Systematic status and biogeography of the Javan and small Indian mongooses (Herpestidae, Carnivora)

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The Javan and small Indian mongooses, ranging from the Middle East to South-east Asia, are considered as two species or as a single species, varying in size and colour from west to east. In order to clarify their systematic status and to define the limits of their ranges, Cytochrome *b* sequences were obtained from 27 specimens, and localities of 392 specimens from museum collections were determined. The phylogenetic analyses revealed that the Javan and Small Indian mongooses grouped in two separate clades with their range limits located in Myanmar. The Javan mongoose is in fact closer to the grey mongoose than to the small Indian mongoose.

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Introduction

The mongooses of genus *Herpestes* are found all across the Old World; at least six species occur in Africa and nine in Asia (Hinton & Dunn 1967; Wozencraft & Gittleman 1989, 1993, 2005). Among them, the small Asian mongooses — the Javan mongoose *Herpestes javanicus* (E. Geoffroy Saint-Hilaire, 1818) and the small Indian mongoose *Herpestes auropunctatus* (Hodgson, 1836) — are considered as two species by some authors (Chasen 1940; Ellerman & Morrison-Scott 1951; Hinton & Dunn 1967; Harrison 1968; Michaelis 1972; Ewer 1973; Medway 1978; Honacki *et al*. 1982; Medway 1983; Wozencraft 1989; Harrison & Bates 1991; Taylor & Matheson 1999), with a zone of sympatry in peninsular Malaysia, or as a single species, *H. javanicus*, varying in size and colour from west to east (Pocock 1937, 1941; Bechthold 1939; Wenzel & Haltenorth 1972; Lekagul & McNeely 1977; Macdonald 1984; Corbet & Hill 1992; Wozencraft 1993, 2005; Roberts 1997; Macdonald 2001).

The ranges of the small Indian and Javan mongooses extend from the Arabian Peninsula across northern India to South-east Asia, although their exact limits vary according to different authors. According to Wozencraft (1993, 2005), *H. javanicus-H. auropunctatus* occurs in Afghanistan, Bangladesh, Bhutan, Cambodia, China, India, Indonesia, Malaysia, Myanmar, Nepal, Pakistan, Thailand and Vietnam. Pocock (1941), Prater (1971), Harrison (1968), Deuve (1972), Lekagul & McNeely (1977), Nellis (1989), Wells (1989), Corbet & Hill (1992) and Roberts (1997) add Iran, Iraq, Laos and Saudi Arabia. Honacki *et al*. (1982) suggest that *H. auropunctatus* ranges from northern Arabia to southern China, Hainan Island and the Malay Peninsula, while *H. javanicus* occurs in Cambodia, Java, the Malay Peninsula, Thailand and central Vietnam. Eight subspecies have been recognized (see Pocock 1941; Ellerman & Morrison-Scott 1951; Wells 1989; Corbet & Hill 1992). However, the taxonomy of these Asian mongooses remains confused.

The type locality of *H. javanicus* is Java while that of *H. auropunctatus* is central Nepal. *H. auropunctatus* (*sensu* Honacki *et al*. 1982) was reviewed by Nellis (1989), mainly on the basis of data from introduced populations, but the distribution map included the range of *H. javanicus*. Wells (1989) showed that the possible sympatry of the small Indian and Javan mongooses was based on misidentification of a specimen from peninsular Malaysia, where he believed that only

H. javanicus occurred. Taylor & Matheson (1999), on the basis of a morphometric analysis, recognized two separate species, with specimens from Java, Vietnam and Thailand as *H. javanicus*, and those from Kashmir, India, Pakistan and China as *H. auropunctatus*.

The small Indian mongoose has been introduced to many different parts of the world, mainly on islands (see review in Tvrtkovic & Krystufek 1990; and in Simberloff *et al.* 2000). The progenitors are believed to have originated from the Indian region (*H. auropunctatus*, *sensu* Honacki *et al.* 1982). In the Adriatic islands, the introduced species has been reported as *H. griseus* (Hirtz 1927), synonym of *H. edwardsii* (see Wozencraft 2005), *Mungos mungo* (Fink 1960), *H. ichneumon* (Van den Brink 1957; Niethammer 1963; Corbet 1978; Görner & Hacketal 1987), *H. edwardsii* (Dulic & Tortic 1960; Toschi 1965; Van den Brink 1972), and *H. auropunctatus* (Tvrtkovic 1982; Tvrtkovic & Krystufek 1990; Mitchell-Jones *et al.* 1999). The identification of the mongoose species introduced in the Adriatic islands has not hitherto been verified using molecular analysis.

According to Simberloff *et al.* (2000), interspecific competition can affect the size of individuals and sexual dimorphism in the small Indian/Javan mongoose. Other mongoose species occur within the geographical range of the small Indian/Javan mongoose. Among them, the grey mongoose *H. edwardsii* is of similar size and ecological characteristics (Creel & Macdonald 1995). The ruddy mongoose *H. smithii*, which is also considered by Simberloff *et al.* (2000) as a possible competitor, has a different activity time (nocturnal vs. diurnal for *H. javanicus* and *H. edwardsii*; Rood 1986). Simberloff *et al.* (2000) consider the small Indian and Javan mongooses to be conspecific and they propose that the size difference observed between the populations in the western (Middle East toward Bangladesh) and in the eastern (South-east Asia; their region VII) parts of their range is due to competition with *H. edwardsii* and *H. smithii* (species that occur in the western and not in the eastern part of the range of the Javan/small Indian mongoose).

The goal of this work is to clarify the systematic status of *H. javanicus* and *H. auropunctatus* and to define the limits of their ranges. Sequences of cytochrome *b* were obtained from 27 specimens, covering the ranges of these species. Cyt *b* has proven to be useful for intraspecific carnivore and species limit studies (Demboski *et al.* 1999; Hosoda *et al.* 1999, 2000; Davison *et al.* 2000; Stone & Cook 2000; Cook *et al.* 2001; Stone *et al.* 2002; Veron *et al.* 2004a). The distribution and range limits of these species were assessed using the localities of specimens from museum collections and from samples used in the molecular study. The grey mongoose, believed to be the sister taxon of *H. javanicus*/*H. auropunctatus* (Veron *et al.* 2004b; Perez *et al.* 2006), was also included in this study. This species is a possible competitor that may, according to

Simberloff *et al.* (2000), impact the morphological variation and speciation of the small Indian/Javan mongoose.

Materials and methods

Molecular analysis

Hair and tissue samples of 18 *H. auropunctatus*/*H. javanicus* and of nine *H. edwardsii* individuals were obtained from various sources (see Acknowledgements) and from different parts of their ranges. Samples are listed in Table 1. *Herpestes naso*, an African species that belongs to the sister clade of the small Asian mongooses, and *H. urva*, a more distantly related Asian species (Veron *et al.* 2004b; Perez *et al.* 2006), were used as outgroups. Eleven sequences from GenBank were also used in the analysis; their geographical origins were obtained from the authors or publications (see Table 1).

DNA extraction, primers, amplification and sequencing were similar to those described by Veron *et al.* (2004a,b). The molecular work was done at the Service de Systématique Moleculaire (CNRS IFR 101), Muséum National d'Histoire Naturelle, Paris.

The data set was analysed with different methods: maximum parsimony (MP) using PAUP* 4.0b10 (Swofford 2001), maximum likelihood (ML) using PhyML (Guindon & Gascuel 2003), and Bayesian inference (BI) using MrBayes 3b4 (Huelsenbeck & Ronquist 2001). The cladistic analysis used heuristic search with random stepwise addition sequence (100 replicates) and TBR branch-swapping (Swofford *et al.* 1996). Likelihood models and parameters were estimated by MODELTEST ver. 3.7 (Posada & Crandall 1998) using the AIC criterion. For BI we used MrBayes 3b4 with flat priors (no *a priori* parameters). The analysis parameters were: four character states (no peculiar weighting scheme for indel, cyt *b* being a coding gene), six substitution types following an invgamma law/shape. Four cold (T = 0.2) Metropolis Coupled Markov Chain Monte Carlo (MCM-CMC) for 3 000 000 generations, with a 'burn-in' period of 30 000 generations and one tree retained every 100 generations, were used (a total of 29 700 trees sampled). The analysis was run twice to check for convergence of the results. To assess statistical support for hypothesized clades, bootstrap (BP) analysis (Felsenstein 1985) with 100 (ML) and 1000 (MP) bootstrap replicates was done, and posterior probabilities (BPP) were calculated in BI. The amount of homoplasy was measured through the consistency index (Kluge & Farris 1969) and the retention index (Farris 1989).

Distribution

Information on specimen locality of small Indian, Javan and grey mongooses was collected in NHM (London), MNHN (Paris), AMNH (New York) and NMNH (Washington). Information from other museums was kindly provided by the

Table 1 Samples and genbank sequences used in the molecular analysis.

Species	DNA sample	Genbank access number	Reference	Geographic origin	Coordinates
H. edwardsii	C-232	AF522336	Veron *et al.* (2004b)	Bahrain	26.00 N, 50.5 E
H. edwardsii	C-233	DQ519050	this study	Bahrain	26.00 N, 50.5 E
H. edwardsii	C-234	DQ519053	this study	Dubai, United Arab Emirates	25.00 N, 55.33 E
H. edwardsii	C-235	DQ519051	this study	Sharjah, United Arab Emirates	25.00 N, 55.75 E
H. edwardsii	C-236	DQ519049	this study	United Arab Emirates	
H. edwardsii	C-237	DQ519052	this study	Iran	
H. edwardsii	C-372	DQ519054	this study	Payradanga, Jhikorgacha, SW, Bangladesh	23.1 N, 89.11 E
H. edwardsii	C-373	DQ519055	this study	Payradanga, Jhikorgacha, SW, Bangladesh	23.1 N, 89.11 E
H. edwardsii	C-381	DQ519056	this study	Payradanga, Jhikorgacha, SW, Bangladesh	23.1 N, 89.11 E
H. edwardsii		AY170107	Yoder *et al.* (2003)	unknown	
H. javanicus	C-129	DQ519058	this study	Kapoe, Thailande	9.58 N, 98.6 E
H. javanicus	C-192	DQ519059	this study	Phu Khio W.S., Thailand	16.5 N, 101.20 E
H. javanicus	C-228	AF522338	Veron *et al.* (2004b)	Georgetown, Guyana	
H. javanicus	C-229	DQ519065	this study	Georgetown, Guyana	
H. javanicus	C-287	DQ519064	this study	Myanmar	
H. javanicus	C-288	DQ519070	this study	Myanmar	
H. javanicus	C-312	DQ519057	this study	Phu Khio W.S., Thailand	16.5 N, 101.20 E
H. javanicus	C-374	DQ519066	this study	Manda, Dhaka, Bangladesh	24.78 N, 88.7 E
H. javanicus	C-375	DQ519067	this study	Manda, Dhaka, Bangladesh	24.78 N, 88.7 E
H. javanicus	C-382	DQ519072	this study	Manda, Dhaka, Bangladesh	24.78 N, 88.7 E
H. javanicus	C-383	DQ519069	this study	Korcula Isl., Croatia	
H. javanicus	C-393	DQ519071	this study	Pakistan	
H. javanicus	C-394	DQ519068	this study	Pakistan	
H. javanicus	C-396	DQ519073	this study	Thailand	
H. javanicus	C-451	DQ519061	this study	Loei Province, Thailand	
H. javanicus	C-452	DQ519062	this study	Muang, Mam Man, Village Ban Rai Muang, Loei Prov., Thailand	17.12 N, 101.40 E
H. javanicus	C-453	DQ519063	this study	Loei Market, Thailand	
H. javanicus	L-1	DQ519060	this study	Cuc Phuong, Vietnam	20.31 N, 105.63 E
H. javanicus		X94926	Ledje & Arnason (1996)	India	
H. javanicus		AY928675	Koepfli *et al.* (2006)	Vinh Yen district, Tam Dao, Vietnam	21.27 N, 105.38 E
H. javanicus		NC006835	Penny & McLenachan, unpubl.	Fiji	
H. javanicus		AY873843	Penny & McLenachan, unpubl.	Fiji	
H. javanicus		AY170108	Yoder *et al.* (2003)	Caribbean islands	
H. javanicus		AB050130	Sekiguchi *et al.* (2001)	Amami, Japan	
H. javanicus		AB050131	Sekiguchi *et al.* (2001))	Amami, Japan	
H. javanicus		AB050128	Sekiguchi *et al.* (2001)	Okinawa, Japan	
H. javanicus		AB050129	Sekiguchi *et al.* (2001)	Okinawa, Japan	
H. naso	4616	AF522339	Veron *et al.* (2004b)	Mikouma, Gabon	
H. urva	C-253	DQ519074	this study	Northern Taiwan	

curators (see Acknowledgements). Additional specimen localities were found in Meiri (2005) and Van Strien (2001). Species identification was checked whenever possible. As some museums had labelled specimens of small Indian/Javan mongooses according to Wozencraft (1993) (*H. javanicus*, which includes *H. auropunctatus*), while others had considered them to be two species (Honacki *et al.* 1982), we grouped all these specimens under *H. javanicus* following Wozencraft (2005). Geographic coordinates of the locality data given for the collection specimens and for the samples were found using Alexandria Digital Library Gazetteer Web Server and placed on a map using ArcView 3.1 (ESRI, Redlands, CA, USA).

Results
Molecular results
Twenty-seven new sequences of the complete cyt*b* gene (1140 bp) were obtained; for three samples (L-1, C-374 and C-375), only 400 bp were obtained owing to their poor state of preservation (GenBank accession numbers listed in Table 1). The data set comprised 26 sequences of *H. javanicus*/*H. auropunctatus*, ten of *H. edwardsii*, one of *H.* sp. from Croatia, one of *H. naso*, and one of *H. urva*.

The model chosen for ML analysis according to the AIC criterion was GTR + G + I.

MP analysis resulted in 3238 trees of 393 steps (CI = 0.69, RI = 0.31); of 1140 characters, 153 were parsimony-informative.
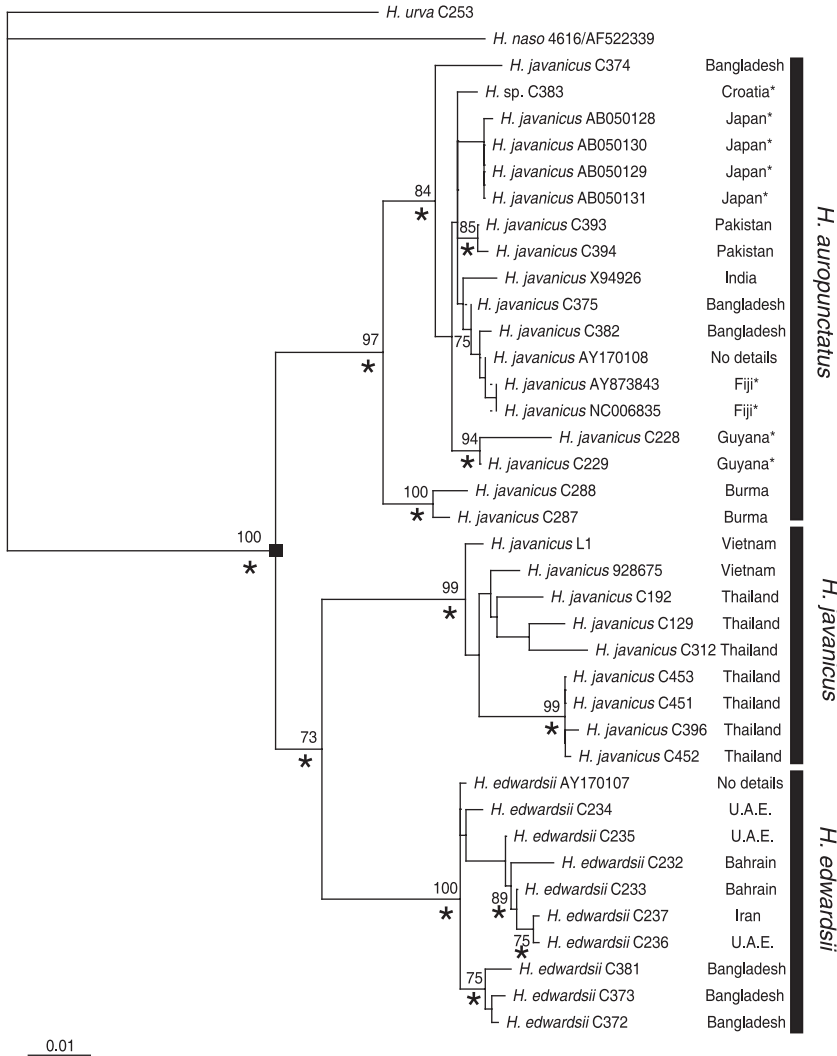
Fig. 1 Phylogenetic tree obtained by maximum likelihood analysis (GTR + G4 + I, bootstrap = 100 replicates). Each specimen is identified by its voucher number or GenBank accession number and its locality. Only bootstrap values > 70 are reported on the tree. Nodes with a star are those found using every analysis method (MP, ML, BI) with good statistical support (BP > 75; BPP > 0.95). Localities annotated with a star are those of introduction. U.A.E.: United Arab Emirates.

The three reconstruction methods gave similar topologies (Fig. 1). Three clades were obtained, corresponding to *H. edwardsii*, *H. auropunctatus* and *H. javanicus* (*sensu* Honacki *et al.* 1982); they were highly supported (respectively BPP = 1.00/1.00/1.00, BP_{ML} = 100/97/99 and BP_{MP} = 100/99/100). The *H. javanicus* clade included specimens of the *javanicus/auropunctatus* complex from Thailand and Vietnam, and the *H. auropunctatus* clade comprised all other specimens from this complex. The samples from introduced mongooses were all within the *H. auropunctatus* clade. This study confirmed the identification of the mongooses introduced to Croatia as *H. auropunctatus* (*sensu* Honacki *et al.* 1982).

H. javanicus was found to be the sister group of *H. edwardsii*, with quite good support (BPP = 1.00, BP_{ML} = 73 and BP_{MP} = 90); *H. javanicus* is thus more closely related to *H. edwardsii* than to *H. auropunctatus*.

Divergences between the three clades are: *H. edwardsii/ H. javanicus* 5.316%, *H. edwardsii/H. auropunctatus* 5.188% and *H. javanicus/H. auropunctatus* 5.698%. Average divergences within *H. auropunctatus*, *H. javanicus* and *H. edwardsii* are 1.952%, 1.769%, and 0.999%, respectively.

Distribution

The 392 specimens of *H. javanicus/H. auropunctatus* provided 272 locality data, and the 288 specimens of *H. edwardsii* provided 163 locality data. Unfortunately, many specimens had unknown or imprecise locality information (see Supplement).

The map (Fig. 2) shows the native distribution of these species. The native distribution of *H. javanicus/H. auropunctatus* includes the following countries: Afghanistan, Bangladesh, Bhutan, Cambodia, China, India, Indonesia, Iran, Iraq, Jordan, Laos, Malaysia, Myanmar, Nepal, Oman, Pakistan, Saudi
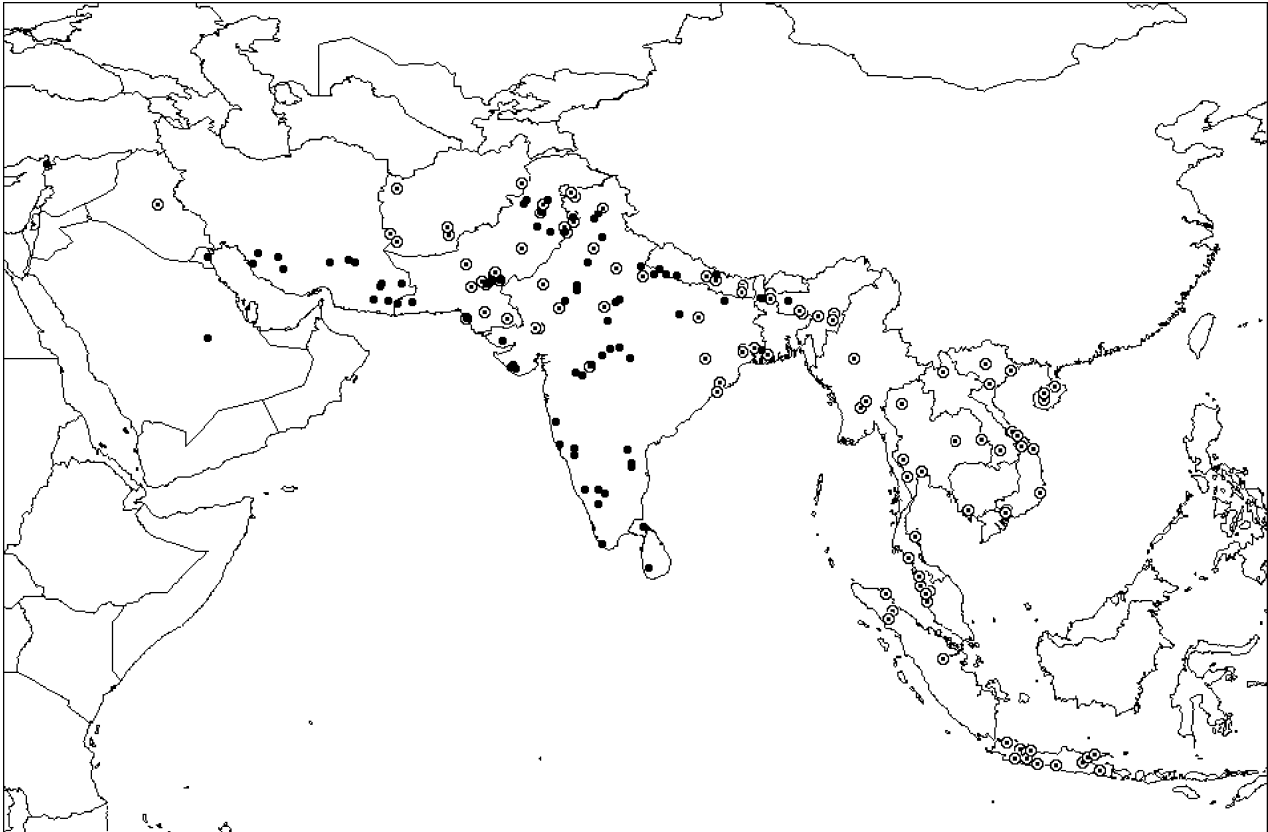
Fig. 2 Distribution map of *Herpestes javanicus* (*sensu* Wozencraft 1993, 2005; including *Herpestes auropunctatus*) (white dots) and *Herpestes edwardsii* (black dots).

Arabia, Thailand and Vietnam. *H. edwardsii* occurs in Afghanistan, Bahrain, India, Iran, Kuwait, Nepal, Pakistan, Saudi Arabia, Sri Lanka, Turkey and United Arab Emirates. This species has not been found in peninsular Malaysia.

Discussion

Systematic status of the Javan and small Indian mongooses

The molecular results support the existence of three distinct clades, which correspond to the Javan mongoose *Herpestes javanicus* (south-east Asia), the small Indian mongoose *H. auropunctatus* (from Middle East to Myanmar) and the grey mongoose *H. edwardsii*, with a mean genetic divergence of 5% between each pair of species. Each of the three clades shows a genetic unity with an inner genetic divergence *c.* 2% for *H. auropunctatus* and *H. javanicus* and 1% for *H. edwardsii*.

The most striking result was the highly supported sister relationship between *H. javanicus* and *H. edwardsii* and not between *H. javanicus* and *H. auropunctatus*, as would have been expected. This clearly shows the invalidity of the definition of *H. javanicus sensu* Wozencraft (1993, 2005). The taxonomic arrangement of Honacki *et al.* (1982) is supported by our results.

This result is congruent with the morphometric study of Taylor & Matheson (1999). Eleven cranial measurements of 15 *Herpestes* species (including *Galerella*, following Wozencraft 1989 and Taylor & Goldman 1993) were included in a principal component analysis, and the results showed a clear separation between *H. auropunctatus* (specimens from China, India, Kashmir and Pakistan) and *H. javanicus* (Java, Thailand and Vietnam). Moreover, their dendrogram on mean values clustered *H. javanicus* with *H. edwardsii*, and not with *H. auropunctatus*.

According to their analysis, the Javan and small Indian mongooses differed in size and also in skull shape. In particular, their study showed the smaller size of the small Indian mongoose. The condylobasal length of the skull of *H. auropunctatus* ranged from 54.9 to 67.1 mm (mean 62.1, $N = 14$) in females, and from 56.3 to 71.5 mm (mean 65.0, $N = 10$) in males. In *H. javanicus*, it ranged from 64.2 to 79.2 mm (mean 72.6, $N = 15$) in females, and from 72.2 to 83.7 mm (mean 78.0, $N = 19$) in males. Body measurements on collection specimens (see Supplement) and in Lekagul & McNeely (1977), Roberts (1997) and Wells (1989), showed that the head and body length of *H. javanicus* ranged from 300 to 415 mm and its tail

length from 210 to 315 mm, while body measurements of *H. auropunctatus* ranged from 250 to 370 mm for head and body length and 192–290 mm for tail length (in some of these references the number of specimens and sex were not provided). Head and body length for specimens from India and Pakistan ranged from 250 to 320 mm, and for specimens from Myanmar from 318 to 370 mm.

The morphometric differences between *H. auropunctatus* and *H. javanicus* observed by Pocock (1941), Corbet & Hill (1992), Taylor & Matheson (1999) and Simberloff *et al.* (2000), were considered by Simberloff *et al.* (2000) as intraspecific size variation reflecting interspecific competition or its absence. According to them, a size difference occurs in both sexes (but is more pronounced in males), revealing an increase of sexual dimorphism in the eastern population, where competition with other similar sized mongooses (*H. edwardsii* and *H. smithii*) did not occur. However, our results show that the eastern population is a different taxon than the one that occurs in sympatry with *H. edwardsii* and *H. smithii*. The two latter species do not show the same morphological variation in the parts of their range where *H. auropunctatus* is absent. This means that we have to reconsider the conclusions of Simberloff *et al.* (2000) about the character displacement and release in the small Indian/Javan mongoose, at least in their native range. However, character release does seem to occur in introduced populations of the small Indian mongoose, as shown by Simberloff *et al.* (2000), but such studies would benefit from clarification of the systematic situation.

With *H. javanicus* and *H. edwardsii* sister taxa, it seems possible that the substantially smaller size of the former relative to the latter reflects character release in the absence of *H. auropunctatus*, which is broadly sympatric with *H. edwardsii* but allopatric with *H. javanicus*. With three specimens of each sex from Myanmar removed from the data of Simberloff *et al.* (2000), the mean sizes of male and female mongooses in their region Asia VII (east of the Irrawaddy River), which they identified as *H. auropunctatus* but we here identify as *H. javanicus*, are substantially smaller than those for any populations of *H. edwardsii* they measured. For *H. javanicus*, mean condylobasal length of the skull was 73.56 mm for males (N = 26), while for females it was 66.98 mm (N = 20). Similar character release resulting in a smaller size in the absence of a smaller putative competitor has been reported for the Irish stoat (*Mustela erminea*) in the absence of the least weasel (*M. nivalis*), with which it co-occurs in Great Britain (Dayan & Simberloff 1994).

Studies of colour variation also concur with our results. According to Pocock (1941) and Corbet & Hill (1992), specimens from Vietnam and Java (*H. javanicus*) are clearly reddish in colour, while specimens from north-west India and Pakistan (*H. auropunctatus*) are pale, and those from Assam and Myanmar are darker and greyish. This is in agreement with our observation of specimens from NHM and the AMNH.

Those from Thailand, Laos and Java are darker and reddish (particularly the head), while those from India, Nepal and Pakistan are paler.

In the *H. javanicus* clade we had samples only from Thailand and Vietnam. However, the morphometric results from Taylor & Matheson (1999) grouped together specimens from Vietnam, Thailand and Java. *H. javanicus* can thus be recognized as in Honacki *et al.* (1982). No specimens from Cambodia, Laos and peninsular Malaysia were available for our molecular study or for the morphometric study in Taylor & Matheson (1999), but they were considered as being part of *H. javanicus* on the basis of their morphology by Pocock (1941). For Ellerman & Morrison-Scott (1951), *H. javanicus* includes three subspecies: *H. j. javanicus* Geoffroy, 1818 (Java), *H. j. exilis* Gervais, 1841 (Indochinese region) and *H. j. peninsulae* Schwartz, 1910 (Thailand, Malay Peninsula).

The placement of specimens from Myanmar in the clade of *H. auropunctatus* differs from the assessment of Simberloff *et al.* (2000), who grouped them with the South-east Asian (region VII) mongooses, corresponding to *H. javanicus*. According to Pocock (1941), the pelage of specimens from Myanmar is very close to that of specimens from Nepal, but he emphasizes that the skull dimensions are larger than those of the western small Indian mongooses, but not much larger than those of *H. javanicus*. Taylor & Matheson (1999) did not include specimens from Myanmar in their study. So the placement of specimens from Myanmar in *H. auropunctatus*, which received high statistical support in our molecular study, cannot be confirmed by any morphometric results. However, mongooses from Myanmar have been considered a separate subspecies, *H. a. birmanicus* Thomas, 1886, included in *H. auropunctatus* by Ellerman & Morrison-Scott (1951) and Michaelis (1972). In our analyses, the specimens from Myanmar are a sister group to the rest of the other small Indian mongooses (from Bangladesh, India, Pakistan, and introduced populations). A similar pattern of a divergent lineage for populations within Myanmar has also been found in Old World fruit bats (the *Cynopterus brachyotis* complex; Campbell *et al.* 2004). The Brahmaputra and Salween Rivers may act as barriers isolating populations, as has been found in gibbon species (Takacs *et al.* 2005).

Chinese populations were assigned to *H. auropunctatus* by Ellerman & Morrison-Scott (1951), Michaelis (1972) and Honacki *et al.* (1982). This was confirmed by the morphometric studies of Taylor & Matheson (1999). However, the precise locality of the Chinese specimens in their study was unknown. Hainan mongooses and southern China populations were grouped in the subspecies *H. a. rubrifrons* J. Allen, 1909 by Ellerman & Morrison-Scott (1951). The coloration of the head of specimens of this subspecies from Hainan (AMNH collection, see Supplement) is reddish, while that of its body is brownish; thus its colour is closer to that of *H. javanicus*

than to that of *H. auropunctatus*. But the specimens' size fits more within the range of that of *H. auropunctatus* than that of *H. javanicus*. The condylobasal length of AMNH specimens is from 59.91 to 66.88 mm (*N* = 8) in females and from 64.28 to 70.60 mm (*N* = 3) in males. Ellerman & Morrison-Scott (1951) recognized five subspecies in *H. auropunctatus*: *H. a. birmanicus*, *H. a. rubifrons*, and *H. a. auropunctatus* Hodgson, 1836 from Nepal and northern India, *H. a. pallipes* Blyth, 1845 from the Middle East to India, and *H. a. siamensis* Kloss, 1917 from northern Thailand. However, the inclusion of the Chinese and northern Thailand populations in *H. auropunctatus* remains to be tested.

The introduced small Indian mongooses included in our study (Caribbean islands, Croatia, Fijian islands, Guyana and Japan) all belong to *H. auropunctatus*. This is in agreement with the history of introduction described by Tvrtkovic & Krystufek (1990) and Simberloff *et al*. (2000). They showed that the mongooses introduced in the Caribbean and Fijian islands came from India and that Japanese (Okinawa) mongooses originated from Bangladesh. Those introduced to Croatia were believed to be from western India. Their identification as *H. auropunctatus* rather than *H. edwardsii* or *H. ichneumon* (as reviewed by Tvrtkovic & Krystufek 1990) or *H. javanicus* is confirmed here.

Distribution

The distributions of the Javan and small Indian mongooses are similar to those described in previously published studies (Pocock 1941; Prater 1971; Harrison 1968; Deuve 1972; Lekagul & McNeely 1977; Nellis 1989; Wells 1989; Corbet & Hill 1992; Roberts 1997; Wozencraft 1993, 2005), to which records from Jordan and Oman must be added. The presence of the Javan/small Indian mongoose in Iran, Iraq, Laos and Saudi Arabia, not mentioned in Wozencraft (1993, 2005), is confirmed. In Indonesia, Honacki *et al*. (1982) mentioned occurrence of the Javan mongoose in Java but not in Sumatra. Its presence in Sumatra, mentioned by Bechthold (1939), was based on the type specimen of *H. rafflesii* Anderson, 1875; however, this was not supported owing to the re-identification of this type specimen as *H. semitorquatus* (Wells 1989, in agreement with Chasen 1940). But *H. rafflesii* is also listed as a synonym of *H. brachyurus* in Wozencraft (1993) and as *H. javanicus* in Wozencraft (2005). However, *H. javanicus tjerapai* Sody, 1949 has been described from Perlak, Aceh, Sumatra, and we also recorded several specimens from Sumatra in different museums (see Supplement).

The distribution of *H. edwardsii* is similar to that described by Wozencraft (1993, 2005), except that we recorded this species in Turkey and the United Arab Emirates and noted its absence in peninsular Malaysia. The record from Turkey extends the known distribution of this species westward.

Biogeography

From specimen distribution and molecular data, the eastern limit of *H. auropunctatus* and the western limit of *H. javanicus* are located in Myanmar; mongooses from Myanmar are in the *H. auropunctatus* clade and not in the *H. javanicus* clade. According to these data, *H. javanicus* and *H. auropunctatus* do not seem to be sympatric. *H. javanicus* and *H. edwardsii* also do not have a sympatric distribution.

The eastern limit of *H. edwardsii* includes Bangladesh, corresponding to the Brahmaputra River limit between the Indian and Indochinese subregions (see Corbet & Hill 1992). The same geographical barrier seems to act for the crab-eating mongoose (*H. urva*) and other small carnivores such as the small-toothed palm civet (*Arctogalidia trivirgata*), the large Indian civet (*Viverra zibetha*), the hog-badger (*Arctonyx collaris*), all occurring east of this barrier, and the Bengal fox (*Vulpes bengalensis*) occurring west of it (Corbet & Hill 1992).

The range limits of *H. javanicus* and *H. auropunctatus* do not correspond to the Brahmaputra River but occur east of it, in Myanmar. The range limit could be the Salween River in Myanmar, which seems to be a geographical barrier for small carnivore species such as the large-spotted civet (*Viverra megaspila*), spotted linsang (*Prionodon pardicolor*), masked palm civet (*Paguma larvata*) and binturong (*Arctictis binturong*) (Corbet & Hill 1992).

Many of the South-east Asian species occur further north-west in the Himalayan region as well, but according to Pocock (1941) the mongooses from this region belong to *H. auropunctatus* rather than to the South-east Asian taxa. Unfortunately, no specimen from the Himalayan region was available for our study, and none was included in the morphometric study of Taylor & Matheson (1999). The morphometric data from Simberloff *et al*. (2000) and our observations of museum specimens in AMNH, NHM and NMNH suggest that the mongooses from Nepal belong to the western taxa rather than to *H. javanicus*, in agreement with the taxonomic arrangement of Pocock (1941). It would be useful to obtain samples from this region in order to test this hypothesis; if proved wrong it would imply a change in the taxonomy of these species, because central Nepal is the type locality of *H. auropunctatus*.

While land connections all over the Sunda shelf existed during the last glacial maximum in the Pleistocene (see review in Meijaard 2003 and 2004a), *H. javanicus* does not occur in Borneo, while it occurs in Sumatra and Java. Other mongoose species occur in Borneo: the short-tailed mongoose *Herpestes brachyurus*, the collared mongoose *H. semitorquatus*, and Hose's mongoose *H. hosei* (Corbet & Hill 1992). What could explain the absence of the Javan mongoose on Borneo? According to Meijaard (2004b), some species may not have used the land connections during the last glacial maximum because of ecological barriers. The habitat in Java was more

open at this time than in Sumatra and Borneo, which may have affected species distributions. This explanation has been suggested to account for the absence of the leopard in Borneo by Payne (1990), Seidensticker (1986), Wong (2002), and Meijaard (2004b).

The ecology of *H. javanicus* has been very little studied in its native range. However, Wells (1989) showed that the Javan mongoose in peninsular Malaysia avoids rainforest and prefers lowland plains, bamboo and young teak plantations, grassland, and paddy and sugarcane fields. This may explain why it did not reach Borneo when land connections existed. Meijaard (2004a) also proposed that physical barriers may have affected the distribution of some species over the Sunda shelf. The landmasses between Java and Borneo, and between peninsular Malaysia and Borneo, were separated by large rivers on the northern Sunda shelf during the last glacial maximum (Meijaard 2003; Meijaard & Groves 2004). Unfortunately, with a very scarce fossil record, dispersal events of mongooses are difficult to date and link to climatic changes and palaeobiogeographical events.

Conclusions

This study has clarified the taxonomic situation of the small Indian/Javan mongoose as comprising two separate clades, with the Javan mongoose being closer to the grey mongoose rather than to the small Indian mongoose. We have attempted to provide more accurate range limits and described possible factors that may have affected their distributions. Previous conclusions on interspecific competition and character release in small Asian mongooses (Simberloff *et al*. 2000) must be reconsidered, as the species investigated has been shown to form three species rather than two. However, their specific status remains to be confirmed by the analysis of nuclear makers, our results being based only on a mitochondrial marker, with divergences between the three clades obtained being close to the intraspecific variation level.

Further investigation is also needed in order to determine precise range limits and to provide a more detailed phylogeography of these Asian mongooses. Identification of Chinese populations as *H. auropunctatus* needs to be checked using samples from South Yunnan, Guangdong, as well as Hainan Island. Investigations of the putative range limits of *H. javanicus* and *H. auropunctatus* could be achieved by obtaining more information and samples from Myanmar. The attribution to *H. auropunctatus* (rather than to *H. javanicus*) of mongooses from the Himalayan region also needs to be verified on the basis of molecular studies. Samples from the Sundaic region (peninsular Malaysia, Java and Sumatra) are needed to test geographical barriers and island isolation in this region, as has been done for other South-east Asian small carnivores (e.g. binturong, see Cosson *et al*. in press).

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Supplement

Available on request from the corresponding author.