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A study of allozyme evolution in African mongooses (Viverridae: Herpestinae)

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Abstract

Using horizontal starch gel electrophoresis, allozyme variation at 18 protein loci was investigated in 48 specimens representing seven species of mongooses (Viverridae: Herpestinae: *Cynictis penicillata, Helogale parvula, Suricata suricatta, Atilax paludinosus, Herpestes ichneumon, Galerella sanguinea* and *G. pulverulenta*) and one species of genet (Viverridae: Viverrinae: *Genetta tigrina*). Fourteen loci were polymorphic, and ten of these varied between species. Phenetic analysis of genetic distances (Nei 1978) suggested a relatively recent and "explosive" radiation of the extant Viverridae. Cladistic analyses (taking as outgroup the genet *Genetta tigrina*), involving distance Wagner trees from genetic distances (Rogers 1972), and parsimony analysis of ordered, multistate locus characters, produced congruent trees which suggested an early origin of *Atilax*, followed by a trichotomous split involving: 1. *Galerella*, 2. *Herpestes* and 3. a "social" lineage, comprising *Helogale, Suricata* and *Cynictis*. Aspects of the molecular phylogeny were supported by palaeontological, morphological, karyological and behavioral evidence. Owing to unequal rates of change in different lineages, phenetic and cladistic analyses of the allozyme data produced discordant trees, and the cladistic approach is to be preferred for analysing phylogenetic relationships among the mongooses.

Introduction

Relationships among the mongooses (Viverridae: Herpestinae) are poorly understood (Wozencraft 1989a). Several, largely conflicting, phylogenetic schemes have been proposed for the mongooses, based on independent studies involving morphological (Gregory and Hellman 1939; Petter 1969; Baker 1987), palaeontological (Hendey 1974), karyological (Fredga 1972) and behavioral (Baker 1987) evidence. Furthermore, a lack of consensus is evident in certain aspects of mongoose classification, such as the status of *Galerella* [subgenus of *Herpestes* (Wozencraft 1989b) or a full genus (Meester et al. 1986)], and the recognition of the mongooses as a separate family (Wozencraft 1989b) or as a subfamily of Viverridae (Rosevear 1974; Meester et al. 1986). Taxonomic instability also exists concerning the numbers of species that should be recognised in certain genera such as *Galerella* (sensu Meester et al. 1986), *Helogale, Bdeogale*, and *Crossarchus* (see Rosevear 1974; Honacki et al. 1982; Goldman 1984; Meester et al. 1986; Watson and Dippenaar 1987; Wozencraft 1989b).

Molecular techniques, including allozyme electrophoresis, have proved to be useful in resolving evolutionary and taxonomic relationships in the carnivoran families Felidae, Canidae and Ursidae (for a review see Wayne et al. 1989). The aim of the present study was to analyse allozyme variation in seven species of Southern African mongooses and one species of genet *Genetta tigrina*, in an attempt to resolve evolutionary and taxonomic relationships in the carnivoran family Viverridae (Herpestinae). Allozyme data were analysed as genetic distances and as qualitative characters, using both phenetic and cladistic (parsimony) approaches.

Material and methods

Tissues (liver, kidney, heart and/or muscle) were collected from 48 specimens representing seven species of Southern African mongooses and one species of genet *Genetta tigrina* and these were stored in liquid nitrogen prior to electrophoretic analysis. Viverrid specimens were collected by live-trapping, shooting and by retrieving tissues from previously frozen carcasses obtained from fresh road kills. In the latter case most carcasses were donated by the Natal Parks Board. In three specimens, carcasses had been de-gutted and only muscle (or muscle and kidney) tissue could be obtained. Of the total sample of specimens collected, 35 specimens, representing eight populations of the yellow mongoose *Cynictis penicillata*, have been previously analysed for within-species allozyme variation at 28 loci (Taylor et al. 1991).

Details of specimens, methods of collection and sample sizes are given in Table 1. Voucher specimens were deposited in the Durban Natural Science Museum, the MacGregor Museum, Kimberley, the National Museum, Bloemfontein, and the Transvaal Museum, Pretoria.

The present study is based on starch (SIGMA: 12.5 %) gel electrophoretic results from 18 genetic loci encoding the following 15 proteins and enzymes (electrophoretic procedures, which are taken mainly from Selander et al. 1971; Shaw and Prasad 1969; Harris and Hopkinson 1976; and Richardson et al. 1986, are described in detail in Taylor et al. 1990): albumin (ALB), catalase (CAT), glucose dehydrogenase (GDH), glutamate-oxaloacetate transaminase (GOT), glycerol dehydrogenase (GCDH), glycerol-3-phosphate dehydrogenase (GPD), haemoglobin (HB), isocitrate dehydrogenase (IDH), lactate dehydrogenase (LDH), malate dehydrogenase (MDH), malic enzyme (ME), phosphogluconate dehydrogenase (PGD), glucosephosphate isomerase (PGI), phosphoglucomutase (PGM), superoxide dismutase (SOD). Haemoglobin was present in sufficient quantities in blood associated with the tissue homogenates to permit its resolution in the present study. Optimum resolution of haemoglobin was obtained using a discontinuous buffer system (in this case, the lithium hydroxide-tris citrate buffer of Selander et al. 1971). Intensity of haemoglobin bands was enhanced by staining with napthyl blue black.

Since muscle tissue only was available from three specimens, both muscle and liver tissues of one individual of *C. penicillata* was examined, to establish the homology of observed staining patterns between the different tissue types.

Electromorphic alleles were described according to their relative mobilities on the gel, with the fastest (most anodal) being designated as A, and successively cathodal alleles being designated as B, C, D etc. Two approaches were taken in the analysis of the allozyme data: 1. analysis of allele frequencies, using the computer program BIOSYS-1 (Swofford and Selander 1989); and 2. cladistic (parsimony) analysis of qualitative allozyme characters, using the computer program PAUP (Swofford 1985). Computer programs were run on an IBM-compatible, XT personal computer.

Analysis of allele frequencis

From the individual genotypes at each locus (including monomorphic loci in which all individuals were scored as AA), allele frequencies were determined and used to calculate genetic distances and similarities (Nei's (1978) and D_N and I, and Rogers' (1972) D_R and S) and mean heterozygosities ($\overline{H}$). In calculating $\overline{H}$, owing to the fact that localities were generally represented by single individuals (with the exception of the yellow mongoose, for which $\overline{H}$ was obtained from Taylor et al. 1990), data were pooled for each species. Genetic distances were summarised using both phenetic (unweighted pair group method with averages (UPGMA) phenogram: Sneath and Sokal 1973) and cladistic (distance Wagner tree: Farris 1972) methods, for Nei's D_N and Rogers' D_R values respectively. Analysis of allele frequency data was based on 17 loci, as missing data for GDH for three species prevented analysis of this locus.

Cladistic analysis of qualitative locus characters

Qualitative allozyme characters may be coded for cladistic analysis by: 1. treating alleles as characters and presence or absence of alleles as character states ("independent alleles model"); and 2. treating the locus as a character and alleles as character states. Although the first approach has the advantage of producing binary characters which are easily ordered using the outgroup method (Watrous and Wheeler 1981), this method can hypothetically give rise to loci having no alleles, and Buth (1984) recommends that the latter approach (treating the locus as character) should be used for cladistic analysis of allozyme data. Several models have been dscribed for ordering multisate locus characters (Mickevich and Mitter 1983), and Buth (1984) recommends that researchers should explicitly state their ordering procedure. However, Swofford (1985) suggests that there is no need to order multistate characters when there is no obvious evolutionary sequence (see also Bezy and Sites 1987; Stasz et al. 1989).

Table 1. **Species and locality data of specimens of eight African viverrid species analysed for allozyme electrophoresis**

Species and locality	n	Method[1]	Tissue[2]
Cynictis penicillata:			
Kaal Plaas Farm, Pretoria, Transvaal	3	T	L, K, H, M
Rhenosterfontein Farm, Cullinan, Transvaal	4	T, S	L, K, H, M
Karroo National Park, Cape Province	1	T	L, K, H, M
Windhoek, Namibia	4	T, R	L, K, H
Victoria West, Cape Province	5	T	L, K, H
Glen Agricultural Coll., Bloemfontein, OFS	15	T, S	L, K, B
Erfdeel Farm, Kroonstad, OFS	2	T	L, K
Riemvasmaak, northern Cape Province	1	T	L, K
Galerella sanguinea:			
Weenen Nature Reserve, Natal	1	T	L, K, M
Blydschap Private Nature Reserve, N. Trvl.	1	T	K, K, H, M
Galerella pulverulenta:			
Karroo National Park, Cape Province	1	T	L, K, H, M
Riemvasmaak, northern Cape Province	1	T	K, H
Atilax paludinosus:			
Hilton, Pietermaritzburg, Natal	1	R	L, K, H, M
Howick, Pietermaritzburg, Natal	1	R	M
Wagondrift Farm, western Cape	1	T	L, K, H, M
Herpestes ichneumon:			
Colchester Farm, Natal	1	R	M
Suricata suricatta:			
On N1, near Kimberley, Cape Province	1	R	L, K, H, M
Helogale parvula:			
Blydschap Private Nature Reserve, N. Trvl.	1	T	L, K, H, M
Genetta tigrina:			
Skewbridge, Pietermaritzburg, Natal	1	R	K, M
Blydschap Private Nature Reserve, N. Trvl.	2	T	L, K, H, M

[1] Methods of collections of specimens: T (live trapped); R (road kill); S (shot). – [2] Tissues collected: L (liver); K (kidney), H (heart); M (muscle); B (blood).

In the present study, the locus was recognised as character, and PAUP was performed on both ordered (using the "relative mobilities model": Mickevich and Mitter 1983) and unordered data, representing allelic variants at ten loci showing interspecific differences. All PAUP analyses were run with the options: MULPARS, SWAP=GLOBAL and ROOT=OUTGROUP, and the genet *Genetta tigrina* was taken as the outgroup. Analyses involving unordered data resulted in 97 equal length trees. A consensus tree, obtained from these trees using the CONTREE program of PAUP, was uninformative in producing an unresolved polychotomy involving six mongoose species. The analysis of ordered data produced six equal length trees, and a more completely resolved consensus tree. For this reason, only the results of the ordered character data are presented in this paper.

Results

Genetic heterozygosities and genetic distances

Of the 18 loci scored, 14 were polymorphic, either between or within species. Of these, ten loci showed consistent allelic differences between species or groups of species (Table 2). From Tables 2 and 3, no allelic variation was found in *Galerella pulverulenta* (Cape grey mongoose), *Atilax paludinosus* (water mongoose), *Herpestes ichneumon* (large grey mongoose), *Suricata suricatta* (suricate) and *Helogale parvula* (dwarf mongoose). Mean

Table 2. **Allelic designations of 14 polymorphic genetic loci for eight species of African Viverridae**
Abbreviations for species explained in Fig. 1. Abbreviations for loci explained in text

Locus	Species							
	Cp	*Gs*	*Gp*	*Ap*	*Hi*	*Ss*	*Hp*	*Gt*
ALB	A	A	A	A	A	A	B	C
CAT	E, G, H	D, F	F	B	C	C	C	A
GDH	E	C	–	–	–	F	D	A, B
GOT-1	A, B	B	B	B	B	B	B	B
GOT-2	A, B	B	B	B	B	B	B	B
GPD	A, B	B	B	B	B	B	B	C
HB	E	C	C	C	C	B	A	D
IDH	A	B	A	A	A	A	A	A
MDH-1	B	B	B	B	B	B	B	A, B
MDH-2	A	A	A	B	A	A	A	B
ME	B	C	B	B	B	A	C	D, E
PGD	A, B, C	C	C	C	C	C	C	C
PGM	A, C	C	C	C	C	C	C	B
SOD	B	B	B	B	B	B	A	B

Table 3. **Estimates of percentage polymorphic loci (%P), mean heterozygosity ($\overline{H}$), and standard error (s.e.) of $\overline{H}$ in eight species of Viverridae**
(data for *Cynictis penicillata* represent the mean for eight populations and were taken from a separate study: Taylor et al. 1990)

Species	N[1]	%P	$\overline{H}$	s.e.
Cynictis penicillata	29.3	6.8	0.026	0.020
Galerella sanguinea	2.0	5.9	0.039	0.039
Galerella pulverulenta	2.0	0	0	0
Atilax paludinosus	2.8	0	0	0
Herpestes ichneumon	1.0	0	0	0
Suricata suricatta	1.0	0	0	0
Helogale parvula	1.0	0	0	0
Genetta tigrina	2.8	11.8	0.051	0.036

[1] Mean sample size per locus.

heterozygosity ($\overline{H}$) was 0.026 in *Cynictis penicillata* (yellow mongoose); 0.039 in *Galerella sanguinea* (slender mongoose); and 0.051 in *Genetta tigrina* (genet; Table 3).

Nei's D_N varies from 0.06 (between *G. pulverulenta* and *H. ichneumon*) to 0.63 (between *G. tigrina* and *S. suricatta*), with a mean of 0.30. Rogers' D_R varies from 0.06 (between *G. pulverulenta* and *H. ichneumon*) to 0.47 (between *G. tigrina* and *S. suricatta*), with a mean of 0.26 (Table 4). The UPGMA phenogram, based on D_N (Fig. 1A), indicates the genetic separatedness of the genets (Viverrinae) from the mongooses (Herpestinae), at a distance of 0.53. Beyond this, no clear groupings are evident, and most splitting events appear to occur over a rather narrow range of genetic distances. The solitary species (*Herpestes, Galerella* and *Atilax*) and the semi-social *Cynictis* are loosely grouped together genetically, and the social species (*Helogale, Suricata*) appear somewhat distinct.

The topology of the outgroup-rooted, distance Wagner trees (Figs. 1B, 1C) is different from the UPGMA phenogram (Fig. 1A). Figure 1B was based on the same data as the UPGMA phenogram. Figure 1C was "optimised" by recording the allelic character states at the ME locus so as to eliminate an obvious convergence (the shared possession of allele C in *G. sanguineus* and *H. parvula*): allele C in *H. parvula* was recoded as D and alleles D and E were recoded as E and F respectively. The "optimised" tree had a "f" value (Farris

Table 4. Values of (A) Nei's (1978) genetic distance (below diagonal) and identity (above the diagonal), and (B) Rogers' (19072) genetic distance (below the diagonal) and similarity (above the diagonal), between eight species of Southern African Viverridae

	Cp	*Gs*	*Gp*	*Ap*	*Hi*	*Ss*	*Hp*	*Gt*
A								
Cp	–	0.78	0.88	0.83	0.88	0.77	0.77	0.60
Gs	0.25	–	0.87	0.78	0.84	0.72	0.78	0.54
Gp	0.12	0.14	–	0.88	0.94	0.76	0.76	0.59
Ap	0.19	0.25	0.12	–	0.88	0.71	0.71	0.65
Hi	0.12	0.17	0.06	0.12	–	0.82	0.82	0.59
Ss	0.27	0.33	0.27	0.35	0.19	–	0.76	0.53
Hp	0.27	0.25	0.27	0.35	0.19	0.27	–	0.59
Gt	0.52	0.61	0.52	0.42	0.52	0.63	0.52	–
B								
Cp	–	0.77	0.88	0.82	0.88	0.76	0.76	0.58
Gs	0.23	–	0.85	0.77	0.83	0.71	0.77	0.53
Gp	0.12	0.15	–	0.88	0.94	0.76	0.76	0.58
Ap	0.18	0.23	0.12	–	0.88	0.71	0.71	0.64
Hi	0.12	0.17	0.06	0.12	–	0.82	0.82	0.58
Ss	0.24	0.29	0.24	0.29	0.18	–	0.76	0.53
Hp	0.24	0.23	0.24	0.29	0.18	0.24	–	0.58
Gt	0.42	0.47	0.42	0.36	0.42	0.47	0.42	–

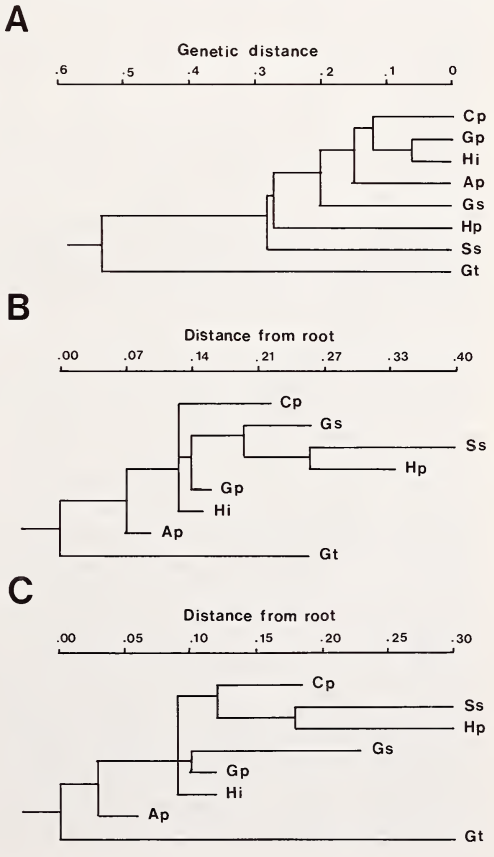

Fig. 1. UPGMA tree (A) and "unoptimised" (B) and "optimised" (C) distance Wagner trees, based on allele frequencies from 17 genetic loci in eight species of Southern African Viverridae. Distance Wagner trees were outgroup-rooted taking the genet *Genetta tigrina* as the outgroup. The procedure for "optimising" the distance Wagner tree in (C) is explained in the text. Abbreviations for species as follows: Ap = *Atilax paludinosus* (water mongoose); Cp = *Cynictis penicillata* (yellow mongoose); Gp = *Galerella pulverulenta* (Cape grey mongoose); Gs = *Galerella sanguinea* (slender mongoose); Gt = *Genetta tigrina* (large-spotted genet); Hi = *Herpestes ichneumon* (large grey mongoose); Hp = *Helogale parvula* (dwarf mongoose); Ss = *Suricata suricatta* (suricate)

1972) of 0.654 and a cophenetic correlation coefficient of 0.965, compared to a "f" value of 1.121 and a cophenetic correlation coefficient of 0.930 in the "unoptimised" tree.

Both distance Wagner trees resulted in the early splitting off of *Atilax*, and the subsequent trichotomous split. In the "unoptimised" tree these three lineages comprise: 1. *Cynictis*; 2. *Galerella*, and the two social genera, *Helogale* and *Suricata*; 3. *Herpestes*. In the "optimised" tree the three lineages comprise: 1. all the social species (*Cynictis, Helogale, Suricata*); 2. *Galerella*; 3. *Herpestes*.

Phylogenetic analysis of discrete allozyme characters

Figure 2A shows one of six trees produced by parsimony, cladistic analysis (PAUP) of ordered, multistate locus characters (the data on which this analysis was based are shown in Table 5). All six trees had a length of 27 and a consistency index of 0.815. Character state changes (i.e. apomorphies) have been superimposed on the tree in Fig. 2A, and homoplasies are indicated by underlining. Figure 2B shows the strict consensus tree obtained from these six trees. Areas of instability, as indicated by unresolved trichotomies on the consensus tree, concern the resolution of the three social species (three of the six trees

Table 5. **Ordered allozyme locus characters used in parsimony cladistic analysis (PAUP) of seven Southern African mongoose species**

Species	ALB	CAT	GDH	HB	IDH	MDH-2	ME	PGM	SOD	GPD
Cp	2	3	3	2	0	1	2	1	0	1
Gs	2	4	1	1	1	1	1	1	0	1
Gp	2	4	–	1	0	1	2	1	0	1
Ap	2	1	–	1	0	0	2	1	0	1
Hi	2	2	–	1	0	1	2	1	0	1
Ss	2	2	4	3	0	1	3	1	1	1
Hp	1	2	2	4	0	1	1	1	0	1
Gt	0	0	0	0	0	0	0	0	0	0

Trees were outgroup-rooted, taking the genet *Genetta tigrina* as the outgroup. Character states (alleles) were ordered using the "relative mobility model", which assumes that alleles closer in mobility on a gel to the allelic state possessed by the outgroup are more primitive than alleles which are further away from the outgroup allele state. Abbreviations of loci explained in text.

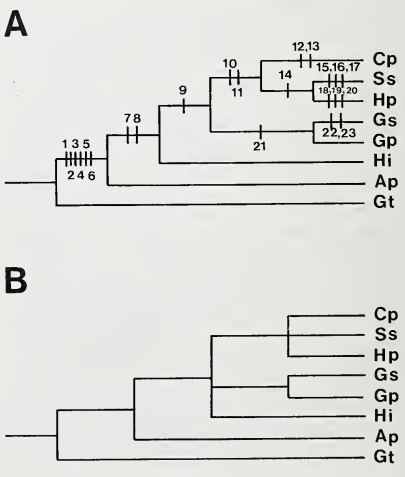

Fig. 2. Cladograms of seven Southern African mongoose species, resulting from phylogenetic analysis using parsimony (PAUP package) of allozyme data, using loci as characters and alleles as character states. Abbreviations for species given in Fig. 1. A: One of six, equal length, most parsimonious cladograms (length = 27; consistency index = 0.815); B: Consensus tree resulting from the six most parsimonious cladograms. Numbers on cladogram (A) represent character state changes as follows (abbreviations of loci explained in text): 1 = GPD (0 → 1); 2 = PGM (0 → 1); 3 = ME (0 → 2); 4 = HB (0 → 1); 5 = CAT (0 → 1); 6 = ALB (0 → 2); 7 = MDH-2 (0 → 1); 8 = CAT (1 → 2); 9 = GDH (0 → 1); 10 = HB (1 → 2); 11 = GDH (1 → 2); 12 = GDH (2 → 3); 13 = CAT (2 → 3); 14 = HB (2 → 3); 15 = SOD (0 → 1); 16 = ME (2 → 3); 17 = GDH (2 → 4); 18 = ME (2 → 1); 19 = HB (3 → 4); 20 = ALB (2 → 1); 21 = CAT (2 → 4); 22 = ME (2 → 1); 23 = IDH (0 → 1)

supported a *Suricata-Helogale* clad, while the other three supported a *Cynictis-Suricata* clade), and the recognition of a *Galerella-Cynictis-Helogale-Suricata* clade (supported by two trees).

The consensus tree in Fig. 2B is similar in overall topology to the "optimised" distance Wagner tree (Fig. 1C), in recognising the early separation of *Atilax*, and the subsequent trichotomy involving the same three lineages (social species, *Galerella* and *Herpestes*).

Discussion

Genetic distance analyses

Allelic variation within species was minimal (**H** = 0–0.051: Table 3). For the ten loci that showed between-species polymorphism, the pattern of distribution of alleles was species and group specific (Table 2). Species differed from one another therefore, in the presence or absence of alleles rather than in allele frequency. These factors promote the stability of dendrograms based on genetic distances (particularly when sample sizes are very small), as shown by Archie et al. (1989), and they also provide suitable qualitative characters for cladistic analysis.

Nei's (1978) genetic identity values (I) between pairs of viverrid species (including the genet *G. tigrina*: Table 4) invariably exceed the mean value for congeneric species given by Thorpe (1982: I=0.54, s.d.=0.17, **n**=824). I values between species of mongooses (Table 4) generally exceed the mean value for incipient species of mammals, given by Ayala (1975: I=0.77). These results suggest a recent radiation of the Viverridae, and are rather surprising, given the fact that mongooses and genets are separated at the subfamily level (or the family level: Wozencaft 1989b), and that most of the species of mongooses included in this study represent separate genera.

However, palaeontological and morphological data provide support for a recent, and somewhat "explosive", radiation of African herpestines. Three lineages of mongooses were present in the Pliocene Langebaanweg deposits, a *Galerella*-type form, a *Herpestes*-type form and a *Mungos*-type form (Hendey 1974, and unpub. data). The close resemblance of the *Mungos* form to *Herpestes* suggested that these two lineages had only recently split (Hendey 1974; furthermore, earlier fossil herpestines are represented only by unspecialised *Herpestes*-type forms: Savage 1978). By the early Pleistocene, fossil representatives of all the extant genera had appeared (Hendey 1974; Savage 1978). On the basis of dental characters and fossile evidence, Petter (1969) suggested a recent origin of the extant African Viverridae. Further allozyme analyses, based on larger numbers of loci, species and specimens, are needed to verify the apparently high genetic similarity between viverrid species.

Comparison of phenetic and cladistic allozyme approaches

Although the two species of *Galerella* are not clustered together on the UPGMA phenogram, they are cladistically similar as shown by the "optimised" distance Wagner (Fig. 1C) and PAUP (Fig. 2) trees. The UPGMA phenogram in Fig. 1A shows a close genetic relationship between *Galerella pulverulenta* and *Herpestes ichneumon* (the two species are separated by a D_N of only 0.06), which would appear to support the argument for including *Galerella* in *Herpestes* (Wozencraft 1989). However, the "optimised" distance Wagner tree (Fig. 1C) and the PAUP consensus tree (Fig. 2B) show *Herpestes* and *Galerella* to be distinct lineages which separated at the same time as the origin of the "social" lineage. The trichotomous split on the cladistic trees in Fig. 1C and Fig. 2 is supported by palaeontological evidence, which shows the existence of three lineages of mongooses in Langebaanweg deposits (3–5 MYA): a *Galerella*-type form, a *Herpestes*-type form and a *Mungos*-type (i.e. social) form (Hendey 1974, and unpub. data).

Buth (1984) has pointed out that UPGMA trees based on electrophoretic data represent the true phylogeny only when the assumption of equal rates of evolution in different lineages is met. The marked difference in topology between the UPGMA phenogram and the cladistic (i.e. distance Wagner and PAUP) trees in this study results from unequal rates of evolution in different lineages of mongooses, as is evident from the distance Wagner trees (Figs. 1B, 1C) and the PAUP tree in Fig. 2A. A similar explanation was given for conflicting phenetic and cladistic analyses of electrophoretic data by Baverstock et al. (1979) and Hillis (1985). Anagenic change (as measured by branch length in the distance Wagner trees in Fig. 1, or by the number of character stage changes in Fig. 2A) appears to occur at a faster rate in the "advanced", social mongooses (*Suricata, Helogale, Cynictis*) than in the "primitive", solitary species (*Galerella, Herpestes, Atilax*), giving rise to an UPGMA tree in which the social species appear to split off before the origin of the extant solitary species. The genetic similarity between *Herpestes, Galerella, Atilax* and *Cynictis* on the UPGMA phenogram is clearly a result of symplesiomorphic (i.e. shared primitive) characters (see Fig. 2A).

Comparison of allozyme and other data sets

Figure 3 illustrates six previous phylogenetic schemes for the Herpestinae, based on morphological, palaeontological, karyological and behavioral evidence. From Fig. 3, there is clearly little consensus regarding phylogenetic relationships among the mongooses. However certain comparisons can be made between the various published phylogenetic schemes and the allozyme trees presented in the present study.

The "optimised" distance Wagner tree (Fig. 1C) and PAUP trees (Fig. 2) support a phylogenetic split between the social and the solitary mongooses. This conclusion is supported by karyological (Fredga 1972), palaeontological (Hendey 1974), and morphological (Gregory and Hellman 1939) evidence (Fig. 3), although Hendey (1974) and Gregory and Hellman (1939) place the "semi-social" genus *Cynictis* closer to *Galerella* than to the social species (Fig. 3A, D). In this respect, from the cladistic analyses of the allozyme data, *Cynictis* separates first from the "social" lineage, and therefore shares greater symplesiomorphic similarity with *Galerella* than do *Helogale* and *Suricata* (this is reflected in the position of *Cynictis* on the UPGMA phenogram in Fig. 1A). Baker (1987) groups *Helogale, Mungos* and *Cynictis* on behavioral grounds, while maintaining that *Suricata* is behaviorally unique (Fig. 3E). However, these behavioral differences in *Suricata* are clearly autapomorphies, and, cladistically speaking, *Suricata* would probably be grouped with *Helogale* and *Mungos* on behavioral grounds.

The close genetic similarity between *Atilax, Herpestes* and *Galerella* (Fig. 1A) is supported by phenetic analyses of behavioral and morphological data (Baker 1987: Fig. 3E, F). However, as shown in the cladistic allozyme trees, and as discussed above, this similarity is symplesiomorphic in nature. The phylogenetic separation of the *Galerella* and *Herpestes* lineages, as suggested by the cladistic, allozyme trees (Figs. 1B, 1C, 2), is supported by palaeontological (Hendey 1974), morphological (Gregory and Hellman 1939; Petter 1969) and karyological (Fredga 1972) data (see Fig. 3). As mentioned above, these results argue against the inclusion of *Galerella* in *Herpestes*, as suggested by Wozencraft (1989b).

Baker (1987) has suggested the possibility of an *Atilax*-like ancestor of the Herpestinae, an idea that is supported by cladistic analysis of allozymes in the present study (Figs. 1B, 1C, 2). Although the earliest mongoose fossils, from the Miocene in Africa and Europe, are generally recognised as unspecialised *Herpestes*-type forms (Savage 1978), a diverse array of these primitive viverrid genera existed during the Miocene, of which many lineages became extinct (e.g. *Kichechia, Leptoplesictis, Herpestides, Legetetia:* Schmidt-Kittler 1987). There need not therefore have been a direct line of descent form the earliest

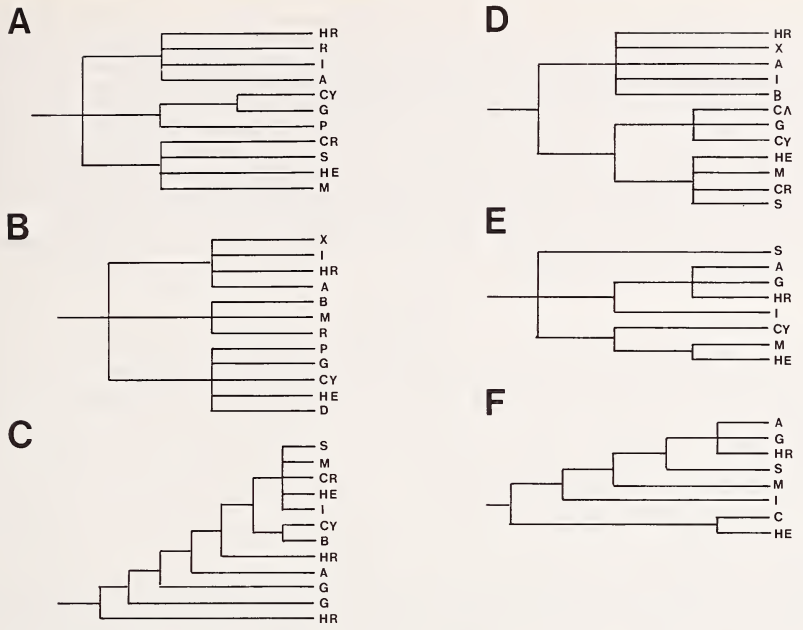

Fig. 3. Dendrograms summarising relationships among genera of mongooses (Hepestinae), based on independent, published studies involving different suites of characters. A: based on palaeontological data, in Hendey (1974, and unpublished phylogenetic tree); B: based on groups identified by Petter (1969) on the basis of size and dental characters; C: modified from Fredga (1972), on the basis of karyological data; D: modified from Gregory and Hellman (1939), based on characters of the skull and teeth; E: based on phenogram from behavior data (Baker 1987); F: based on phenogram from morphological data (Baker 1987). Abbreviations of genera are as follows: A = *Atilax*; B = *Bdeogale*; CA = *Calogale*; CR = *Crossarchus*; CY = *Cynictis*; D = *Dologale*; G = *Galerella*; HR = *Herpestes*; HE = *Helogale*; I = *Ichneumia*; M = *Mungos*; P = *Paracynictis*; R = *Rhynchogale*; S = *Suricata*; X = *Xenogale*

unspecialised viverrids to all of the extant species (HENDEY, pers. comm.), and it is quite plausible that a more recent *Atilax*-like ancestoral species gave rise to the apparently recent (Pliocene and early Pleistocene) extant mongoose radiation.

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Zusammenfassung

Untersuchungen zur Evolution afrikanischer Mangusten (Viverridae: Herpestinae) aufgrund von Allozymen

Durch waagerechte Stärkegel-Elektrophorese wurden die Unterschiede der Allozyme an 18 Proteinloci bei 48 Exemplaren von sieben Mangustenarten (Viverridae: Herpestinae: *Cynictis penicillata, Helogale parvula, Suricata suricatta, Atilax paludinosus, Herpestes ichneumon, Galerella sanguinea* and *G. pulverulenta*) und bei einer Ginsterkatze (Viverridae: Viverrinae: *Genetta tigrina*) untersucht.

14 Loci waren polymorph und 10 waren zwischenartlich unterschiedlich. Eine phenetische Analyse der genetischen Abstände (Nei 1978) deutet auf eine verhältnismäßig junge "explosive" Artenbildung der untersuchten Viverridae. Kladistische Analysen (wobei *Genetta tigrina* als Außengruppe betrachtet wurde) die durch "Wagner-Bäume" der genetischen Abstände (Rogers 1972) und Sparsamkeitsanalyse geordneter Eigenschaften multipler Loci gewonnen wurden, ergaben übereinstimmende Dendrogramme, die eine frühe Abzweigung von *Atilax* zeigen, mit einer darauffolgenden Aufspaltung in die drei Stämme: 1. *Galerella*, 2. *Herpestes* und 3. eine Gruppe sozialer Arten mit *Helogale*, *Suricata* und *Cynictis*. Diese Befunde werden durch paläontologische, morphologische, karyologische und ethologische Vergleiche gestützt. Wegen ungleicher Veränderungsgeschwindigkeiten der verschiedenen Linien, führten die phenetischen und kladistischen Analysen der Allozyme zu widersprüchlichen Dendrogrammen. Der kladistischen Methode wird für die Ermittlung phylogenetischer Beziehungen hier der Vorrang gegeben.

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