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Molecular systematics and origin of sociality in mongooses (Herpestidae, Carnivora)

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Abstract

The Herpestidae are small terrestrial carnivores comprising 18 African and Asian genera, currently split into two subfamilies, the Herpestinae and the Galidiinae. The aim of this work was to resolve intra-familial relationships and to test the origin of sociality in the group. For this purpose we analysed sequences of the complete cytochrome *b* gene for 18 species of Herpestidae. The results showed that the mongooses were split into three clades: (1) the Malagasy taxa (Galidiinae and *Cryptoprocta*), (2) the true social mongooses and (3) the solitary mongooses, each group being also supported by morphological and chromosomal data. Our results suggested unexpected phylogenetic relationships: (1) the genus *Cynictis* is included in the solitary mongoose clade, (2) the genera *Liberiictis* and *Mungos* are sister-group, and (3) the genus *Herpestes* is polyphyletic. We examined the evolution of the sociality in mongooses by combining behavioural traits with the cytochrome *b* data. Some of the behavioural traits provided good synapomorphies for characterizing the social species clade, showing the potential benefit of using such characters in phylogeny. The mapping of ecological and behavioural features resulted in hypothesizing solitary behavior and life in forest as the conditions at the base of the mongoose clade.

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1. Introduction

The extant mongooses (Herpestidae) comprise 18 genera and 37 species of small terrestrial carnivores, found mainly in Africa, with 8 species of the genus *Herpestes* occurring in Asia. The recognition of the mongooses as a separate family by Gregory and Hellman (1939) has been confirmed by several studies (Bugge, 1978; Fredga, 1972; Hunt, 1987; Neff, 1983; Radinsky, 1975; Veron, 1995; Wozencraft, 1989; Wurster, 1969), although it was not followed by some authors who continued to include the mongooses in the Viverridae (Coetzee, 1977; Dargel, 1990; Ewer, 1973; Kingdon, 1977; Rosevear, 1974; Taylor, 1988; Simpson, 1945; Skinner and Smithers, 1990).

The phylogenetic relationships among the mongooses have been studied on the basis of morphological features (Baker, 1987; Gregory and Hellman, 1939; Hendey, 1974; Petter, 1969, 1974; Pocock, 1919; Stains, 1983; Veron, 1995; Wozencraft, 1989), karyological data (Couturier and Dutrillaux, 1985; Fredga, 1972) and allozymes (Taylor et al., 1991). Until the present study, the relationships within the Herpestidae have never been investigated using DNA sequencing data. Wozencraft (1989) considered three subfamilies, namely: (1) the Galidiinae, consisting of the Malagasy species, including the genera *Galidia*, *Galidictis*, *Mungotictis*, and *Salanoia*, (2) the Herpestinae, including the genera *Atilax*, *Bdeogale*, *Herpestes*, *Ichneumia* and *Rhynchogale*, and (3) the Mungotinae, with the genera *Crossarchus*, *Cynictis*, *Dologale*, *Helogale*, *Liberiictis*, *Mungos*, *Paracynictis* and *Suricata*. Wozencraft (1989) noted that the relationships within the Mungotinae were poorly understood and suggested two monophyletic groups within

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the Herpestinae: the *Herpestes*–*Atilax* clade and the *Ichneumia*–*Bdeogale*–*Rhynchogale* clade. Many authors (see Allen, 1924; Rosevear, 1974; Wozencraft, 1993) placed four small African species of *Herpestes* (*flavescens*, *pulverulentus*, *sanguineus*, and *swalius*) in a separate genus, *Galerella*, but this group was not recovered by the morphometric study of Taylor and Matheson (1999). The Liberian mongoose (*Liberiictis kuhni*), seen alive for the first time in 1989 (Taylor, 1992) has been live-trapped and studied for the first time in Ivory Coast by A. Dunham, providing new data on its behaviour. The phylogenetic relationships of this species are unknown but it has been suspected to be close to *Crossarchus* (Hayman, 1958; Honacki et al., 1982).

The family is currently split into two subfamilies, the Herpestinae (which includes the Mungotinae) and the Galidiinae (Wozencraft, 1993). Some recent studies (Veron, 1995; Veron and Catzeffis, 1993; Yoder et al., 2003) showed that the Malagasy carnivores currently placed in the Viverridae (*Cryptoprocta*, *Eupleres*, and *Fossa*) (Wozencraft, 1993) form a monophyletic group with the Malagasy mongooses (Galidiinae) which are the sistergroup of the other mongooses (Herpestinae).

In some species of mongooses, groups larger than a single family unit are found, and in some cases, individuals live in cohesive packs which forage and den together (Rood, 1983). Ecological and behavioural studies of the dwarf mongoose (*Helogale parvula*) (Creel and Waser, 1997; Rasa, 1973, 1977, 1987; Rood, 1978, 1980, 1983, 1987, 1990), the meerkat (*Suricata suricatta*) (Clutton-Brock et al., 1999; Ewer, 1963), the common cusimanse (*Crossarchus obscurus*) (Booth, 1960; Ewer, 1973; Goldman, 1987; Goldman and Dunham, in press; Rosevear, 1974) and the banded mongoose (*Mungos mungo*) (Cant, 2000; De Luca and Ginsberg, 2001; Hinton and Dunn, 1967; Neal, 1970; Rood, 1975) revealed that they live in cohesive social groups (packs) larger than a single family unit (Rood, 1975), breed cooperatively (lactation of multiple females, adult group members helping to guard and feed the young, coordination system of vigilance, see Clutton-Brock et al., 1999) and forage in packs. The yellow mongoose (*Cynictis penicillata*) lives in pairs or family groups in habitat similar to that of the meerkat (Cavallini, 1993b; Earle, 1981; Wenhold, 1990). The behavioural and ecological studies of the solitary mongooses have included the marsh mongoose (*Atilax paludinosus*) (Baker, 1988, 1989; Ray, 1997), the small Indian mongoose (*Herpestes javanicus*) (Cavallini and Serafini, 1995; Gorman, 1979), the Egyptian mongoose (*Herpestes ichneumon*) (Ben Yaacov and Yom-Tov, 1983; Delibes et al., 1984; Palomares and Delibes, 1992, 1993), the long-nosed mongoose (*Herpestes naso*) (Ray, 1997), the slender mongoose (*Galerella sanguinea*) (Baker, 1980; Jacobsen, 1982; Rood, 1989; Rood and Waser, 1978; Waser et al., 1994) and the Cape grey mongoose

(*Galerella pulverulenta*) (Cavallini, 1992; Cavallini and Nel, 1990).

Some solitary mongooses have revealed more complex social systems and inter-individual contacts than expected (Palomares and Delibes, 1993, 2000) as well as a tendency to become gregarious in some conditions (see Cavallini and Nel, 1990 for *Galerella pulverulenta*; Rood, 1989; Rood and Waser, 1978; Waser et al., 1994 for *Galerella sanguinea*; Ben Yaacov and Yom-Tov, 1983; Palomares and Delibes, 1993 for *Herpestes ichneumon*; Waser and Waser, 1985 for *Ichneumia albicauda*).

Almost nothing is known about the social behaviour of the black-footed mongoose (*Bdeogale nigripes*) or of the bushy-tailed mongoose (*Bdeogale crassicauda*) (Kingdon, 1977), but the latter is believed to be nocturnal and solitary (Sale and Taylor, 1970; Skinner and Smithers, 1990; Taylor, 1987). The behaviour of Asian species (*Herpestes brachyurus*, *H. edwardsii*, *H. javanicus*, *H. palustris*, *H. semitorquatus*, *H. smithii*, *H. urva*, *H. vitticollis*) is also poorly known but these species are believed to be solitary (Gorman, 1979; Roberts, 1977) and diurnal (Santiapillai et al., 2000).

The social mongooses are generalized to have diurnal activity, live in open habitat and feed largely on invertebrates, whereas the solitary species are generalized to be nocturnal, live in forested habitats, feed on small vertebrates as well as invertebrates, and larger in size than the social mongooses (Gorman, 1979; Rood, 1986). Carnivores are believed to be primitively solitary, nocturnal forest-dwellers (Rood, 1983) and this is also thought to be the primitive condition for mongooses (Gorman, 1979; Gregory and Hellman, 1939; Savage, 1978).

The social mongooses were suspected to be close together (subfamily Mungotinae; Wozencraft, 1989) but the origin of sociality and of other life traits in the mongooses has never been tested in a phylogenetic framework. The aim of this study was to resolve intra-familial relationships among Herpestidae and to test if the social mongooses really form a monophyletic group, or if sociality has been acquired independently several times in this group (see Rood, 1986). This will also demonstrate if behavioural traits could be appropriate characters for phylogenetic investigations. Mitochondrial cytochrome *b* has been shown to be useful for elucidating intra-familial relationships within the Carnivora (Dragoo et al., 1993; Dragoo and Honeycutt, 1997; Gaubert et al., in press; Geffen et al., 1992; Koepfli and Wayne, 1998; Kurose et al., 2000; Ledje and Arnason, 1996; Masuda and Yoshida, 1994; Masuda et al., 1996; Veron and Heard, 2000). The present study provides a new data set of complete cytochrome *b* sequences for 18 species, belonging to 12 different genera of Herpestidae. Seven ecological and behavioural traits have been studied in order to test their evolution in a phylogenetic framework.

2. Materials and methods

Sequencing work was undertaken at the Service Commun de Systématique Moléculaire at the Muséum National d'Histoire Naturelle, Paris.

The samples used in this study are presented in Table 1. Samples came from diverse sources (see Acknowledgements). When available, two different specimens of the same species were sequenced. Our sampling

represents 17 species of Herpestinae belonging to 11 genera, and 1 species of Galidiinae, totalizing 18 species belonging to 12 genera of Herpestidae. Among the subfamily Herpestinae, the three genera *Bdeogale*, *Dologale*, and *Paracynictis* were not represented. The 10-lined mongoose (*Mungotictis decemlineata*) (Galidiinae) and the Malagasy fossa (*Cryptoprocta ferox*) (Viveridae) were included in the ingroup because the Herpestidae and the Malagasy carnivores are believed to form a

Table 1
List of samples

Genus	Species	DNA #	GenBank #	References	Locality	Museum #, Zoo
<i>Atilax</i>	<i>paludinosus</i>	C-110	AF522324	This study	Kenya	
<i>Atilax</i>	<i>paludinosus</i>	C-158	AF522325	This study	Centr. African Rep.	R-12061
<i>Crossarchus</i>	<i>alexandri</i>	C-109	AF522326	This study	Unknown, captivity	
<i>Crossarchus</i>	<i>obscurus</i>	C-187	AF522327	This study	Ivory Coast	
<i>Cynictis</i>	<i>penicillata</i>	C-111	AF511060	Gaubert et al. (in press)	South Africa	
<i>Cynictis</i>	<i>penicillata</i>	C-66	AF522328	This study	South Africa	
<i>Galerella</i>	<i>pulverulenta</i>	C-164	AF522329	This study	South Africa	B-8121
<i>Galerella</i>	<i>pulverulenta</i>	C-165	AF522330	This study	South Africa	B-8122
<i>Galerella</i>	<i>sanguinea</i>	C-167	AF522331	This study	South Africa	DM-5644
<i>Galerella</i>	<i>sanguinea</i>	C-168	AF522332	This study	South Africa	B-8120
<i>Helogale</i>	<i>parvula</i>	C-140	AF522333	This study	Unknown, captivity	NMS
<i>Helogale</i>	<i>parvula</i>	C-245	AF522334	This study	South Africa	TM-39553
<i>Helogale</i>	<i>hirtula</i>	C-134	AF522335	This study	Unknown, captivity	M-98.1937
<i>Herpestes</i>	<i>edwardsii</i>	C-232	AF522336	This study	Bahrain	SDP
<i>Herpestes</i>	<i>ichneumon</i>	C-21	AF511059	Gaubert et al. (in press)	Spain	
<i>Herpestes</i>	<i>ichneumon</i>	C-246	AF522337	This study	South Africa	TM-39272
<i>Herpestes</i>	<i>javanicus</i>		X94926	Ledje and Arnason (1996)	Arnason (1996)	
<i>Herpestes</i>	<i>javanicus</i>	C-228	AF522338	This study	Guyana	ROM-107489
<i>Herpestes</i>	<i>naso</i>	C-16	AF522339	This study	Gabon	
<i>Herpestes</i>	<i>naso</i>	C-242	AF522340	This study	Gabon	
<i>Ichneumia</i>	<i>albicauda</i>	C-79	AF511058	Gaubert et al. (in press)	Saudi Arabia	
<i>Ichneumia</i>	<i>albicauda</i>	C-160	AF522341	This study	Centr. African Rep.	R-NC0137
<i>Liberictis</i>	<i>kuhni</i>	C-188	AF522342	This study	Ivory Coast	
<i>Liberictis</i>	<i>kuhni</i>	C-230	AF522343	This study	Liberia	ROM-102286
<i>Rhynchogale</i>	<i>melleri</i>	C-243	AF522344	This study	South Africa	DM-7176
<i>Suricata</i>	<i>suricatta</i>	C-67	AF522345	This study	South Africa	NZP
<i>Suricata</i>	<i>suricatta</i>	C-117	AF522346	This study	South Africa	NZP
<i>Mungos</i>	<i>mungo</i>	C-78	AF522347	This study	Unknown, captivity	ZGH
<i>Mungos</i>	<i>mungo</i>	C-190	AF522348	This study	Unknown, captivity	ZDK
<i>Mungotictis</i>	<i>decemlineata</i>	C-46	AF511061	Gaubert et al. (in press)	Madagascar	
<i>Cryptoprocta</i>	<i>ferox</i>	C-13	AF511070 (AF125139)	Veron and Heard (2000); Gaubert et al. (in press)	Madagascar	PZM
<i>Hemigalus</i>	<i>derbianus</i>	C-40	AF511067 (AF125143)	Veron and Heard (2000); Gaubert et al. (in press)	Unknown, captivity	SZG
<i>Arctogalidia</i>	<i>trivirgata</i>	C-35	AF511068 (AF125140)	Veron and Heard (2000); Gaubert et al. (in press)	Unknown, captivity	M-1998.1970
<i>Prionodon</i>	<i>pardicolor</i>	C-163	AF522349	This study	Cambodia	
<i>Viverra</i>	<i>zibetha</i>	C-34	AF125146	Veron and Heard (2000); This study	Vietnam	
<i>Nandinia</i>	<i>binotata</i>	C-126	AF522350	This study	Ivory Coast	ROM
<i>Crocuta</i>	<i>crocuta</i>	C-70	AF511064	Gaubert et al. (in press)	Unknown	
<i>Hyaena</i>	<i>hyaena</i>	AM-60	AF511063	Gaubert et al. (in press)	Unknown	
<i>Felis</i>	<i>catus</i>		AB004237	Yoshida et al., unpubl.		
<i>Panthera</i>	<i>leo</i>		AF053052	Cracraft et al. (1998)		
<i>Panthera</i>	<i>tigris</i>		X82301	Arnason et al. (1995)		

Abbreviations for Museum specimen number: B, National Museum Bloemfontein, South Africa; DM, Durban Museum, South Africa; M, Museum National d'Histoire Naturelle, France; NMS, National Museums of Scotland, Scotland; R, University of Rennes, France; ROM, Royal Ontario Museum, Canada; TM, Transvaal Museum, South Africa. Abbreviations for Zoological parks: NZP, National Zoological Garden, Pretoria, South Africa; PZM, Zoological Park of Montpellier, France; SDP, Sharjah Desert Park, United Arab Emirates; SZG, Singapore Zoological Garden; ZDK, Zoo Dvur Kralové, Czech Republic; ZGH, Zoologischer Garten, Halle, Germany.

monophyletic group (Flynn and Nedbal, 1998; Veron and Catzeffis, 1993; Yoder et al., 2003). Ten species belonging to other families of Feliformia (three Felidae, two Hyaenidae, one Nandiniidae, and four Viverridae) were sequenced or obtained from GenBank and used as outgroups (see Table 1).

Total genomic DNA extraction from hair and tissue samples followed the method of Kocher et al. (1989), with an extended digestion time (until 24 h). The amplification of cytochrome *b* was performed in a reaction volume of 25 µl using TAQ polymerase (Appligene) with the same conditions as described in Veron and Heard (2000).

A total of 6 primers were used for amplification and sequencing:

L 14724 (short): 5'-GATATGAAAAACCATCGTT G-3' (modified from Irwin et al., 1991);
 L 14841: 5'-CATCCAACATCTCAGCATGATGAA A-3' (modified from Kocher et al., 1989);
 L 15146: 5'-CATGAGGACAAATATCATTCTGA G-3' (reverse of H 15149, from Kocher et al., 1989);
 H 15149: 5'-AAACTGCAGCCCCTCAGAATGA TATTGTCCTCA-3' (Kocher et al., 1989);
 H 15553: 5'-TAGGCAAATAGGAAATATCATTCTGGT-3' (Ducroz et al., 1998);
 H 15915 (short): 5'-TTCATCTCTCCGGTTTACA AGAC-3' (modified from Irwin et al., 1991);

where the letters L and H refer to the light and heavy strands, respectively, and the number refers to the position of the 3' end of the oligonucleotide according to the numbering system for the human sequence (Anderson et al., 1981). The PCR products were purified directly from PCR mixture or from an agarose gel (MinElute PCR Kit) and sequenced directly in both forward and reverse direction by cycle sequencing with dye-labelled terminators and an automated sequencer (CEQ 2000 DNA Analysis System, Beckman). Sequences were aligned by eye using MUST (Philippe, 1993) and BioEdit version 5.0.6 (Hall, 1999).

Phylogenetic analyses were performed using Neighbour Joining (NJ), Maximum Parsimony (MP), and Maximum Likelihood (ML) methods with PAUP*4.0b10 (Swofford, 2001). Uncorrected distances were used to generate NJ tree and distance matrix. MP analysis used heuristic search with random stepwise addition, TBR branch-swapping, and ACCTRAN optimization. The amount of homoplasy was measured through the Consistency Index (CI) (Kluge and Farris, 1969) and the Retention Index (RI) (Farris, 1989). Likelihood models and parameters were estimated using ModelTest version 3.06 (Posada and Crandall, 1998), and the selected model was GTR (Rodriguez et al., 1990) with proportion of invariant site (I) and Gamma distribution (G).

Both equal and unequal weighting schemes were used (transversions weighted 2–4 times over transitions, ac-

cording to transition: transversion ratio, using the step matrix command of PAUP). We did not perform an analysis with transversions only, because such an approach ignores informative transition substitutions (Björklund, 1999; Gaubert et al., in press). Bootstrap resampling was performed using 100 (ML) and 1000 (MP, NJ) replications. The Decay Index (DI; Bremer, 1988) was calculated using TreeRot.v2 (Sorenson, 1999) in order to estimate node support in MP trees.

Social behaviour and other life history traits were taken from the literature (Albignac, 1976; Baker, 1988, 1989; Ben Yaacov and Yom-Tov, 1983; Cavallini, 1992; Cavallini, 1993a,b; Cavallini and Nel, 1990; Estes, 1991, 1993; Ewer, 1973; Goldman and Taylor, 1990; Haltenorth and Diller, 1977; Kingdon, 1977; Nellis, 1989; Ray, 1997; Rood, 1983; Rood and Waser, 1978; Santapillai et al., 2000; Skinner and Smithers, 1990; Taylor, 1972, 1975, 1987; Taylor and Meester, 1993; Van Staaden, 1994; Wenhold, 1990) and personal communications from Z. Balmforth, C. Baker, and A. Olson, and from new observations in the wild by A. Dunham for the Liberian mongoose and the common cusimanse. We selected seven ecological and behavioural characters (see Rood, 1975, 1983, 1986 for description of these traits):

- Activity: diurnal/nocturnal,
- Habitat: forest or dense vegetation/open or semi open habitat,
- Pack foraging: considered as ‘obligate’ pack foraging; coded present when always observed in a species; mongooses known to forage alone more frequently than in pack, were not considered as pack foragers,
- Social: mongooses have been considered as social when they live in stable cohesive group containing more than one adult male and one adult female, and denning together,
- Social antipredator behaviour:
 - Alarm call: when a predator is detected, alarm calls cause the group members to run to cover,
 - Bunching: pack members form a tight bunch, and frequently stand up while approaching the predator, generally causing its retreat,
- Alloparental behaviour: babysitting: group members other than the parents also take care of the young.

These seven eco-ethological data were then coded into a matrix (see Table 2) and the six ethological characters (activity, pack foraging, sociality, alarm call, bunching, and babysitting) were included in a combined analysis with the cytochrome *b* data set in order to test the phylogenetic contribution of ethological traits, as they have proved to constitute appropriate characters for phylogenetic reconstruction (De Queiroz and Wimberger, 1993; Stuart et al., 2002). The partitioned Bremer support (PBS; Baker and DeSalle, 1997) was estimated for the three codon positions and ethological

Table 2

Ecological and behavioural characters (references in text; taxonomy follows Wozencraft, 1993)

	Activity	Habitat	Pack foraging	Social >1 pair	Social antipredator behavior		Alloparental behavior Babysitting 0: absent
					Alarm call	Bunching	
	0: nocturnal	0: forest or dense veget	0: no	0: no	0: absent	0: absent	
	1: diurnal	1: open or semi open habitat	1: yes	1: yes	1: present	1: present	1: present
Herpestidae							
Galidiinae							
<i>M. decemlineata</i>	1	0	1	1	1	1	?
Herpestinae							
<i>H. edwardsii</i>	1	1	0	0	?	0	0
<i>H. ichneumon</i>	1	0;1	0	0;1	0;1	0	0;1
<i>H. javanicus</i>	1	1	0	0	0;1	0	0
<i>H. naso</i>	1	0	0	0	0	0	0
<i>I. albicauda</i>	0	1	0	0	0	0	0
<i>C. penicillata</i>	1	0;1	0	1	1	?	1
<i>R. melleri</i>	0	1	0	0	0	0	0
<i>G. sanguinea</i>	1	0;1	0	0	?	0	0
<i>G. pulverulenta</i>	1	0;1	0	0	0	0	0
<i>A. paludinosus</i>	0	0	0	0	0	0	0
<i>S. suricatta</i>	1	1	1	1	1	1	1
<i>Hel. hirtula</i>	1	1	1	1	1	?	1
<i>Hel. parvula</i>	1	1	1	1	1	0	1
<i>C. alexandri</i>	1	0	1	1	1	1	1
<i>C. obscurus</i>	1	0	1	1	1	1	1
<i>M. mungo</i>	1	0;1	1	1	1	1	1
<i>L. kuhni</i>	1	0	1	1	1	1	?
Viverridae							
<i>P. pardicolor</i>	0	0	0	0	0	0	0
<i>V. zibetha</i>	0	0	0	0	0	0	0
<i>A. trivirgata</i>	0	0	0	0	0	0	0
<i>H. derbyanus</i>	0	0	0	0	0	0	0
<i>C. ferox</i>	0	0	0	0	0	0	0
Nandiniidae							
<i>N. binotata</i>	0	0	0	0	0	0	0
Felidae							
<i>F. catus</i>	0	0	0	0	0	0	0
<i>P. leo</i>	1	1	1	1	?	?	1
<i>P. tigris</i>	0	0	0	0	0	0	0
Hyaenidae							
<i>C. crocuta</i>	0	1	1	1	?	?	0
<i>H. hyaena</i>	0	1	0	0	0	0	0

traits using TreeRot.v2. The seven ecological and behavioural characters were also mapped on MP molecular trees in order to determine the relative probability of ancestral conditions of eco-ethological traits following two methods of parsimony: the method of Bremer (1992), based on the Camin & Sokal parsimony (only the reversions are allowed), and a method implemented in the software MacClade version 4.0 (Maddison and Maddison, 2000), based on Wagner parsimony, which allows for optimization through both reversions and convergences (Swofford and Maddison, 1987). We consider that congruence between the results from these two methods gives a high confidence to our results.

3. Results

Complete (1140 bp) cytochrome *b* sequences were obtained for the Herpestidae and outgroup species (GenBank accession numbers are given in Table 1), with the final data matrix consisting of 41 sequences representing 29 taxa.

Several studies have reported the presence of nuclear copies of mitochondrial genes (Arctander, 1995; Collura and Stewart, 1995; Fukuda et al., 1985; Kornegay et al., 1993; Smith et al., 1992; Sorenson and Fleischer, 1996). Characteristics of such sequences are frameshifts and nonsense/stop codons within the open reading frame, but there was no evidence of these among our sequences.

The average relative nucleotide frequencies within the Herpestidae sequences are A: 30.0%, G: 13.5%, C: 30.6%, and T: 25.9%. These results are very similar to those found in other carnivorae sequences reported in GenBank or found in previous studies (Koepfli and Wayne, 1998; Veron and Heard, 2000; Gaubert et al., in press). The transition:transversion ratio ranges from 0 to 17.86, with a mean of 3.44, in the overall taxa included in the analyses. Raw pairwise distances between species ranged from 5.8% to 23.8% among the Feliformia species included in the study, while distances among the ingroup (Herpestidae and the Malagasy taxa *Cryptoprocta* and *Mungotictis*) ranged from 5.8 to 20.2%. Distances within species of Herpestidae ranged from 0.0% to 6.7%. Distance values are summarized in Table 3. These results are very similar to those observed in other studies at similar systematic levels in the Carnivora (Dragoo et al., 1993; Koepfli and Wayne, 1998; Masuda et al., 1996; Veron and Heard, 2000). Plots of the number of transitions against the percentage of sequence divergence (not shown) revealed that transitions appeared to be saturated among distantly related taxa, so weighting schemes that increase the level of phylogenetic signal provided by transversions were used (see Section 2).

For the analyses, a data set with a total of 1140 bp was used, which included 568 variable sites and 472 informative characters.

The MP analysis yielded one tree of 2621 steps ($CI=0.33$; $RI=0.51$) represented in Fig. 1. The ML analysis yielded one tree ($-\ln L = 12247.02616$) represented in Fig. 2 with parameters. The NJ tree is shown in Fig. 3. The trees obtained with the different weighting schemes (not shown) yielded a similar pattern for the well-supported clades.

All trees supported the monophyly of the Herpestinae. The sister relationship of the Malagasy taxa (*Cryptoprocta*, *Mungotictis*) with the mongooses is not well supported (MP and ML trees), but the Malagasy narrow-striped mongoose (*Mungotictis*) and the fossa (*Cryptoprocta*) are sister-taxa. Within the mongooses (Herpestinae), two clades were found:

- (1) the small social mongooses (*Helogale*, *Crossarchus*, *Mungos*, and *Liberiictis*), with a strong support (bootstrap value of 99% in the ML tree, 95% in the NJ tree and 78% in the MP tree), with the meerkat (*Suricata*) as sister-group in the ML and MP trees, whereas in the NJ tree, the meerkat is located at the base of the mongoose clade. The Liberian mongoose (*Liberiictis*) is the sister-group of the banded mongooses (*Mungos*), and the dwarf mongooses (*Helogale*) are closely related to the common cuscimane (*Crossarchus*);
- (2) other mongooses, including *Herpestes*, *Galerella*, *Rhynchogale*, *Cynictis*, *Ichneumia*, and *Atilax* (bootstrap value of 91% in NJ tree and 54% in MP tree). The relationships within this clade are not well sup-

ported but the genus *Herpestes* does not appear monophyletic. The two Asian mongooses (*Herpestes edwardsii* and *Herpestes javanicus*) are sister-group (bootstrap value of 100% in all trees). The long-nosed mongoose *Herpestes naso* groups with the marsh mongoose *Atilax paludinosus*. The systematic position of the Egyptian mongoose *Herpestes ichneumon* is not resolved, as well as that of the two species of the genus *Galerella*. Furthermore, the monophyly of this genus is found only in ML and NJ trees with a low support.

The analysis done with the combination of molecular and ethological data provided a topology similar to the trees obtained with molecular data only, and agrees with the results of the MP and ML analyses in placing *Suricata* at the base of the clade of small social mongooses (Fig. 4). PBS estimations revealed that ethological characters do not carry a conflicting phylogenetic signal compared to cytochrome *b*. Instead, conflicting signals mostly appeared among the three codon positions of the mitochondrial gene (data not shown) as found in a similar analysis on the Viverinae subfamily (Gaubert et al., in press). The ethological characters support the position of *Suricata* at the base of the small social mongooses (PBS: 0 (cytochrome *b*)/5 (eco-ethological characters)). The estimation of homoplasy for ethological characters gave values of CI generally higher than for cytochrome *b* sites (Table 4).

The estimated ancestral conditions of eco-ethological characters are given in Table 5. The Bremer's method (Bm) and MacClade (MC) estimations yielded roughly congruent results, except in the case of pack foraging (see Table 5). The two methods suggest that the ancestral conditions for the clade Herpestidae + Malagasy taxa were most probably life in forest and absence of social behaviour (no group >1 pair, absence of alarm call, bunching and baby-sitting (equivocal with Bm for the latter)). However, the estimations of ancestral states for “social,” “alarm call,” and “bunching” become ambiguous when the genus *Suricata* is placed as the sister-species to the other mongooses (following the NJ topology based on cytochrome *b* sequences only). The estimation for the ancestral state concerning activity is diurnal via Bm, but ambiguous in any cases with MC. However, MC estimated the ancestral condition to be diurnal at the node grouping the Herpestinae (Malagasy taxa excluded).

4. Discussion

4.1. Monophyly of the mongooses

The relationships between the different families of Feliformia are not well supported, as already reported in

Table 3
Pairwise comparison of the sequence data

	C.f.	M.d.	H.e.	H.j.	H.j.	I.a.	I.a.	C.p.	C.p.	R.m.	G.s.	G.s.	H.i.	H.i.	G.p.	G.p.	H.n.	H.n.	A.p.	A.p.	S.s.	S.s.	H.h.	H.h.	H.p.	H.p.	C.a.	C.o.	M.m.	M.m.	L.k.	L.k.	P.p.	V.z.	A.t.	H.d.	F.c.	P.l.	P.t.	C.c.	H.b.
C.f.C13	15.7	16.3	17.8	16.8	19.1	19.7	18.6	18.5	17.3	17.6	17.3	17.7	18.1	17.8	17.8	18	17.2	18.6	17.6	18.9	19.2	18.8	20.2	17.8	20.1	19.5	19.3	16.6	19.6	19.6	20.1	19.5	20.5	22.7	19.3	20.3	20.3	19.4	18.5		
M.d.C46	0.24	16	16.3	15.5	19.7	19.4	18	17.5	17.3	19.2	18.5	17.6	17.2	18.2	17.9	16.1	15	17.9	17.2	18.1	18.7	18.6	19.8	17.2	18.9	19	18.3	15.8	20.2	20.2	19.7	19.9	19.7	21.2	18.3	20.4	19.4	17.9	17.4		
H.e.C232	0.37	0.39	6.2	5.8	11	11.4	10.8	10.5	11.1	11.7	11.7	9.4	9.9	10	10.1	11.4	11	11.5	10.4	14.3	14.6	14.4	14.9	13.1	13.6	12.4	13.6	11.6	13.9	13.9	18.3	17.4	18.3	19.5	19.1	17.3	16.7				
H.j.	0.35	0.40	0.15	2.3	11.2	11.5	10.8	11	11.7	12.4	12.2	11.1	11.7	10.5	10.6	11.3	10.7	12	11.3	14	14.4	14.1	14.2	12.1	14.7	13	15.1	12	14.4	14.4	19.5	18.8	18.7	19.6	18.6	20.4	20.4	17.7	17.7		
H.j.C228	0.38	0.43	0.14	0.22	10.9	11.2	10.4	10.2	11.6	11.7	11.7	10.1	10.7	9.4	9.6	11.1	10.6	11.1	10.9	14.1	14.2	14.4	14.1	12.3	14.8	13.5	14.3	11.8	14.3	14.3	18.7	18.5	18.1	19.9	17.5	19.3	19.2	17.2	17.2		
I.a.C79	0.32	0.30	0.18	0.19	0.20	2.4	10.9	11	12	11.4	11.8	10.8	11.3	11.3	12.1	11.3	12.7	12	16.2	15.8	15.7	16.1	14.5	16.1	15.3	16.3	13.6	16.1	16.1	21.2	20.1	20.4	20.9	20	21.9	21.9	18.7	19.2			
I.a.C160	0.30	0.31	0.18	0.17	0.20	0.17	11.3	11.2	11.7	12	12.5	10.7	11.2	12.2	12.1	12	11.1	13.4	12	16.6	16.2	15.4	16.2	14.4	16.1	15.3	16.6	13.6	15.6	15.6	21.9	20.7	21.3	21.4	20.3	22.5	22.6	18.9	19.5		
C.p.C111	0.32	0.32	0.14	0.12	0.16	0.11	0.11	0.9	11.4	12.1	13	9.3	9.8	11.5	11.8	13.2	12.3	11.6	10.8	14.9	15.6	14.4	15.3	13	15.5	15.4	14.1	12.9	14.6	14.6	19	19.1	20.1	22	19.9	21.1	20.7	19.2	17.9		
C.p.C66	0.31	0.33	0.12	0.12	0.15	0.11	0.09	0.44	11.2	12.4	12.8	9.4	9.6	11.7	11.7	13.2	12	11.7	10.7	14.9	15.3	14.2	15.6	12.8	15.7	15.4	14.2	12.7	14.7	14.5	19	19.6	20.2	22.1	19.9	21.3	20.6	19.1	17.8		
R.m.C243	0.37	0.36	0.18	0.20	0.21	0.16	0.11	0.11	11.3	11.7	12.2	12.1	12	12.3	11.4	11	13.2	12.6	15	15.7	13.7	14.8	14	15	13.4	14.6	13.3	14.5	14.5	19.6	18.5	19.9	19.9	19.1	21.3	21.5	18.7	18.9			
G.s.C167	0.34	0.30	0.15	0.14	0.17	0.13	0.12	0.07	0.06	0.17	3.5	10.1	10.1	10.7	10.6	13.1	12.4	12.4	12.5	16.5	16	14.6	15.2	13.9	15.3	14.9	15	13.2	15.6	15.6	20.4	20.4	20	22.3	21.1	21.6	22.6	19.3	18.7		
G.s.C168	0.34	0.29	0.14	0.14	0.17	0.12	0.11	0.07	0.05	0.15	0.11	10.4	10.1	10.7	10.7	12.1	11.8	12.3	12.1	16.1	15.6	14.6	15.5	14.1	16	15.5	14.6	13.2	15.1	15.1	19.5	20.4	19	21.8	19.9	20.8	21.7	18.9	18.4		
H.i.C21	0.33	0.34	0.16	0.13	0.17	0.12	0.10	0.08	0.05	0.13	0.07	0.07	1.9	9.3	9.4	11.9	11.6	10.5	10.1	14.9	14.7	13.1	14.4	12.6	12.8	13.4	14.1	12.5	14.3	14.3	19.9	19	19.9	20.8	19.6	19.9	21	18.5	17.4		
H.i.C246	0.33	0.34	0.15	0.14	0.18	0.13	0.12	0.09	0.07	0.13	0.09	0.07	0.11	10	10.1	11.8	11.5	11	10	14.8	14.8	13.2	14.8	12.3	12.9	13.4	14	12	14.5	14.5	19.7	18.4	20	20.5	19.4	20.1	21.2	18.5	17.2		
G.p.C165	0.34	0.33	0.16	0.14	0.19	0.12	0.10	0.09	0.07	0.14	0.07	0.07	0.05	0.07	0.6	11.7	11.1	11.7	11.8	15.1	15	13.8	15.9	13.5	15.5	14.9	15.4	13	15.1	15.1	20.5	19.6	19.2	21	20.7	21.1	21.5	18.8	17.8		
G.p.C164	0.34	0.34	0.16	0.14	0.19	0.12	0.10	0.08	0.06	0.14	0.08	0.07	0.07	0.09	0.33	11.8	11.3	11.8	12	15	15.2	14.1	15.8	13.7	15.3	14.7	15.4	13.3	15.1	15.1	20.6	19.6	19.1	21.1	20.3	20.7	21.3	18.8	17.9		
H.n.G416	0.33	0.35	0.11	0.12	0.15	0.11	0.09	0.07	0.05	0.14	0.08	0.07	0.07	0.09	0.09	1.4	10.7	10.4	15.1	15.5	15	16.3	13.9	15.2	15.2	15.4	13.4	14.8	14.8	20.1	20.3	19.8	21.8	18.8	21.7	20.6	18.8	17.1			
H.n.C242	0.35	0.39	0.11	0.14	0.15	0.11	0.11	0.07	0.06	0.12	0.10	0.08	0.08	0.08	0.11	0.11	0.21	10.3	10.2	14.7	15.3	15.1	15.7	14	14.4	14.3	13.3	14.8	14.8	19.4	19.6	18.8	21.7	18.3	21.1	19.8	18.3	16.6			
A.p.C110	0.32	0.34	0.14	0.13	0.16	0.13	0.10	0.09	0.07	0.14	0.10	0.08	0.08	0.10	0.10	0.10	0.10	0.08	10	6.6	16.1	16.2	15.7	15	13.3	15.2	15.4	15.1	13.2	16.4	16.4	21.2	19.8	20.3	22.1	19	20.5	20.9	17.9	18.3	
A.p.C158	0.34	0.35	0.18	0.18	0.21	0.18	0.16	0.14	0.12	0.17	0.14	0.12	0.14	0.14	0.14	0.14	0.12	0.13	0.11	14.9	15.3	14.9	14.6	13.6	13.4	14.1	14.1	11.9	14.5	14.5	20.2	17.8	19	21.9	18.8	20.8	21.2	17.4	16.6		
S.s.C67	0.34	0.37	0.24	0.23	0.25	0.23	0.21	0.21	0.19	0.23	0.20	0.19	0.20	0.20	0.22	0.22	0.17	0.20	0.20	0.24	2.8	16.3	17	14.9	17.2	16.4	17.8	15.1	16.6	16.5	21.5	19.5	21.6	23.1	19.4	21.6	22.2	20.4	20.2		
S.s.C117	0.34	0.37	0.25	0.23	0.25	0.25	0.23	0.22	0.20	0.24	0.23	0.22	0.22	0.24	0.24	0.19	0.21	0.22	0.25	0.18	16	17.1	15.2	18	17.1	17.6	15.4	17.2	17.2	21.2	19.6	21.6	23.8	20	21.5	22.1	20.1	19.6			
H.h.C134	0.41	0.41	0.27	0.28	0.29	0.25	0.26	0.22	0.22	0.24	0.25	0.25	0.27	0.27	0.28	0.27	0.22	0.23	0.26	0.24	3.9	13.7	13.3	15.1	12.8	15.8	15.8	15.8	22.3	21.5	20	22.8	19.9	22.6	22	19.4	19.3				
H.p.C140	0.39	0.41	0.31	0.31	0.33	0.29	0.23	0.25	0.27	0.28	0.27	0.29	0.30	0.28	0.28	0.26	0.27	0.29	0.33	0.25	0.26	0.24	3.9	13.7	13.3	15.1	12.8	15.8	15.8	15.8	22.3	21.5	20	22.8	19.9	22.6	22	19.4	19.3		
H.p.C245	0.36	0.38	0.24	0.26	0.27	0.23	0.23	0.18	0.19	0.21	0.22	0.21	0.23	0.23	0.23	0.23	0.19	0.20	0.23	0.25	0.19	0.20	0.12	0.31	11.9	11.7	12.7	11.8	13.1	13.1	13.1	19.7	18.7	17.1	20.7	18.2	19.3	19.3	17.6	17.3	
C.a.C109	0.37	0.41	0.29	0.27	0.28	0.26	0.25	0.21	0.20	0.24	0.25	0.23	0.27	0.27	0.25	0.25	0.22	0.25	0.24	0.28	0.22	0.22	0.18	0.23	0.14	8	15.1	13.7	14.3	21.7	19.9	21.1	22.3	20.7	22	23.2	21.1	19.3			
C.o.C187	0.37	0.39	0.30	0.28	0.29	0.27	0.25	0.21	0.21	0.26	0.25	0.23	0.25	0.25	0.25	0.25	0.21	0.23	0.23	0.26	0.22	0.23	0.24	0.24	0.17	0.19	15.2	13.3	14.8	14.8	14.8	21	20.2	20.2	21.8	19.9	21.9	21.7	19.8		
M.m.C78	0.38	0.42	0.31	0.24	0.28	0.26	0.23	0.25	0.25	0.26	0.25	0.27	0.27	0.26	0.26	0.26	0.26	0.30	0.21	0.23	0.21	0.13	0.18	0.20	6.7	14.2	14.2	20.1	19.5	18.9	21.4	19.9	21.5	20.7	19.4	19.7					
M.m.C190	0.39	0.40	0.28	0.23	0.25	0.25	0.19	0.20	0.22	0.23	0.21	0.23	0.24	0.25	0.24	0.20	0.22	0.23	0.27	0.19	0.21	0.12	0.16	0.08	0.15	0.09	11.8	11.8	16.9	16.9	16.5	19.1	17.3	19.6	17.9	16.2	17				
L.k.C188	0.38	0.40	0.32	0.28	0.31	0.27	0.27	0.25	0.24	0.28	0.26	0.26	0.27	0.28	0.28	0.24	0.26	0.26	0.23	0.17	0.21	0.22	0.22	0.19	0																

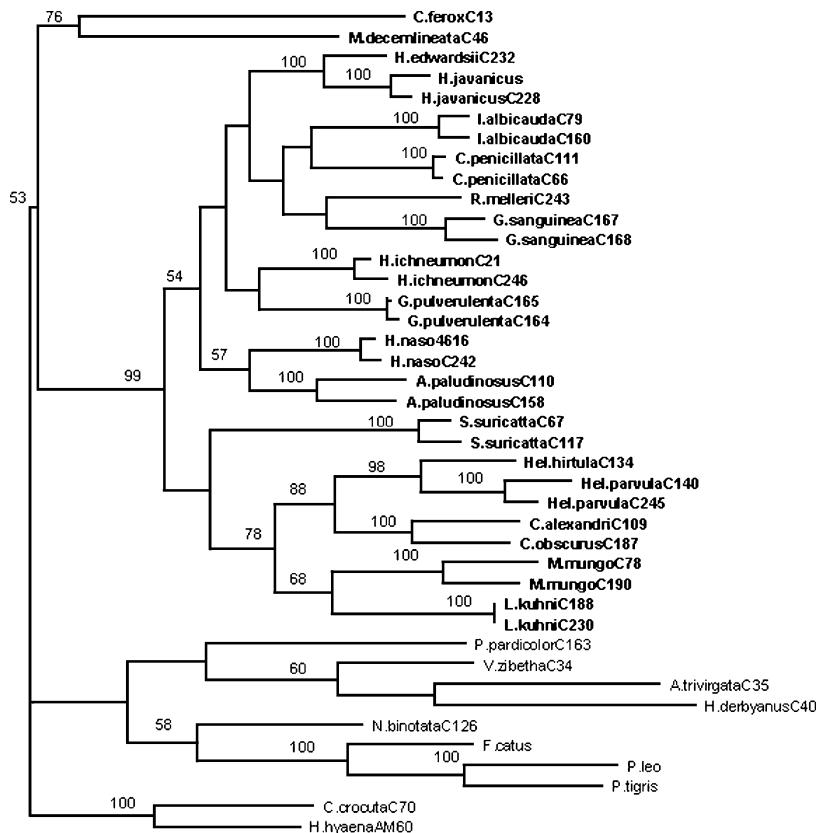


Fig. 1. MP phylogram (2621 steps; CI = 0.33; RI = 0.51). Number above branches represent bootstrap values superior to 50% (1000 replicates) (Herpestidae in bold type).

previous cytochrome *b* analyses (Gaubert et al., in press; Veron and Heard, 2000) and a nuclear gene would be an appropriate marker for improving the basal resolution within this group (Flynn and Nedbal, 1998; Gaubert et al., in prep.; Yoder et al., 2003). The sister relationship of the Malagasy taxa to the mongooses is not well supported, but the fossa (*Cryptoprocta*) and the Malagasy narrow-striped mongoose (*Mungotictis*) are close together with a relatively strong support. The close relationship of the fossa with the mongooses has been previously found (Veron and Catzeffis, 1993) and the sister relationship of the other Malagasy carnivores with the mongooses has been also confirmed elsewhere (Yoder et al., 2003). The monophyly of the mongooses has been found previously with morphological data (Veron, 1995) as well as its separation from the Viverridae (Bugge, 1978; Gregory and Hellman, 1939; Hunt, 1987; Neff, 1983; Radinsky, 1975; Veron, 1995; Wozencraft, 1989) and is again confirmed here.

4.2. The systematic position of the yellow mongoose

The separation of the mongooses into three clades is in agreement with the recognition of three subfamilies proposed by several authors (Galidiinae, Mungotinae, and Herpestinae; see Wozencraft, 1989). This taxonomic

scheme, however, places the yellow mongoose (*Cynictis penicillata*) together with the small social mongooses (*Crossarchus*, *Dologale*, *Helogale*, *Liberiictis*, *Mungos*, *Paracynictis*, and *Suricata*) in the Mungotinae (Wozencraft, 1989), but our results suggest that this species should be excluded from this group (contrary to Baker, 1987; Bininda-Emonds et al., 1999; Taylor et al., 1991; Veron, 1995; Wozencraft, 1989) and included in the solitary mongooses group. According to the phylogeny obtained, the presence of social traits in *Cynictis* (groups >1 pair, presence of alarm call and baby sitting), as well as in the true social mongooses (*Suricata*, *Mungos*, *Liberiictis*, *Crossarchus*, and *Helogale*), is the result of convergence in behaviours. In fact, while several authors (Dorst and Dandelot, 1972; Fitzsimons, 1919; Roberts, 1951; Walker, 1964) mentioned that a single colony of *Cynictis penicillata* could consist of as many as 40–50 individuals, this assertion resulted certainly from confusion with *Suricata*. Mean colony sizes of only 3.9, 4.1, and 8 individuals of *C. penicillata* were observed by Zumpt (1976), Lynch (1980), and Earle (1981), respectively. According to Earle (1981), Taylor and Meester (1993), and Wenhold and Rasa (1994), the yellow mongoose hunts alone and its social behaviour is only slightly more developed than that of the Egyptian mongoose (*Herpestes ichneumon*) when it becomes social

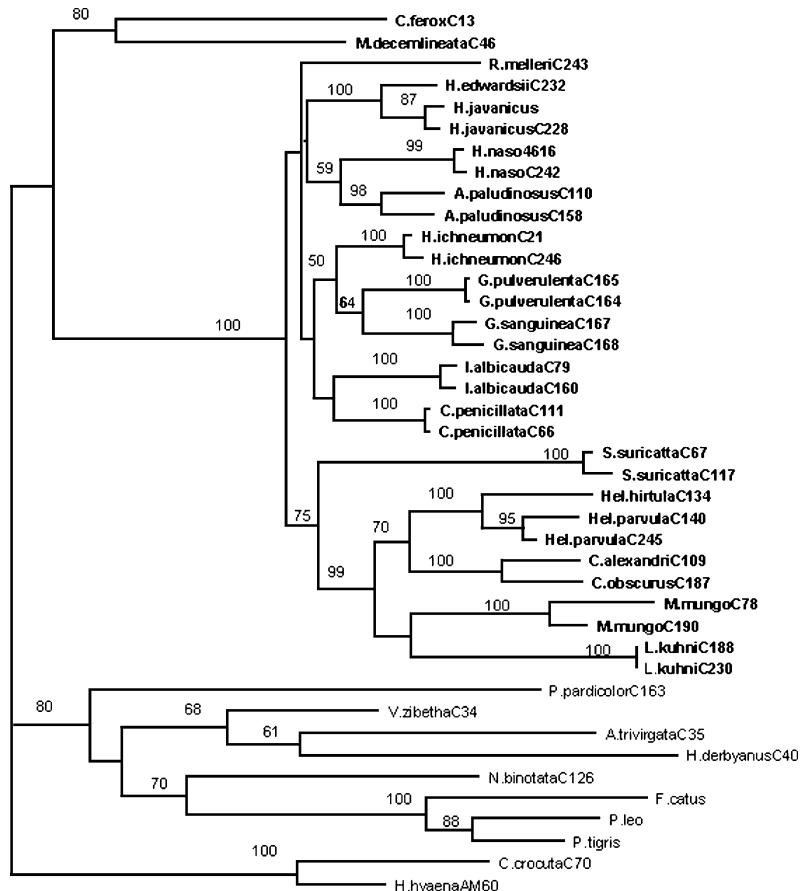


Fig. 2. ML tree ($-\ln L = 12247.02616$). The tree was generated using GTR model (Rodriguez et al., 1990) with proportion of invariant site ($I = 0.4519$) and Gamma distribution shape parameter ($G = 0.9131$) with estimated substitution of $A-C = 0.4316$, $A-G = 10.6103$, $A-T = 0.7720$, $C-G = 0.4406$, $C-T = 11.4885$ and $G-T = 1.0000$, and base frequencies of $A = 0.3551$, $C = 0.3701$, $G = 0.0797$, $T = 0.1952$ and $I = 0.4519$, and $G = 0.9131$. Number above branches represent bootstrap values superior to 50% (100 replicates). Thickness of the branches represents the result of the branch length test (Felsenstein, 1981); thick branches: different from 0 ($P < 0.001$), thin branches: different from 0 ($0.001 < P < 1$), branches which are not significantly different from 0 are collapsed (Herpestidae in bold type).

(Ben Yaacov and Yom-Tov, 1983). On the other hand, Z. Balmforth (pers. com.) regularly observed six individuals from one group foraging within sight of each other, showing that they can forage in small groups, as was previously mentioned by Earle (1981). However, the yellow mongoose is not obligate pack foragers as the other true social mongooses. The morphological features that prompted several authors to consider the yellow mongoose close to the small social mongooses (Petter, 1969; Veron, 1995; Wozencraft, 1989) apparently are the result of convergence in ecological and behavioural characteristics (open habitat, insectivorous diet, social family life, diurnal activity, and communal burrows). Similarly, Gregory and Hellman (1939) believed in an independent parallel evolution of *Cynictis* and *Suricata*, and Pocock (1919) already suggested on the basis of morphological features that the yellow mongoose could be close to *Ichneumia*, which is the result obtained in both ML and MP trees (but with bootstrap values inferior to 50%). These two genera also share a similar number of chromosomes ($2N = 36$) and

are the only members of this clade for which males have a distinct Y chromosome (Fredga, 1972; Pathak and Stick, 1976; Wurster and Benirschke, 1968).

4.3. The systematic position of the Liberian mongoose

The new data on the social behaviour of the Liberian mongoose (*Liberiictis kuhni*) collected by A. Dunham in Tai N. P. (Ivory Coast) show that the species is commonly observed in foraging packs of 4–6 individuals, though larger groups are occasionally observed. Our phylogenetic results show that the Liberian mongoose is closely related to the other small social mongooses and that it is closer to the banded mongoose (*Mungos*) rather than to the cusimanse genus (*Crossarchus*) as previously supposed (Hayman, 1958; Honacki et al., 1982). However, it does not share the dental formula of the small social species (40 teeth in *Liberiictis* and 36 in *Mungos*, *Helogale*, *Crossarchus*, and *Mungos*) (Haltenorth and Diller, 1977; Kingdon, 1977), has smaller cheek-teeth in relation to the greater size of the skull (Hayman, 1958;

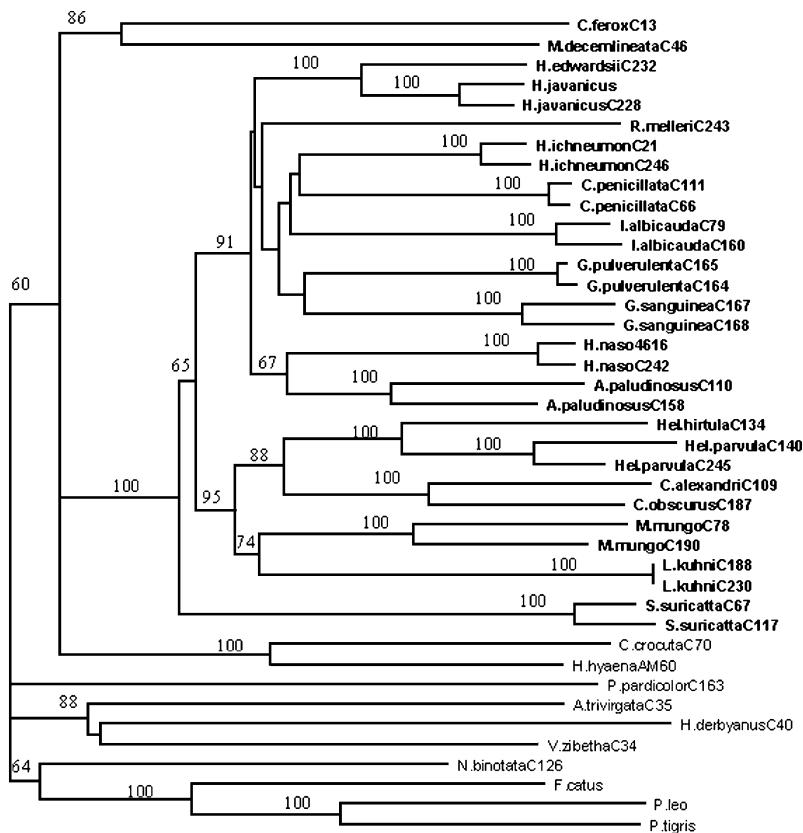


Fig. 3. NJ tree (Herpestidae in bold type). Number above branches represent bootstrap values superior to 50% (1000 replicates).

Schlitter, 1974) and is slightly larger than the other social mongooses (up to 2.4 kg compared to less than 1 kg in *Helogale* and *Suricata*, and less than 2 kg in *Crossarchus* and *Mungos*; Rood, 1986; Taylor and Dunham, in press; up to 2.25 kg is mentioned in Rosevear, 1974 for a female of *Mungos mungo*), but it shares their social behaviour characters (see Table 2). The differences observed are most likely adaptations to a diet specialized on earthworms (Taylor and Dunham, in press).

4.4. The social mongooses: a monophyletic group

Results show that the true social mongooses, defined as living in stable social groups larger than a single family unit, breeding cooperatively and foraging in packs, become a monophyletic group after the exclusion of *Cynictis*. The meerkat (*Suricata*) is the sister-taxon of the clade containing the other social mongooses (in 2 of the 3 analyses, as well as in the combined analysis), which is congruent with the recognition of this species as a very distinct taxon, which had already been placed in a separate subfamily (Suricatinae) by Pocock (1919). In fact, its morphology is specialized in relation to its ecological habits as a burrow-dwelling, insectivorous, diurnal, savannah species. Its close relationship with the other social mongooses is not very well supported here but is congruent with many other data (morphological,

data: Gregory and Hellman, 1939; karyological data: Fredga, 1972; paleontological and morphological data: Hendey, 1974; allozyme: Taylor et al., 1991). The clade of the true social mongooses is also supported by chromosomal data ($2N = 36$; unknown in *Liberiictis*) (Fredga, 1972; Todd, 1966) as well as some morphological characters: absence of first upper and lower premolar (except in *Liberiictis*), shape of the cheek teeth, shape of the tympanic bullae (Veron, 1994) and small size (less than 2–2.4 kg) (Rood, 1986).

4.5. The solitary mongooses

Besides the clade containing the true social small mongooses, we found a clade containing the solitary mongooses, including the species of *Atilax*, *Cynictis*, *Galerella*, *Herpestes*, *Ichneumia*, and *Rhynchogale*. They share some morphological characters: first upper premolar present (but variable in *Atilax*), shape of the cheek teeth, shape of the tympanic bullae (Veron, 1994) and large size (up to around 5 kg) (Novak, 1999). In this clade, some mongooses share a particular chromosomal feature, the Y chromosome being translocated onto an autosome, resulting in a different number of chromosomes in male and female (Fredga, 1972; Pathak and Stick, 1976; Wurster and Benirschke, 1968). This occurs in *Atilax paludinosus* (Female: $2N = 36$; male: $2N = 35$),

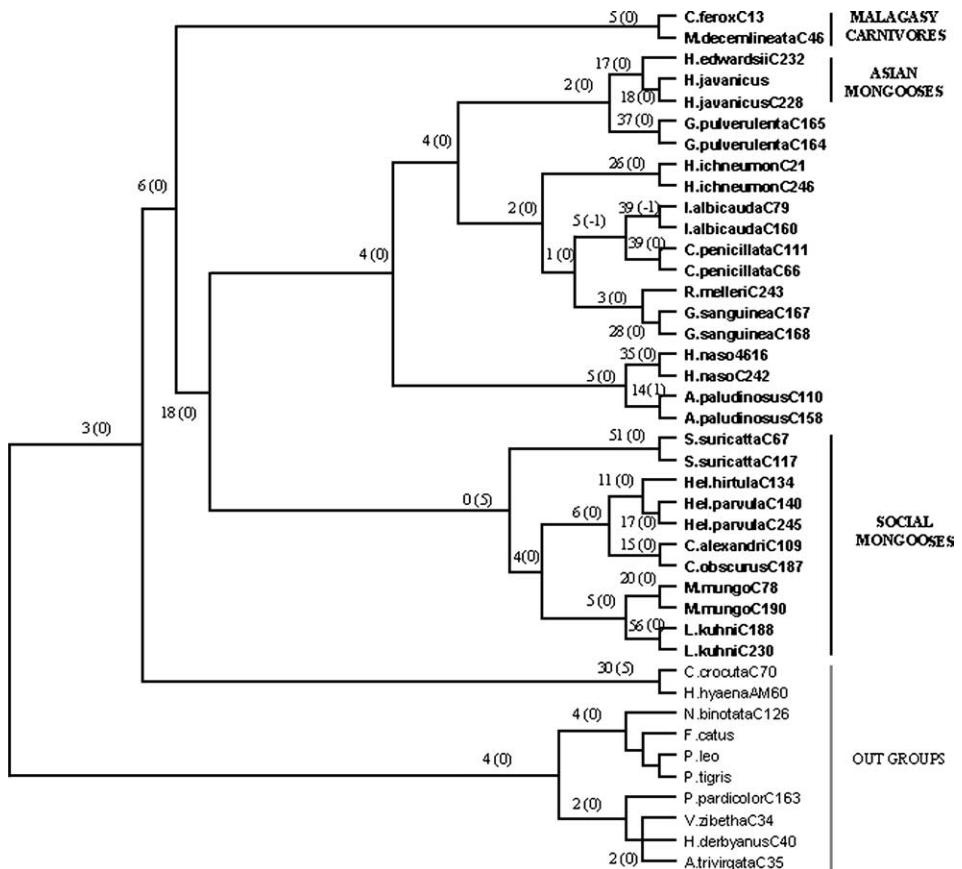


Fig. 4. MP tree (2650 steps, CI = 0.334) resulting from combined analysis with DNA and eco-ethological characters (see Table 2) (Herpestidae in bold type). Number on branches represent Decay Indices for the whole data matrix, in brackets are shown the DI values representing the contribution of the eco-ethological characters for each node of the ingroup (estimated via the procedure of Partitioned Bremer Support).

Table 4
Estimation of homoplasy for eco-ethological characters

Character	CI
1141 (Activity)	0.333
1142 (Pack foraging)	0.500
1143 (Social)	0.400
1144 (S.a.b.—alarm call)	0.667
1145 (S.a.b.—bunching)	0.667
1146 (baby-sitting)	0.667

CI values in this case were calculated manually by visualising character changes on MacClade. S.a.b. is used for "Social anti-predator behaviour."

Galerella pulvulenta (40, 39), *Galerella sanguinea* (42, 41), *Herpestes javanicus* (36, 35), *Herpestes edwardsii* (36, 35), *Herpestes ichneumon* (44, 43), but not in *Ichneumia* and *Cynictis* ($2N = 36$) (Fredga, 1972; Pathak and Stick, 1976; Wurster and Benirschke, 1968).

4.6. *Herpestes* is not monophyletic

Most of the relationships within the clade of the solitary mongooses are poorly supported. One major

point is that the genus *Herpestes* does not appear monophyletic, which has never been suggested before (see reviews in Bininda-Emonds et al., 1999; Taylor and Matheson, 1999; Taylor et al., 1991). In all trees, the two Asian *Herpestes* species (*H. javanicus* and *H. edwardsii*) are sister-species. The monophyly of the Asian *Herpestes* species is also supported by their chromosome formula: $2N = 36$ in female and $= 35$ in male, in *H. javanicus*, *H. edwardsii*, *H. fuscus*, and *H. urva* (Fredga, 1972). The long-snouted mongoose (*Herpestes naso*) and the marsh mongoose (*Atilax paludinosus*) are sister-species but with a low support. Although these two species display a strong external resemblance (see Colyn and Van Rompaey, 1994; Rosevear, 1974), they have not been considered to be closely related (Bininda-Emonds et al., 1999). The monophyly of the genus *Galerella* is not well supported, but was found in both the ML and NJ trees. The species of *Galerella* are placed in the genus *Herpestes* by some authors (see Taylor and Goldman, 1993; Wozencraft, 1989) but their inclusion in a separate genus was supported by allozyme (Taylor et al., 1991) and some morphological data (see Rosevear, 1974), whereas the craniometric study of Taylor and

Table 5
Estimation of ancestral condition for eco-ethological traits

Eco-ethological traits	Bremer's method				MacClade
	G	L	G/L	AC	
Activity: nocturnal	4 (4)	7 (8)	0.57 (0.5)	0.29 (0.25)	ambiguous
Activity: diurnal	7 (8)	4 (4)	<u>1.75 (2)</u>	<u>0.88 (1)</u>	(ambiguous) *
Habitat: forest	9 (9)	8 (8)	<u>1.125</u>	<u>1</u>	X (X)
Habitat: open or semi-open	8 (8)	9 (9)	0.89	0.79	
Pack foraging: no	2 (2)	2 (3)	1 (0.67)	0.67 (0.45)	X (ambiguous)
Pack foraging: yes	2 (3)	2 (2)	<u>1 (1.5)</u>	<u>0.67 (1)</u>	
Social (>1 pair): no	6 (6)	3 (5)	<u>2 (1.2)</u>	<u>1 (0.6)</u>	X (ambiguous)
Social (>1 pair): yes	3 (5)	6 (6)	0.5 (0.83)	0.25 (0.42)	
S.a.b.—alarm call: absent	8 (8)	6 (7)	<u>1.33 (1.14)</u>	<u>1 (0.86)</u>	X (ambiguous)
S.a.b.—alarm call: present	6 (7)	8 (8)	0.75 (0.875)	0.56 (0.66)	
S.a.b.—bunching: absent	9 (9)	6 (6)	<u>1.5</u>	<u>1</u>	X (ambiguous)
S.a.b.—bunching: present	6 (6)	9 (9)	0.67	0.45	
Baby-sitting: absent	7 (7)	7 (7)	1	1	X (X)
Baby-sitting: present	7 (7)	7 (7)	1	1	

G, number of necessary gains under forward Camin–Sokal parsimony; L, number of losses under reverse Camin–Sokal parsimony; AC, Ancestral Condition. For the Bremer's method, it corresponds to G/L quotients rescaled to a maximum value of 1 by dividing with the largest G/L value within each character. In order to assess the impact of phylogenetic hypotheses on the estimation of AC, we reconstructed the ancestral state with 1/“*Suricata* sister-species to the clade of the other small social mongooses” (MP and ML tree) and 2/“*Suricata* sister-species to all the other mongooses (Malagasy taxa excluded)” (NJ tree; values between parentheses). X indicates the Ancestral Condition estimated using MacClade. The most probable estimations for the ancestral conditions are underlined. * AC is assumed to be “diurnal” at the node grouping the Herpestidae.

Matheson (1999) did not support the monophyly of this genus. Here, we found that the two species of *Galerella* were genetically quite distant from each other (10.6 and 10.7%), but their placement in a separate genus or in *Herpestes* cannot be confidently established with the present data and need further studies.

4.7. Evolution of social behaviour and ecological traits

The two methods of parsimony used for estimating ancestral conditions from characters mapped on the phylogenetic trees yielded interesting hypotheses about the condition at the node grouping the Herpestidae and the Malagasy carnivores. The results are quite surprising concerning the period of activity, which is believed to be primitively nocturnal for the Carnivora as a whole (Gorman, 1979; Gregory and Hellman, 1939; Savage, 1978) yet we found it to be “diurnal” (but see Section 3). These results do depend on taxon sampling, trait coding, and tree pattern, and should be considered with caution since, as shown above, most of the relationships among the solitary mongooses are not well supported. Moreover, dealing with polymorphic characters in such estimations may prove problematic. However, the general congruency between the two methods of estimation strengthens the confidence we can have in the ancestral state reconstructions. The results also suggested that the “proto-mongooses” were primitively solitary and had no social anti-predator

behaviour. Our estimations also determined social behavioural traits as having appeared at the base of the clade of social mongooses, which is in accordance with the hypothesis of Gorman (1979).

When included as characters in the data matrix, ethological traits proved to be less homoplastic than cytochrome *b* sites. The traditional point of view that considers ethological characters as subjected to high convergence (for a review, see Stuart et al., 2002) is here rejected, as was already concluded by De Queiroz and Wimberger (1993) and McLennan and Mattern (2001) on the basis of a comparison between morphological and behavioural characters. Ethological characters provided a strong contribution for the support of the clade of the social mongooses (see values of PBS) and some of them (social, pack foraging, alarm call, and babysitting) provided synapomorphies for characterizing this monophyletic group.

Some male associations (cohesive association of males sharing the same home range, see Rood, 1989) have been observed in non-social mongooses (see Rood and Waser, 1978, 1989 for the slender mongoose *Galerella sanguineus*; see Cavallini and Nel, 1990 for the Cape grey mongoose *Galerella pulverulenta*), and Cavallini and Nel (1990) suggested that the sociality in the Cape grey mongoose may have been underestimated due to the methods of study, which are often based on sightings and in which travelling animals are more likely to be encountered. Waser et al. (1994) showed that some

male associations in the slender mongoose (*G. sanguineus*) can last a very long time (at least 7 years). In the same way, some studies on *Herpestes ichneumon* lead to the reconsideration of the sociality of this species (Ben Yaacov and Yom-Tov, 1983; Palomares and Delibes, 1993). The behavioural study of the least known non-social species would help us to understand the factors that could favour the evolution of the sociality in mongooses.

Rood (1986) compared the social structures of mongooses to other ecological traits and concluded that all the social mongooses were small (adult weight of <2 kg), diurnal, and primarily insectivorous, but the Liberian mongoose was not classified because of the lack of data on its social structure. This species is now known to be social, diurnal and to feed on invertebrates (A. Dunham, pers. obs.), but its weight can be up to 2.4 kg (Haltenorth and Diller, 1977; Taylor and Dunham, in press). No solitary species combines the first three traits listed above but pair or family-living species do, like the yellow mongoose (*Cynictis penicillata*) (Rood, 1986). All the group-living and family-living species live in open habitats, except *Crossarchus* and *Liberiictis*. In *Herpestes* and *Galerella*, there is a great variability of ecological traits, but the remaining solitary mongooses (*Atilax*, *Bdeogale*, *Ichneumia*, *Paracynictis*, and *Rhynchogale*) are all nocturnal and feed on invertebrates (Rood, 1986). So, the assumption that social mongooses are diurnal, small and invertebrate eaters appears true, but the assumption that the solitary species are nocturnal, large and feed on small vertebrates is not true for all species. Moreover, it has been shown that diet can be very variable in the same species, the major dietary item being sometimes different according to the location and the season (see review in Cavallini and Nel, 1990 for *Galerella pulverulenta*; in Simberloff et al., 2000 for *Herpestes javanicus*; in Taylor and Meester, 1993 for *Cynictis penicillata*). Similarly, in the social species, behavioural features are variable and complex, making it difficult to define and code characters, and thus underlining the need for further studies.

4.8. The origin of sociality in mongooses

The availability and renewability of invertebrate food may decrease the costs of group living, and predation risk (higher in open habitat) may have been the main selective pressure promoting the sociality in mongooses (Palomares and Delibes, 1993; Rood, 1986; Waser, 1981). The abundance of shelters providing suitable cover constructed by other animals, may allow communal denning in African mongooses (Rood, 1986). The appearance of extensive areas of grassland during the late Miocene and Pliocene periods promoted a radiation of artiodactyls and may have favoured the evolution of insectivorous small carnivores. We can observe today

that the abundance of ungulates that leave large quantities of dung, thereby promoting the abundance of dung beetles, may favour the banded mongooses that feed on these insects. Such abundant food resource may have facilitated group formation in mongooses (Rood, 1986). In the same way, the Resource Dispersion Hypothesis (see Carr and Macdonald, 1986; Macdonald, 1983) states that the quality and dispersion of resources influence the social structure of population in a given habitat. However, Nel and Kok (1999) underlined that it does not explain why similar-sized sympatric species with the same activity pattern and greatly overlapping diets exhibit marked difference in foraging group size, and why a species retains the same foraging group sizes in different parts of its geographic range, even when contribution of prey categories changes. In order to search for the reason why *Cynictis* are solitary foragers (but see Z. Balmforth observations above) whereas *Suricata* are obligate pack foragers, Nel and Kok (1999) compared their diet in different habitats. These authors, as well as Gorman (1979), Cavallini (1993b), Rasa et al. (1992) proposed hypotheses based on predation risk, interspecific and intra-specific competition, difference in microhabitat use, spectrum of prey, and the propensity for capturing small vigilant vertebrate prey (less disturbed by small foraging groups). In fact, none of these can explain the differences in foraging behaviour between these two sympatric species, and our phylogenetic results suggest that they are the result of their individual history.

Even if some feliforms dated at 19.6 MA may be early herpestids (*Legetetia*, *Kichechia*), the first fossil that can unequivocally be considered as a true herpestid is *Leptolesictis*, and is found in the early Miocene (17.8 MA) in Africa (Hunt, 1996). The same genus is found in Europe in middle Miocene deposits, and Schmidt-Kittler (1987) believed that African and Asian early mongooses derived from immigrants from southern Asia. However, herpestids are unknown in Asia before the late Miocene (Barry, 1985; Barry et al., 1980). The Miocene herpestids are carnivore, slightly different from extant *Herpestes*, whereas fossils closer to the true social mongooses are not found before the Plio-Pleistocene in Africa. This suggests that the first mongooses were vertebrate eaters and that the changing environment favoured insectivorous species during the Pliocene and led to the current diversity. Our estimations of the ancestral conditions for the mongooses were solitary and diurnal forest animals that became social at the base of the clade grouping the African social Herpestidae, which is congruent with such hypothesis. As said above, environment and abundance of arthropods in open habitats of Africa may have favoured the occurrence of sociality as had been observed in other African carnivores (Waser, 1981; Rood, 1986).

5. Conclusions

The main difficulty in doing molecular systematics of small carnivores is to find material, particularly for the rare and elusive species as we already discussed elsewhere (Veron and Gaubert, 1999; Veron and Heard, 2000). The opportunity offered by the acquisition of samples of species of mongooses never studied with molecular methods allowed us to assess the phylogenetic relationships of the small social mongooses and to test the monophyly of this group. We showed that behavioural traits could provide good synapomorphies, confirming the potential usefulness of such characters in systematics.

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