Aspects of carnivoran evolution in Africa

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Abstract

This thesis concerns the evolution of African small carnivorans, with emphasis on East African Viverridae and Herpestidae (Carnivora, Mammalia). Viverridae and Herpestidae are two Old World feliform (belonging to the cat branch) carnivoran families with a confusing, and sometimes even misleading, taxonomic and systematic history, in addition to a scarce fossil record.

A new genus and species from Fort Ternan, western Kenya, dated to ca 14 Mya (million years ago), was described and tentatively assigned to the Viverridae. The excellent preservation of this material has the potential to shed much light on the evolution of feliform carnivorans from Africa. The fossil record of Carnivora from Laetoli, a Pliocene hominid-bearing site in northern Tanzania, was also described and placed in an evolutionary context. The age of the fossil fauna from Laetoli ranges from 4.3 Mya to 2.5 Mya. The fossil material from this site is remarkable for two reasons: it is extensive in both number of taxa represented and amount of fossil material, especially of small carnivorans, and it is fossilized and preserved under aeolian conditions. In addition to these paleontological studies, two studies concerning extant Viverridae and Herpestidae were conducted. First, the phylogeography of the white-tailed mongoose, *Ichneumia albicauda*, (Herpestidae), was examined, with the tentative conclusion that its origin is southern African. Second, the ecomorphology and biogeography of African and Eurasian Viverridae and Herpestidae was analysed in order to investigate if these features can be used to help assess their evolutionary history in the absence of fossils. The pattern that emerges in this study is that the species of Viverridae and Herpestidae do not generally overlap in ecomorphology where they overlap geographically, which indicates considerable competitive interactions between the families in both Africa and Eurasia.

Keywords: Carnivora, Evolution, Africa, Viverridae, Herpestidae

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To Jasmine, Sam, Sophie and Nicholas

تقدیم به خانواده‌ام،
با عشق

LIST OF ORIGINAL PUBLICATIONS AND MANUSCRIPTS

This thesis is based on the following papers, referred to in the text by their Roman numerals:

I. Werdelin, L. & Dehghani, R. In press. Carnivora. *In*: Harrison, T. (ed.) Paleontology and Geology of Laetoli, Tanzania: Human Evolution in Context. Vertebrate Paleobiology and Paleoanthropology Series, Springer, Dordrecht.

II. Dehghani, R. & Werdelin, L. 2008. A new small carnivoran from the Middle Miocene of Fort Ternan, Kenya. Neues Jahrbuch für Geologie und Palaeontologie Abhandlungen, 248: 233-244.

III. Dehghani, R., Wanntorp, L., Pagani, P, Källersjö, M., Werdelin, L. and Veron, G. Submitted. Phylogeography of the White-tailed Mongoose (Herpestidae, Carnivora, Mammalia) - a phylogenetic study based on partial mtDNA of the control region (D-loop)

IV. Wesley-Hunt, G. D., Dehghani, R. and Werdelin, L. Manuscript. Comparative ecomorphology and biogeography of Herpestidae and Viverridae

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This thesis is not to be regarded as a publication in the sense of the International Code of Zoological Nomenclature (ICZN, 1999), and scientific names mentioned in it should not be cited in any form.

Contents

Setting the stage

For over 15 million years, carnivorans have been the dominant predators in Africa. Their first appearance in the African fossil record occurred at least 19 million years ago, and coincided with the first semi-permanent land bridge between Eurasia and Africa. Carnivorans evolved 65 million years ago and were already circum-Arctic in their distribution well before they reached Africa, some 45 million years later. The first African carnivorans migrated from Eurasia and are members of the Felidae, Viverridae and Herpestidae, three modern carnivore families. There remain difficulties in determining the patterns of migration and endemic radiation in the African later Tertiary. In this thesis, I have, together with collaborators: revised and described new material of Carnivora from Laetoli, a 3.7 million year old fossil-bearing locality in northern Tanzania, eastern Africa (paper I); described a new small carnivoran from the Middle Miocene, ca 14 Ma, of Fort Ternan, western Kenya (paper II); examined the phylogeography of the white-tailed mongoose (Herpestidae) (paper III), and; applied ecomorphological traits of the Viverridae and Herpestidae (Carnivora) to better understand their paleobiogeography and current distribution (paper IV).

The main focus of this thesis is to further our understanding of the evolution of carnivorans in Africa, with emphasis on Viverridae and Herpestidae, aiming at increasing our knowledge about their fossil history, biogeography and ecomorphology. In order to put these groups in a wider context, I will start with a general introduction to the order Carnivora, their inclusive group.

The Order Carnivora (Bowdich, 1821)

Introduction

The diverse order Carnivora, consisting of 15 extant families comprising about 280 species of placental mammals, occurs naturally throughout the world except in Australia, New Guinea, New Zealand, Antarctica, and many oceanic islands (Wozencraft, 2005). One species, *Canis familiaris*, the domestic dog, was apparently actively introduced to Australia by humans in ancient times and subsequently managed to establish viable populations there. Even in modern times, there are cases of introduced species as a result of human activity. The mongoose populations found on the West Indies are one example (Nowak, 1999). Not all members of the order are carnivorous. Therefore, membership in this order merely reflects shared phylogenetic history, not shared dietary adaptations. Members of the order Carnivora are referred to as “carnivorans”, while the term “carnivore” refers to any organism that includes a significant amount of meat in its diet.

Carnivorans have teeth and claws adapted for catching and eating prey. The order Carnivora is characterized by functional specializations for shearing in the fourth upper premolar (P4) and the first lower molar (m1) (Figure 1d). These teeth, called carnassials, have a blade-like morphology. The principal carnassial shear of P4/m1 remains as the central character complex that unites members of the order Carnivora, despite its secondary loss in some carnivoran taxa. Functionally, this adaptation increases the efficiency of meat-slicing, as the blades of the carnassials move past each other in a scissor-like action. Many carnivorans hunt in packs and are social. Other features shared by all carnivores include: a fusion of certain bones in the foot (scaphoid, lunar, and centrale bones) to form the scapholunar, an ossified auditory bulla [although secondarily lost in *Nandina binotata*, the African palm civet, which has a cartilaginous bulla (Hunt, 1974)], a relatively undeveloped/reduced collar bone (clavicle), and a penis containing an elongated bony structure known as the baculum or os penis (lost in hyenas) (Macdonald, 2001). In addition, there are a few other general “carnivore” characters concerning the carnivoran body plan and modes of life, but these are more variable between families and species of Carnivora.

With respect to morphology and life history of the taxa included, the Order Carnivora is extremely heterogenous in many respects. The smallest living carnivoran is the least weasel *Mustela nivalis* (Mustelidae) with an adult weight around 35-40 g, whereas the largest living carnivoran is the brown or grizzly bear, *Ursus arctos* (Ursidae), with a recorded weight of 780 kg for an adult male. The members of this order show a wide variety of dietary preferences, including species that are entirely carnivorous, insectivorous, frugivourous, herbivorous or omnivorous. Further, carnivorans inhabit a wide range of habitats around the world, including both terrestrial and aquatic environments, and have cursorial, arboreal, fossorial or aquatic modes of life (Nowak, 1999). These kinds of wide-ranging adaptations in morphological traits, with several cases of parallel and convergent evolution, have resulted in difficulties for researchers concerned with carnivoran systematics. Another impediment to a better understanding of carnivoran diversification patterns is the fact that systematic and evolutionary studies of the two speciose families Viverridae and Herpestidae have been neglected. The situation is, however, being amended through recent molecular studies (Viverridae: Gaubert et al., 2004a, b; Herpestidae: Veron et al., 2004). In contrast, the systematics and evolution of some other carnivore families have been given considerable attention (Hyaenidae: Werdelin and Solounias, 1991; Koepfli et al., 2006; Canidae: Tedford et al., 1995; Lindblad-Toh et al., 2005; Felidae: Johnson et al., 2006).

History of classification

In 1758, meat-eating mammals were referred to the order Ferae by Linneaus. At that time and the first half of the 19th century, carnivorous species were mainly grouped together on the basis of morphological characters of the dentition (Cuvier, 1800, 1817; Gray, 1821). However, the criterion ‘meat-eating’ was not satisfying and led to homoplasy when arranging taxa (Cuvier, 1800; Flower, 1869). Therefore, Turner’s (1848) classification of the order Carnivora represented a new view in the field of systematics, identifying essential differences regarding basicranial morphology at the familial level. From the time of Turner’s classification and about 100 years onwards, to the mid 20th century, areas in focus in carnivoran systematic studies went through different trends, for example combining cranial-, postcranial-, and soft anatomy (Flower, 1869; Flower and Lydekker, 1891; Huxley, 1880) and taking fossil material into account (Simpson, 1945).

In early studies of carnivoran interrelationships, the creodonts, an extinct group of mammalian carnivores, were considered to be included within Carnivora (Cope, 1880; Matthew, 1909; see also Linnaeus, 1758; Savage, 1977). The Creodonta first appeared in the Paleocene, about 59 million years ago, and were the dominant meat eaters of the Paleocene and Eocene. Like the members of Carnivora, they had the feature of carnassial shear, a meat-eating adaptation that gave both groups the necessary tools to dominate the carnivore niche. However, the specific teeth adapted as carnassials differed between creodonts and carnivorans, as well as within

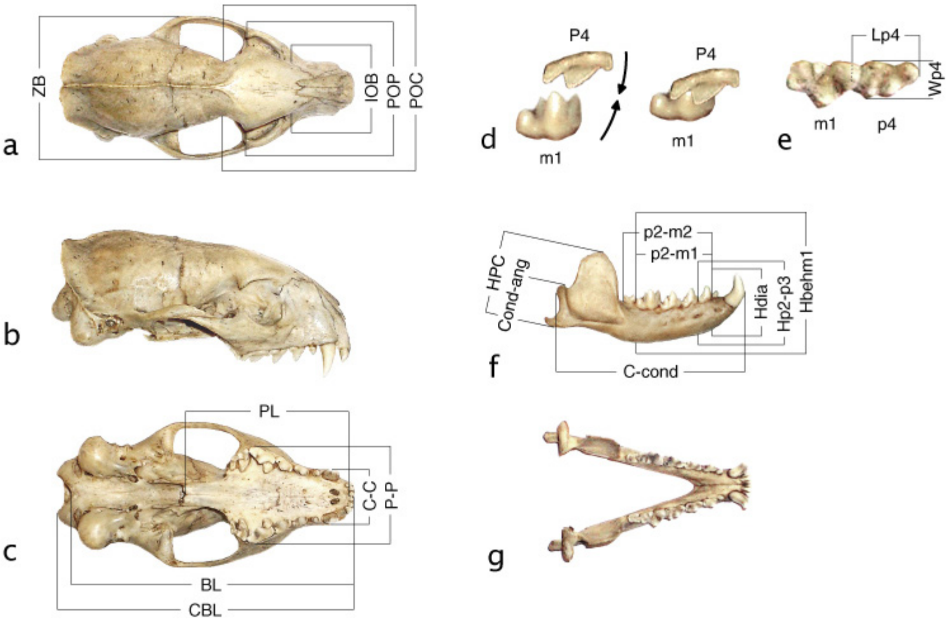


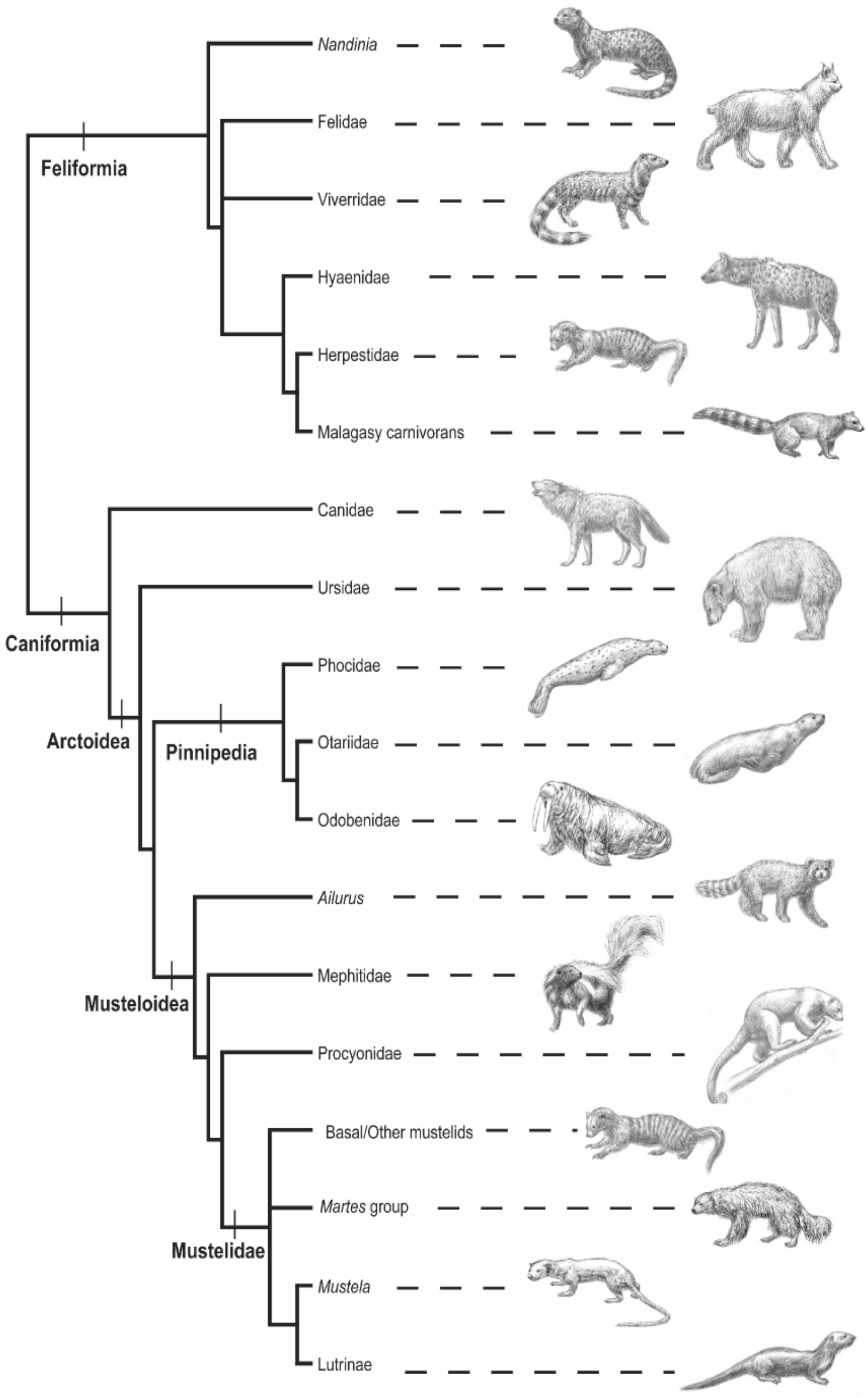
Figure 1. Photographs showing different views of the skull and mandible in a recent mongoose (*Herpestes ichneumon* NRM VE A581268) together with a selection of craniodental measurements used in carnivoran paleontology. Definition of measurements below. **1a**. Skull, dorsal view. **1b**. Skull, right lateral view. **1c**. Skull, ventral view. **1d**. Left: the carnassials, upper P4 and lower m1, right lateral view; the arrows show the shearing motion. Right: the carnassials in occlusion. **1e**. Right p4 and m1 in occlusal view. **1f**. Right mandibular ramus, lateral view. **1g**. Mandible, occlusal view. Length of skull from anterior face of incisors to posterior end of occipital condyles (Condylobasal length, CBL) in this specimen = 99.46 mm. Hbehm1 = dorsoventral depth of mandible behind m1; C-C = width of skull between buccal margins of canines, P-P = width of skull between buccal margins of P4, IOB = least infraorbital width, POC = least width at post-orbital constriction, and, ZB = greatest width of skull at zygomatic arches, C-cond = length of mandible from anterior end of canine to posterior end of condyle, HPC = height of the coronoid process, cond-ang = height from condyle to angular process, p2-m1 = length of tooth row from p2 to m1 inclusive, p2-m2 = length of tooth row from p2 to m2 inclusive, Hdia = least depth of mandible at diastema, Hp2-p3 = depth of mandible between p2 and p3, BL = length of skull from anterior face of incisors to anterior end of foramen magnum, CBL = length of skull from anterior face of incisors to posterior end of occipital condyles, PL = length of bony palate at midline, and POP = greatest width of skull at postorbital processes.

creodonts. The creodonts finally went extinct in the Late Miocene, about 9 million years ago (Flynn et al., 1988; Polly, 1996, 1999; Lewis, 1999).The relationships between Creodonta and Carnivora became one of the focal areas in carnivoran phylogenetics. From being considered an ingroup within the Carnivora, via the view that they constitute the ancestors of the carnivoran order, the creodonts are today considered a separate order of carnivorous mammals sharing common ancestry with the Carnivora (Savage, 1977; Flynn and Galiano, 1982; Martin, 1989; Wyss and Flynn, 1993;).

Present phylogenetic status

Although carnivoran systematics are constantly revised, there is a consensus that Carnivora is a monophyletic group and that two main crown-group lineages are recognized within the order: the Feliformia (cat-like carnivorans), including the extant families Felidae (cats), 'Viverridae' (civets, genets and linsangs) (probably paraphyletic, and thus, placed within quotation marks (Gaubert and Veron, 2003), Eupleridae (Malagasy Carnivora), Nandiniidae (African palm civet), Herpestidae (mongooses) and Hyaenidae (hyaenas and the aardwolf); and the Caniformia (dog-like carnivorans), including the extant families Canidae (dogs, wolves, coyotes, jackals and foxes), Ursidae (bears), Otariidae (seals and sea-lions), Odobenidae (walruses), Phocidae (true seals), Mustelidae (weasels, badgers and otters), Mephitidae (skunks and stink badgers), Procyonidae (raccoons and relatives) and Ailuridae (red panda) (Figure 2) (Flynn et al., 2005; Wozencraft, 2005). This bipartite grouping was first recognized by Cuvier (1800) and later formalized by Kretzoi (1945) and is generally accepted today (Flynn and Nedbal, 1998; Flynn et al., 2005; Wozencraft, 2005).

Figure 2. Opposite page. A schematic phylogeny of the Carnivora. Illustrations of representative taxa for major lineages include (from top): *Nandinia binotata;* Felidae (*Lynx rufus*); Viverridae (*Viverra zibetha*); Hyaenidae (*Crocuta crocuta*); Herpestidae (*Mungos mungo*); Malagasy carnivorans (*Eupleres goudotii*); Canidae (*Canis lupus*); Ursidae (*Ursus americanus*); Phocidae (*Phoca vitulina*); Otariidae (*Zalophus californianus*); Odobenidae (*Odobenus rosmarus*); Ailuridae (*Ailurus fulgens*); Mephitidae (*Mephitis mephitis*); Procyonidae (*Potosflavus*); Mustelidae, basal/other mustelids [generalized schematic representing diverse taxa (African polecat and striped marten, badger, etc.)]; Mustelidae, *Martes*-group (*Gulo gulo*); Mustelidae, *Mustela* (*Mustela frenata*); Mustelidae, Lutrinae (*Lontra canadensis*) (From Flynn et al., 2005).


Nandinia
Felidae
Viverridae
Hyaenidae
Herpestidae
Malagasy carnivorans
Feliformia
Canidae
Ursidae
Phocidae
Otariidae
Odobenidae
Caniformia
Arctoidea
Pinnipedia
Ailurus
Mephitidae
Procyonidae
Musteloidea
Basal/Other mustelids
Martes group
Mustela
Lutrinae
Mustelidae

Viverridae (Gray, 1821) and Herpestidae (Bonaparte, 1845)

Present phylogenetic status

Historically, both Viverridae and Herpestidae have a long and confusing taxonomic and systematic history. Until recently, Viverridae (sensu stricto) and Herpestidae have been placed together in the Viverridae (sensu lato), in which the herpestids were allocated to a subfamily of their own, Herpestinae (Winge, 1895; Gregory and Hellman, 1939). This traditional merging, however, was questioned on morphological grounds, and many authors agreed on a series of anatomical differences, especially of the scent glands and basicranium (Hunt, 1974, 1987; Hunt and Tedford, 1993; Wozencraft, 1989; Wyss and Flynn, 1993). As is the case in many groups of organisms, the phylogeny of Viverridae and Herpestidae has been extensively revised in recent years on account of the increasing use of molecular methods. Today, there is a consensus that "Herpestinae" neither belongs within the family Viverridae, nor represents the sister group of Viverridae, but instead a separate family Herpestidae is recognized, which is the sister-group of the Hyaenidae (Flynn and Nedbal, 1998; Flynn et al., 2005).

Beside the family rank revisions of the Viverridae and Herpestidae, intra-familial studies have shown that the former family, even after separation of the Herpestidae, is paraphyletic. There are now morphological and molecular data showing that the African palm civet, *Nandinia binotata*, (Hunt, 1974; Flynn and Nedbal, 1998; Flynn et al., 2005) and the oriental linsangs, *Prionodon linsang* and *P. pardicolor*, (Gaubert and Veron, 2003; Gaubert et al., 2004b) fall outside the true viverrids (Hunt, 1974; Flynn et al., 2005), *contra* the former definition of Viverridae including these genera (Simpson, 1945; Wozencraft, 1989, 1993). *Nandinia* is now considered the sister taxon to all other extant feliform carnivorans and is consequently placed in a family of its own, the Nandiniidae (Flynn et al., 2005). The linsangs, on the other hand, are currently considered the extant sister group to the family Felidae. It has further been shown that *Osbornictis piscivora*, the aquatic genet, should be synonymised with and included in the genus *Genetta* in order to make that genus monophyletic (Gaubert, 2004a, b). In Herpestidae, there is reason to question the monophyly of the genus *Herpestes* (Veron et al., 2004), with species from both Africa and Asia. Malagasy Carnivora, which have traditionally been thought to have a dual origin from separate migrations of Herpestidae and Viverridae, have in recent studies been shown to be monophyletic and, closely allied with the Herpestidae (Flynn et al., 2005; Gaubert et al., 2005). Thus, the Malagasy Carnivora (*Fossa* and *Eupleres*, previously regarded as Viverridae, *Galidia*, *Galidictis*, *Mungotictis* and *Salanoia*, previously regarded as Herpestidae; and the enigmatic *Cryptoprocta*, previously placed in both Viverridae and Herpestidae, as well as Felidae) seem to have a single origin from an African herpestid ancestor (Yoder et al., 2003).

Fossil history in brief

The present distribution of the Viverridae and Herpestidae (excluding a few introduced populations) is Africa and South and Southeast Asia. Both families are diverse and ecologically varied, but their fossil record is extremely poor and difficult to interpret (Hunt, 1996; Werdelin, 2003). Both Viverridae and Herpestidae must have originated by the late Oligocene, around 25 Ma, and the feliform radiation in the Old World started to really accelerate by the end of the early and the beginning of the middle Miocene, around 17-16 Ma (Werdelin, 1996). Neither viverrids nor herpestids reached North America, which suggests that their center of radiation was at relatively low latitudes, thus making it difficult for them to move through northern Asia and across the Bering land bridge (Martin, 1989). One striking aspect regarding extant species of African carnivorans is the fact that very few of them have a definite fossil record in eastern Africa (Werdelin and Lewis, 2005). Nevertheless, a good portion of our knowledge about the evolutionary history of Viverridae and Herpestidae is from Mio-Pliocene eastern African material. The carnivoran fossils from this region are found in association with early hominids and other mammals, and the small carnivoran fossils, especially herpestid finds, are the result of extensive sieving operations.

Viverridae: The oldest basicranial material referred to Viverridae is the early Miocene (more than 20 Ma) genus *Herpestides* known from France (Hunt, 1991) and eastern Africa (Schmidt-Kittler, 1987). This genus was long thought to be a herpestid (Beaumont 1967), but more recent studies of its auditory bulla have led to it being reassigned to the Viverridae (Hunt, 1991, 1996; Hunt and Tedford, 1993). *Herpestides* is the oldest known viverrid with a modern auditory bulla. Many older taxa have been referred to the family Viverridae, but only on the basis of dental characters, which are of doubtful diagnostic value at the generic level. From the middle Miocene (ca. 14 Ma) of Kenya there is a specimen with complete cranium and upper dentition tentatively assigned to the Viverridae (paper II). The oldest material referable to a modern genus is likely to be specimens from Late Miocene (ca. 6.2-5.5 Ma) from Ethiopia referred to *Genetta* (Haile-Selassie, 2001). However, specimens from Lothagam, Kenya, referred to cf. *Genetta* are slightly older and would therefore be the oldest representatives of a modern viverrid genus if the generic attribution is confirmed (Werdelin, 2003). Many fossil Viverridae from Africa represent large forms, sometimes much larger than their living equivalents. The Pliocene (3.7 Ma) *Viverra leakeyi* from Laetoli, Tanzania, represents one such example (paper 1). From this locality we also have material assigned to *Genetta*.

Herpestidae: Due to their primitive dentition, many middle and late Miocene Herpestidae have been placed in extant genera, notably *Herpestes*, whilst earlier fossils have been placed in genera such as *Leptoplesictis*, of somewhat uncertain systematic position (Hunt, 1996). This has complicated understanding of the evolutionary history of the family. Herpestids are not known prior to the late Miocene in Asia, where they are found in the Siwalik beds of Pakistan and in the Bahe fauna of north China, material that is as yet undescribed. As it is, the oldest known material belonging in extant herpestid genera may be that from Late Miocene (ca. 7 Ma) of Chad questionably referred to *Galerella sanguinea* (Peigné et al., 2005). As with Viverridae, there is Pliocene (3.7 Ma) herpestid material from Laetoli, Tanzania, representing *Herpestes*, *Galerella*, *Helogale* and *Mungos*, some of which may represent the oldest instances of the extant species (paper I). All fossil material assigned to Viverridae and Herpestidae from Laetoli is referred to extant genera and sometimes species.

Methodological framework

Carnivoran paleontology

Carnivorans are usually underrepresented in the fossil record compared to other vertebrate taxa due to their mode of life as top predators. Smaller Carnivora are also usually underrepresented in the fossil record compared to the larger forms, which is clearly the case in the east African Pliocene-Pleistocene fossil record (Werdelin and Lewis, 2005), in this thesis represented by the fossil material from Laetoli (Paper I). The reason for this lies mainly in the nature of the fossil deposits of the region and in the nature of their study. In vertebrate paleontological studies, fossils in the form of skeletal remains of teeth, cranial and postcranial constitute the raw study material. Fortunately, the skeleton of carnivorans includes a lot of morphological information, which is useful in both systematic and ecological studies. Both life-history traits and behavioural traits can be inferred from the morphology of carnivorans. In the present studies (papers I and II), the focus is on dental and cranial fossil material, due to preservation, taphonomy (the study of the course of events between the time of death of an organism to the time of its discovery as a fossil) and collecting techniques employed.

The importance of dental morphology in carnivoran paleontology

In mammals, teeth are the most readily preserved body parts, and consequently, many mammals are described on the basis of a few teeth (Lucas, 1979; Ginsburg, 1999). Teeth are of special significance in carnivoran studies, and especially in paleontology, due to their usefulness in carnivoran systematics, since a single tooth can be used to obtain reliable taxonomic identifications (Damuth and MacFadden, 1990). There are many kinds of specializations that separate species from each other. Variation within species in dental morphology tends to be limited compared to differences between species, so a few teeth can provide important and decisive systematic information (Damuth and MacFadden, 1990; pers. obs.). Further, teeth connect morphology to ecology through diet (Van Valkenburgh, 1989; Jernvall et al., 1996). Therefore, it is possible to obtain information on diet and prey preferences by examining teeth. Furthermore, it is possible to estimate body mass in carnivorans by studying dental morphology (Van Valkenburgh, 1988, 1991, 1996; Van Valkenburgh and Binder, 2000). Hence, in a wider perspective, it is possible to address questions regarding various ecological and functional traits such as locomotion, hunting strategies and carcass transport, habitat preference and larger-scale patterns of guild structure. Figure 1 shows a selection of craniodental measurements commonly used in carnivoran studies of morphological nature.

Ecomorphology

Ecological morphology, or ecomorphology, is the study of the relationship between the functional design of organisms and the environment (Wainwright and Reilly, 1994), or to put it in another way, the study of the relationship between the ecological role of an individual and its morphological adaptations (Ricklefs, 1990). In paleontology, ecomorphological studies are a combination of morphological and paleoecological questions, issues sometimes difficult to separate and many times applied in combination. Morphological studies are carried out at the species level and generally in analogy with extant species, thereby making it possible to reconstruct paleoenvironment and paleoecology for the time period under investigation, enabling the investigation of morphological variation over time and the tracking of adaptive shifts (Van Valkenburgh, 1994). Further, it is possible to study different kinds of interactions between species, such as competition, and how communities have evolved over time (Janis et al., 2000). It is important to remember, however, that it is the morphology of the studied organisms that provides ecologically significant information. In paper IV, ecomorphology is used to examine the biogeography of Viverridae and Herpestidae.

Comparative morphology

Both qualitative and quantitative methods have been employed in the morphological comparisons in this thesis (papers I, II and IV). To qualitatively study morphology and morphological traits, simply means that the specimens are studied by eye, described and compared to relevant material.

Measurements taken on the teeth and skeletons (here confined to the cranium) constitute the raw data used in the following quantitative methods:

Bivariate methods: The quantitative methods used are mostly limited to standard bivariate techniques when fossil material is studied. This is due to the fragmentary (paper I) and/or limited (paper II) nature of the material.

In the bivariate diagrams, the raw data were transformed into $\log_{10}$ in order to normalize the distribution of the variables. Craniodental measurements used are standard for carnivorans (Werdelin and Solounias, 1991). Figure 1 show a selection of cranial and dental measurements commonly used in carnivoran paleontology (length and width of additional teeth not shown). The use of bivariate methods renders possible identification and similarities and differences between taxa analysed statistically.

Multivariate methods: Principal Components Analysis (PCA) is a multivariate statistical method used to reduce and interpret large multivariate data sets with some underlying linear structure to lower dimensions for analysis and is extensively used in morphometric studies. In paper II, this method was used to complement the bivariate statistics. In order to help assess the ecology of a new fossil taxon, measurements of the upper dentition of the referred specimen and a number of African small feliform Carnivora were taken. The resulting correlation matrix was then used to carry out a Principal Components Analysis in PAST 1.7 (Hammer et al., 2001).

Principal Coordinates Analysis (PCO) is another multivariate statistical method analogous to PCA and used in paper IV. A dissimilarity matrix was calculated from coded characters and plotted into morphospace using the first and second axis of a Principal Coordinate Analysis (PCO) (see Wesley-Hunt 2005 for discussion). A morphospace is a representation of the possible form, shape or structure of an organism. Each axis of the morphospace corresponds to a variable which describes some set of characters of the organism. Each point in the morphospace represents an individual organism. This method enables the investigation of a whole variety of morphological characters. The purpose of this study is to document the pattern of morphological diversity, here represented by 16 dental characters and body size, by investigating patterns of morphospace occupation. The dental characters describe the entire tooth row and capture the complexity present in carnivorans. In addition to the ecological importance of body mass in carnivorans, the use of dentition permits ecological inferences to be made since teeth and diet are closely related, and, thereby ecologically significant.

Phylogeographic study

Phylogeography is the study of the biogeography of populations (Avise, 2000). This is generally done by studying the distribution of molecular sequences or markers that allow for the reconstruction of the distributional history of a species. In paper III, tissue samples from individuals of the white-tailed mongoose, *Ichneumia albicauda*, from different localities were collected in order to study its phylogeography. The obtained phylogeny from DNA sequences of the mitochondrial genome served as basis for a discussion regarding the place of origin and subspecies distribution of the white-tailed mongoose, as well as a test of some older taxonomic hypotheses.

The papers in brief

I. Pliocene Carnivora from Laetoli, Tanzania

A total of 936 catalogued specimens of Carnivora from Laetoli were studied. Laetoli is a Pliocene site in northern Tanzania. The fossil material from the site comes from several levels: the Lower Laetolil Beds (ca. 4.3-3.7 Ma), the Upper Laetolil Beds (ca. 3.7-3.4 Ma), and the Ndolanya Beds (ca. 2.5 Ma). A feature distinguishing this material from that of most other African Pio-Pleistocene sites is that it accumulated and was fossilized in a fully terrestrial environment. This is significant since the fossil specimens found at this locality sample a somewhat different environmental context than material from elsewhere.

The material consists of dental, cranial and post-cranial material, of which the former two were the focus of this study. The material is described, analyzed and taxonomically identified. The study includes both qualitative (morphological comparisons) and quantitative analyses (bivariate methods). Much of the material is in a fragmented state, creating difficulties for species-level identification.

The Laetoli specimens are attributed to six carnivore families: Canidae, Mustelidae, Viverridae, Herpestidae, Hyaenidae and Felidae, and represent about 30 species-level taxa. In comparison to other Pliocene eastern African carnivore faunas, Laetoli shows several important features: the material is extensive; representing both smaller and larger Carnivora and the diversity of small carnivorans is unique within east Africa. It is the oldest site in Africa to have a diverse canid sample. It includes many definite and possible first occurrences, such as *Canis* and *Otocyon* (Canidae), *Proteles* and *Crocuta* (Hyaenidae) and *Panthera* (two species) and *Acinonyx* (Felidae).

II. A new carnivoran from Fort Ternan, Kenya

The complete cranium and upper dentition of a new genus and species of a small feliform carnivoran from the Middle Miocene (ca. 14 Ma) of Fort Ternan, western Kenya, is described. This new taxon, *Kanuites lewisae*, currently only known from this locality, is tentatively assigned to the family Viverridae on the basis of dental characters and external features of the auditory bulla and basicranium. Ecologically, *Kanuites* probably filled a niche similar to that occupied by modern-day genets (Viverridae). In addition, this new form has, in view of its excellent preservation, potential in the future to shed much light on the evolution of feliform carnivorans in Africa.

III. Phylogeography of the white-tailed mongoose

The phylogeography of the white-tailed mongoose, *Ichneumia albicauda*, (Herpestidae, Carnivora) is studied using sequence data from the mitochondrial control region (D-loop). The current distribution of *I. albicauda* is wide-ranging, from sub-Saharan Africa to southern Africa (it is absent in some areas), and along coastal areas of the southern half of the Arabian Peninsula. An intraspecific phylogeny was obtained and used to address questions regarding the biogeography, subspecies division and tail tip coloration of *I. albicuda*. The tail tip is usually white, but occasionally black in individuals from West Africa.

Based on the phylogenetic pattern of *Ichneumia albicauda*, we hypothesize that the species originated in South Africa and from there spread across the African continent and further to the Arabic Peninsula. Further, our results partly support the traditional division into six subspecies. The color polymorphism of the tail-tip, however, seems to reflect variation at the individual level, rather than being of phylogenetic significance.

IV. Ecomorphology in Viverridae and Herpestidae

Ecological morphology, ecomorphology, is used to study the diversification and biogeography of Viverridae and Herpestidae. Dental characters and body size, characters that are significant in Carnivoran ecology, are used to assess viverrid and herpestid morphospace occupation. This approach adds a new perspective to the understanding of the present distribution of these families. The morphological characters were mapped for a set of viverrid and herpestid species and then plotted in morphospace using Principal Coordinates Analysis.

The result is that when taxa from both Africa and Eurasia are included in the analysis, the two families overlap in morphospace. This is, however, not the case when the taxa are analysed continent by continent, where there is little or no overlap. The pattern of morphospace occupation may be the result of ecological competition and order of appearance on the continents.

Svensk sammanfattning (Summary in Swedish)

Ordningen Carnivora, rovdjur, är en av de mest artrika däggdjursordningarna. Denna ordning består av två huvudgrupper, Feliformia, kattartade rovdjur, och Caniformia, hundartade rovdjur, med uppenbara skillnader i morfologi (organismers anatomiska struktur) och ekologi (organismers relation till sin omvärld). Ett hinder för att bättre förstå rovdjurens diversifieringsmönster är att systematiska och evolutionära studier av de två mest artrika familjerna av Feliformia, Viverridae (sibetkatter) och Herpestidae (mangustrar), har varit starkt eftersatta, i motsats till andra rovdjursfamiljer såsom kattdjur, hyenor och hunddjur, vilkas systematik och evolution ägnats stor uppmärksamhet. Målet med detta projekt har varit att fylla igen viktiga luckor i vår kunskapsbas om dessa familjers evolutionshistoria under sen tertiär tid, dvs. från ca 15 miljoner år bakåt i tiden och fram till idag, med fokus på afrikanska former.

För att kunna studera biogeografiska mönster, dvs. de bakomliggande orsaker som kan förklara de nu levande viverrid- och herpestidarternas geografiska utbredning och förekomst, har mer detaljerad kunskap om de fossilfynd som gjorts, deras fylogenetiska position (släktskapsförhållanden) och ekologiska och morfologiska egenskaper behövts. Afrikanska fossil, jämförande anatomi, samt genetiskt material har utgjort grunden i denna avhandling. De enskilda studierna beskriver och reviderar 3,7 miljoner år gamla rovdjursfossil från Laetoli i norra Tanzania (I), beskriver ett nytt rovdjurssläkte från Fort Ternan, västra Kenya, vilket är 14 miljoner år gammalt (II), studerar utbredningsmönster hos *Ichneumia albicauda*, vitsvansad manguster, en nu levande afrikansk herpestid (III), samt försöker förklara utbredningen av recenta (nulevande) arter av viverrider och herpestider genom att analysera deras morfologi och ekologi i kombination med deras geografiska utbredning (IV).

Slutsatserna i de två förstnämnda studierna av fossila rovdjur är att: 1) det fossila materialet från Laetoli är anmärkningsvärt i två avseenden, dels är det omfattande i både antal arter och mängden fossil, vilket är unikt för tidsperioden i Östafrika vad beträffar de mindre rovdjuren, dels att det har fossiliserats direkt på land, och 2) rovdjursmaterialet från Fort Ternan i Kenya är mycket välbevarat och har många likheter med recenta viverrider. I de två sistnämnda studierna, som behandlar recenta viverrider och herpestider, tyder resultaten på att: 1) den vitsvansade mangustern *Ichneumia albicauda* är av sydafrikanskt ursprung och därifrån har spridit sig över den afrikanska kontinenten och vidare till den Arabiska halvön, och

2) att arter av viverrider och herpestider generellt inte överlappar varandra morfologiskt och ekologiskt när deras geografiska utbredningsområde sammanfaller, vilket tyder på konkurrens mellan familjerna i både Afrika och Eurasien.

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