986) also supported this relationship. In fact, Herrington and I both base placement of *P. tigris* on the same character, enlargement of the processus muscularis (see character 23). The phylogenetic position of *H. yagouaroundi* is in partial concordance with Collier and O'Brien's (1985) immunological results (fig. 59), in which it is closely related to *Panthera* and relatives.

*Leptailurus serval* switched from a position within component 17 on the cranial tree (fig. 51) to become part of a poorly resolved area of the morphological cladogram, as sister taxon of *Prionailurus bengalensis*. Until further evidence supports this sister-group relationship, this is interpreted as a possible result of noise in the data, or as a side effect of the successive weighting algorithm. Note that on the unweighted tree (appendix 2), *L. serval* came out as sister group of *Felis* plus *Otocolobus manul*, and that the cranial tree supports a very similar phylogenetic status. Hemmer (1978) and Herrington (1986) have also suggested a similar relationship for *L. serval*.

Finally, component 8 of the cranial cladogram might well be an indication of a sister-group relationship between clades 8 and 15 of the morphological cladogram. In fact, a major component of one of the 18 equally parsimonious trees from the morphological data matrix unites *Felis* plus *Lynx* (and relatives) with the *Panthera* and relatives grouping as indicated by component 8 of figure 52. Other species are also part of this major clade.

Extant felid phylogenetics is a subject with a complex history. Better corroborated hypotheses of phylogenetic relationship, founded on new morphological complexes as well as new molecular data, await further study. Extant and fossil felids remain to be combined in a single data matrix for a more complete understanding of the history of the Felidae.



## REFERENCES

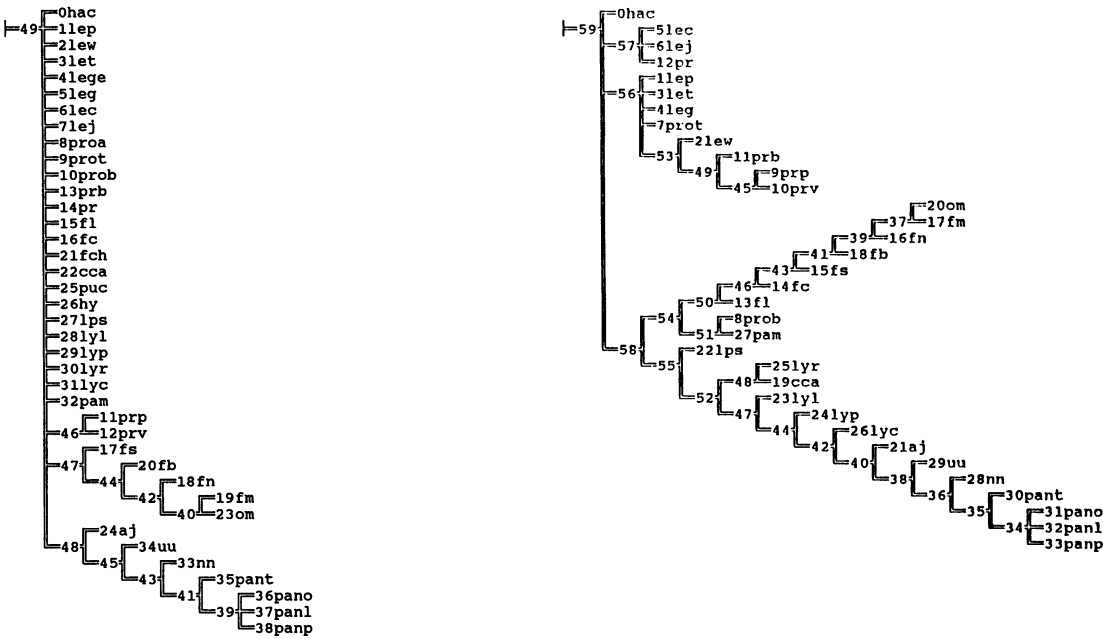
- Berta, A.  
1988. Quaternary evolution and biogeography of the large South American Canidae (Mammalia: Carnivora). Univ. Calif. Publ. Geol. Sci. 132: 149 pp.
- Biknevicius, A.  
1990. Biomechanical design of the mandibular corpus in carnivores. Ph.D. diss., Johns Hopkins Univ., Baltimore, 249 pp.
- Carpenter, J. M.  
1988. Choosing among multiple equally parsimonious cladograms. *Cladistics* 4(3): 291–296.
- Cifelli, R. I.  
1982. The petrosal structure of *Hyopsodus* with respect to that of some other ungulates and its phylogenetic implications. *J. Paleontol.* 56(3): 795–805.
- Collier, G. E., and S. J. O'Brien  
1985. A molecular phylogeny of the Felidae: immunological distance. *Evolution* 39(3): 473–487.
- Davis, D. D., and H. E. Story  
1943. The carotid circulation in the domestic cat. *Zool. Ser., Field Mus. Nat. Hist.* 28: 5–47.
- Fagen, R. M., and K. S. Wiley  
1978. Field paedomorphosis, with special reference to *Leopardus*. *Carnivore* 1(2): 72–81.
- Farris, J. S.  
1969. A successive approximations approach to character weighting. *Syst. Zool.* 18: 374–385.  
1988. Hennig86 (version 1.5) reference. Distributed by the author. New York: 41 Admiral Street, Port Jefferson Station 11776.
- Field, H. E., and M. E. Taylor  
1950. An atlas of cat anatomy. Chicago: University Press, 75 pp.
- Fischer, G.  
1817. *Adversariorum Zoologorum Fasciculus primus*: 1. de Nexu corporum naturalium in universum. 2. de Systemate Mammalium. 3. de Mammalium generibus. *Memoires de la Societe Imperiale des Naturalistes de Moscou*. IV Zoologie.
- Flower, W. H.  
1869. On the value of the characters of the base of the cranium in the classification of the Order Carnivora, and on the systematic position of *Bassaris* and other disputed forms. *Proc. Zool. Soc. London* 1869: 4–37.
- Flynn, J. J., and H. Galiano  
1982. Phylogeny of Early Tertiary Carnivora, with a description of a new species of *Protictis* from the Middle Eocene of northwestern Wyoming. *Am. Mus. Novitates* 2725: 64 pp.
- Flynn, J. J., N. A. Neff, and R. H. Tedford  
1988. Phylogeny of the Carnivora. In M. J. Benton (ed.), *The phylogeny and classification of the tetrapods*, vol. 2: Mammals. Systematics Association Special Volume no. 35B, pp. 73–116. Oxford: Clarendon Press.
- Gaunt, W. A.  
1959. The development of the deciduous cheek teeth of the cat. *Acta Anat.* 38(3): 188–212.
- Gray, J. E.  
1821. On the natural arrangement of vertebrate animals. *London Med. Repos.* 15: 296–311.  
1867. Notes on the skulls of the cats (Felidae). *Proc. Zool. Soc. London* 1867: 258–277, 874–876.
- Haltenorth, T.  
1937. Die verwandtschaftliche Stellung der Grosskatzen zueinander. *Z. Saugetierkd.* 11: 32–105, and 12: 97–44.  
1953. *Die wildkatzen der Alten Welt*. Leipzig: Geest & Portig, 117 pp.
- Hemmer, H.  
1978. The evolutionary systematics of living Felidae: present status and current problems. *Carnivore* 1: 71–78.  
1981. Die Evolution der Pantherkatzen model zur überprüfung der brauchbarkeit der hennigschen prinzipien der phylogenetischen systematik für wirbeltierpaläontologische studien. *Paläont. Z.* 55(1): 109–116.
- Hennig, W.  
1966. *Phylogenetic systematics*. Urbana: Univ. Illinois Press, 263 pp.
- Herrington, S. J.  
1986. Phylogenetic relationships of the wild cats of the world. Unpub. Ph.D. diss., Univ. Kansas, Lawrence, 421 pp.
- Hunt, R. M., Jr.  
1974. The auditory bulla in Carnivora: an anatomical basis for reappraisal of carnivore evolution. *J. Morphol.* 143(1): 21–76.  
1987. Evolution of the aeluroid Carnivora: significance of auditory structure in the

- ninravid cat *Dinictis*. Am. Mus. Novitates 2886: 74 pp.
1989. Evolution of the aeluroid Carnivora: significance of the ventral promontorial process of the petrosal, and the origin of basicranial patterns in living families. Am. Mus. Novitates 2930: 32 pp.
- Jardine, Sir W.  
1834. The naturalist's library: Mammalia, vol. 2; the natural history of the Felinae. Edinburgh: W. H. Lizars et al., 276 pp.
- Jayne, H.  
1898. Mammalian anatomy. Part. I. The skeleton of the cat. Philadelphia: J. B. Lippincott.
- Macintyre, G. T.  
1972. The trisulcate petrosal pattern of mammals. In T. Dobzhansky, M. K. Hecht, and W. C. Steere (eds.), Evolutionary biology 6: 275–302. New York: Appleton-Century-Crofts.
- MacPhee, R. D. E., M. J. Novacek, and G. Storch  
1988. Basicranial morphology of early Tertiary erinaceomorphs and the origin of primates. Am. Mus. Novitates 2921: 42 pp.
- Maddison, W. P., M. J. Donoghue, and D. R. Maddison  
1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83–103.
- Mazak, V.  
1968. Note sur les caractères craniens de la sous-famille des Pantherinae (Carnivora; Felidae). Mammalia 32: 670–676.
- Mickevich, M. F., and N. Platnick  
1989. On the information content of classifications. Cladistics 5(1): 33–47.
- Müller, P.  
1973. Historisch-biogeographische Probleme des Artenreichtums der südamerikanischen Regenwälder. Amazoniana 4(3): 229–242.
- Nawa, A.  
1967. Shapes of Felidae pupils. J. Mammal. Soc. Japan 3: 72–73.
- Neff, N. A.  
1982. The big cats. New York: Harry Abrams, 243 pp.  
1983. The basicranial anatomy of the Nimravidae (Mammalia: Carnivora) character analyses and phylogenetic inferences. Ph.D. diss., City Univ., New York, 643 pp.
- Nelson, G.  
1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. Syst. Zool. 27: 324–345.  
1979. Cladistic analysis and synthesis: principles and definitions, with a historical note on Adanson's "Familles des plantes" (1763–1764). Ibid., 28: 1–21.  
1985. Outgroups and ontogeny. Cladistics 1: 29–45.
- Nelson, G., and N. Platnick  
1981. Systematics and biogeography. Cladistics and vicariance. New York: Columbia Univ. Press, 567 pp.
- Novacek, M. J.  
1986. The skull of leptictid Insectivora and the higher-level classification of eutherian mammals. Bull. Am. Mus. Nat. Hist. 183: 1–112.
- Patterson, C.  
1982. Morphological characters and homology. In K. A. Joysey, and A. E. Friday (eds.), Problems of phylogenetic reconstruction, pp. 21–74. London and New York: Academic Press.
- Peters, G.  
1987. Acoustic communication in the genus *Lynx* (Mammalia: Felidae)—comparative survey and phylogenetic interpretation. Bonn. Zool. Beitr. 38(4): 315–330.
- Pinna, M. C. C. de  
1991. Concepts and tests of homology in the cladistic paradigms. Cladistics 7(4).
- Pocock, R. I.  
1907. Notes upon some African species of the genus *Felis*, based upon specimens recently exhibited in the Society's gardens. Proc. Zool. Soc. London 1907: 329–350, 656–677.  
1916a. On the hyoidean apparatus of the lion (*F. leo*) and related species of Felidae. Ann. Mag. Nat. Hist., ser. 8, 18: 222–229.  
1916b. The structure of the auditory bulla in existing species of Felidae. Ibid., 18: 326–334.  
1917a. On the external characters of the Felidae. Ibid., 19: 113–136.  
1917b. The classification of existing Felidae. Ibid., 20: 329–350.
- Rieppel, O. C.  
1988. Fundamentals of comparative biology. Basel: Birkhauser Verlag, 202 pp.
- Salles, L. O.  
1991. Felid phylogenetics: extant taxa, skull morphology. M.A. diss., City University, New York, 282 pp.
- Scrocchi, G. J., and S. P. Halloy  
1986. Notas sistematicas, ecologicas, etologicas y biogeograficas sobre el gato andino *Felis jacobita* Cornalia (Felidae, Carnivora). Acta Zool. Lilloana 38: 2.

- Severtzon, M. N.  
1857–58. Notice sur la classification multiseriale des carnivores, spécialement des felides, et les études de zoologie générale qui s'y rattachent. *Rev. Mag. Zool.* 9(2): 389–391, 433–439; 10(2): 3–8, 145–150, 192–199, 241–426, 385–393.
- Sonntag, C.  
1923. The comparative anatomy of the tongues of Mammalia. VIII. Carnivora. *Proc. Zool. Soc. London* 9: 129–153.
- Szalay, F. S.  
1969. Mixodectidae, Microsyopidae, and the insectivore primate transition. *Bull. Am. Mus. Nat. Hist.* 140(4): 193–330.
- Van Valen, L.  
1966. Deltatheridia, a new order of mammals. *Bull. Am. Mus. Nat. Hist.* 132(1): 1–176.
- Weigel, I.  
1956. Das Fellmuster der wildlebenden Katzenarten und der Hauskatze in vergleichender und stammesgeschichtlicher Hinsicht. *Säugetierkd. Mitt.* 9: 1–120.
- Weitzman, S. H., and S. V. Fink  
1985. Xenurobryconin phylogeny and putative pheromone pumps in glandulocaudine fishes (Teleostei: Characidae). *Smithson. Contrib. Zool.* 421: 1–118.
- Werdelin, L.  
1981. Evolution of lynxes, *Ann. Zool. Fenn.* 18: 37–71.  
1983. Morphological patterns in the skull of cats. *Biol. J. Linnean Soc.* 19: 375–391.
- Wiley, E. O.  
1981. *Phylogenetics. The theory and practice of phylogenetic systematics.* New York: Wiley, 439 pp.
- Wozencraft, W. C.  
1984. A phylogenetic reappraisal of the Viverridae and its relationships to other Carnivora. Vol. 1, pp. 546 and Vol. 2, pp. 476. Ph.D. diss., Univ. Kansas, Lawrence.  
1989. The phylogeny of recent Carnivora. In J. L. Gittleman (ed.). *Carnivore behavior, ecology, and evolution.* Ithaca: Comstock, pp. 495–535.
- Wyss, A. R.  
1987. The walrus auditory region and the monophyly of Pinnipeds. *Am. Mus. Novitates* 2871: 31 pp.

APPENDIX 1

On the right, the unweighted Nelson consensus of 1348 most parsimonious trees resulted from the first cranial data analysis, where all 38 felids are considered; and on the left the weighted tree represented in figure 51.

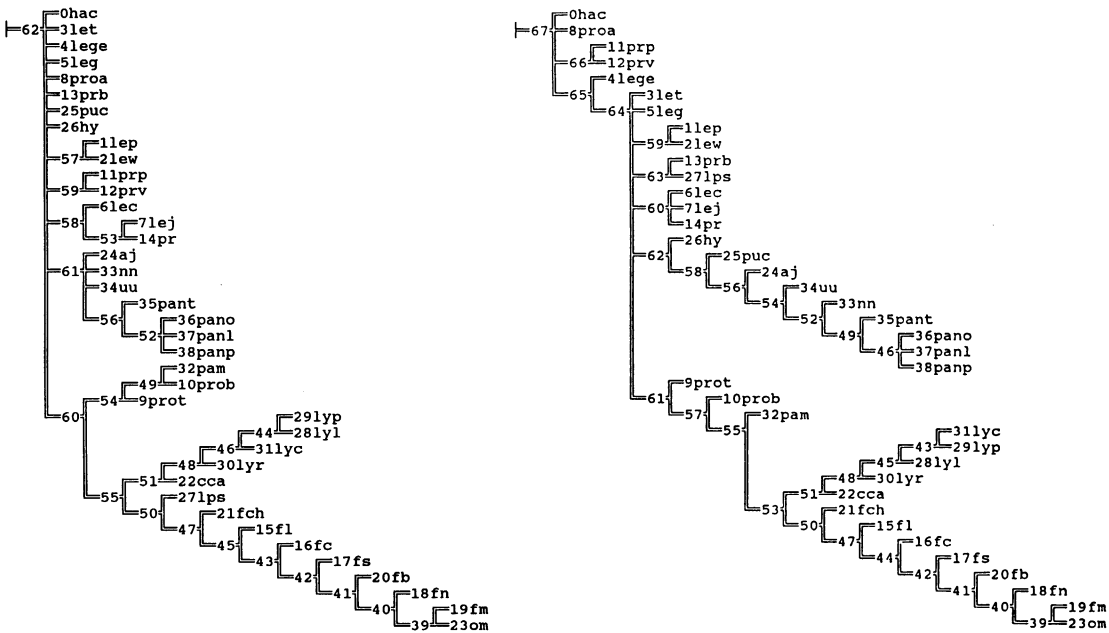


Taxonomic abbreviations

hac	hypothetical common ancestral	fm	<i>Felis margarita</i>
lep	<i>Leopardus pardalis</i>	fb	<i>Felis bieti</i>
lew	<i>Leopardus wiedii</i>	fch	<i>Felis chaus</i>
let	<i>Leopardus tigrina</i>	ca	<i>Caracal caracal</i>
lege	<i>Leopardus geoffroyi</i>	om	<i>Otocolobus manul</i>
leg	<i>Leopardus guigna</i>	aj	<i>Acinonyx jubatus</i>
lec	<i>Leopardus colocolo</i>	puc	<i>Puma concolor</i>
lej	<i>Leopardus jacobita</i>	hy	<i>Herpailurus yagouaroundi</i>
proa	<i>Profelis aurata</i>	lps	<i>Leptailurus serval</i>
prot	<i>Profelis temmincki</i>	lyl	<i>Lynx lynx</i>
prob	<i>Profelis badia</i>	lyp	<i>Lynx pardina</i>
prp	<i>Prionailurus planiceps</i>	lyr	<i>Lynx rufus</i>
prv	<i>Prionailurus viverrina</i>	lyc	<i>Lynx canadensis</i>
prb	<i>Prionailurus bengalensis</i>	pam	<i>Pardofelis marmorata</i>
pr	<i>Prionailurus rubiginosa</i>	nn	<i>Neofelis nebulosa</i>
fl	<i>Felis lybica</i>	pant	<i>Panthera tigris</i>
fc	<i>Felis cafra</i>	pano	<i>Panthera onca</i>
fs	<i>Felis silvestris</i>	panl	<i>Panthera leo</i>
fn	<i>Felis nigripes</i>	panp	<i>Panthera pardus</i>

APPENDIX 2

On the right, the unweighted Nelson consensus of 409 equally parsimonious trees resulted from the morphological character analysis of 57 characters for 38 taxa; and on the left the weighted tree represented in figure 52. (Abbreviations are spelled out in appendix 1.)



## APPENDIX 3

Derived character information from Pocock, 1917b, associated with the numbered nodes shown in figure 55:

## Pocock's Character Types

Node 1: Suspensorium of hyoid imperfectly ossified, its inferior portion consisting of a larger or shorter elastic tendon conferring great mobility upon the larynx.

Node 3: (a) Suspensorium of hyoid normally ossified, holding the larynx close to the base of the skull, and restricting its movement. (b) Furnished digits' tips (fore and hind feet), with at least a single cutaneous lobe protecting the retracted claw on the inner side of the digits 2 and 3 and on the outer side 4 and 5.

Node 4: (a) Nasal depressed. (b) Mesopterygoid fossa elongated.

Node 5: (a) Rarely complete sagittal ridge. (b) Nasal compressed above. (c) Anterior border of maxilla vertical or nearly vertical. (d) Occipital crest not appreciably concave above condyles and considerably broader at that point than condylar width.

Node 6: Postcanine space quite small.

Node 7: (a) Feet fully webbed. (b) Hair on neck reversed in direction of growth. (c) Lacrimal extends higher above malar arch within orbit.

Node 8: (a) Nasal little broader. (b) Occipital area much broader, especially over summit and across mastoid process.

Node 9: Front of mesopterygoid fossa lanceolate.

Node 10: (a) Back of maxilla inclined well beyond lacrimal foramen. (b) Condyle high above angular. (c) Malar crest close to its inferior edge. (d) Coronoid process narrower.

Node 11: Deep postorbital constriction.

Node 12: Groove partition of bulla passing from stylomastoid foramen to basioccipital suture.

Node 13: Bulla groove partition rising some distance from crest of tympanic annulus.

Node 14: Suborbital edge of palate not deeply notched.

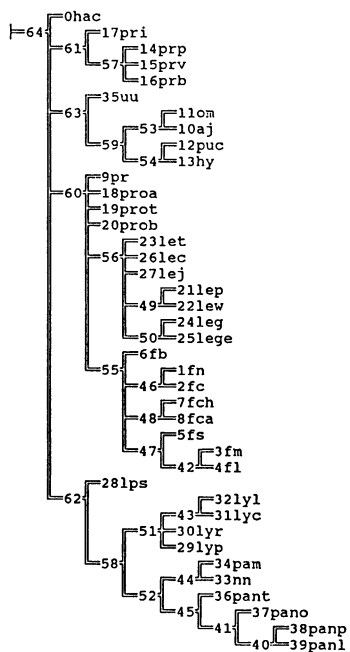
Node 15: (a) Nasal branch of maxilla broad above nasal, then abruptly pointed. (b) Rhinarium reduced.

Autapomorphies for species branching off from nodes 0 and 3:

*Acinonyx jubatus*: Total suppression of cutaneous lobes guarding claws.

*Neofelis nebulosa*: (a) Occiput angular above. (b) Posterior part of nasal width greater. (c) Anterior rim of mesopterygoid fossa evenly ovate, antero-lateral border. (d) Mandible greatly elevated anteriorly. (e) Symphyseal region nearly vertical.

*Puma concolor*: (a) Groove of partition rising close to crest of tympanic annulus. (b) Palatine foramen very large in orbit. (c) Palate broad. (d) Sides of posterior elongation of palate widely divergent. (e) Occiput wide across mastoids. (f) Nasal bones end rather abruptly.



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