



urn:lsid:zoobank.org:pub:EB6AF6D6-36E7-4677-87E8-D72C42A273AF

Molecular systematics and biogeography of the Hemigalinae civets (Mammalia, Carnivora)

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Abstract. Due to the difficulty in obtaining samples, the systematics of the Hemigalinae civets has not been fully resolved. The aim of this study was to clarify the relationships of the species and the intraspecific diversity within this subfamily, and to explore the environmental factors that might have affected its evolution. Using two mitochondrial and two nuclear markers, we confirmed that the Hemigalinae comprises Owston's civet, the otter civet, Hose's civet and the banded civet, but also the Sulawesi palm civet (formerly included in the Paradoxurinae). Our study showed that the banded and Owston's civets are sister species, and suggested that Hose's civet is sister to these two. Within the banded civet, we observed a high divergence between individuals from the Mentawai Islands and those from Sumatra and Borneo (while the latter two were not strongly divergent), likely due to the deep sea channel between the Mentawai Islands and Sumatra. Unexpectedly, the Sumatran and Peninsular Malaysian individuals were not closely related, despite the fact that these two regions have repeatedly been connected during the last glaciations. No high polymorphism was found within Owston's civet, although three groups were obtained: southern China, northern Vietnam and central Vietnam, which might be related to Pleistocene climatic fluctuations.

Keywords. Southeast Asia, phylogeography, civets, Viverridae, molecular systematics.

Veron G., Bonillo C., Hassanin A. & Jennings A.P. 2017. Molecular systematics and biogeography of the Hemigalinae civets (Mammalia, Carnivora). *European Journal of Taxonomy* 285: 1–20. <http://dx.doi.org/10.5852/ejt.2017.285>

Introduction

The subfamily Hemigalinae (Viverridae) comprises four species: Owston's civet *Chrotogale owstoni* Thomas, 1912, the otter civet *Cynogale bennettii* Gray, 1837, Hose's civet *Diplogale hosei* (Thomas, 1892), and the banded civet *Hemigalus derbyanus* (Gray, 1837), that are found in Southeast Asia and southern China (Jennings & Veron 2009; Fig. 1). Very little is known about their ecology, but they seem to be nocturnal, mainly terrestrial, and are primarily found in tropical forests (Veron *et al.* 2006; Jennings & Veron 2009; Jennings *et al.* 2013). The banded civet and otter civet occur mainly in the lowlands, while Hose's civet is primarily found at higher elevations (Veron *et al.* 2006; Jennings *et al.* 2013); Owston's civet seems to be found both in lowland and montane forests (Jennings & Veron 2009). These species are of conservation concern, with the otter civet listed as Endangered and the other three as Vulnerable by the IUCN (2015), although there is a scarcity of data about their current population trends and sensitivity to environmental disturbance (Schreiber *et al.* 1989; Jennings & Veron 2009; Jennings *et al.* 2013). The destruction and degradation of tropical forests are clearly major threats to this group (Meijaard & Sheil 2008; Corlett 2009; Jennings *et al.* 2013). Despite these threats, little molecular systematics work has been done on this group; knowledge of their phylogenetic diversity, intraspecific genetic diversity and structure, and population differentiation is crucial for defining conservation priorities and for the identification of evolutionarily significant units (ESUs, Ryder 1986; Moritz 1994; Haig 1998; Isaac *et al.* 2007).

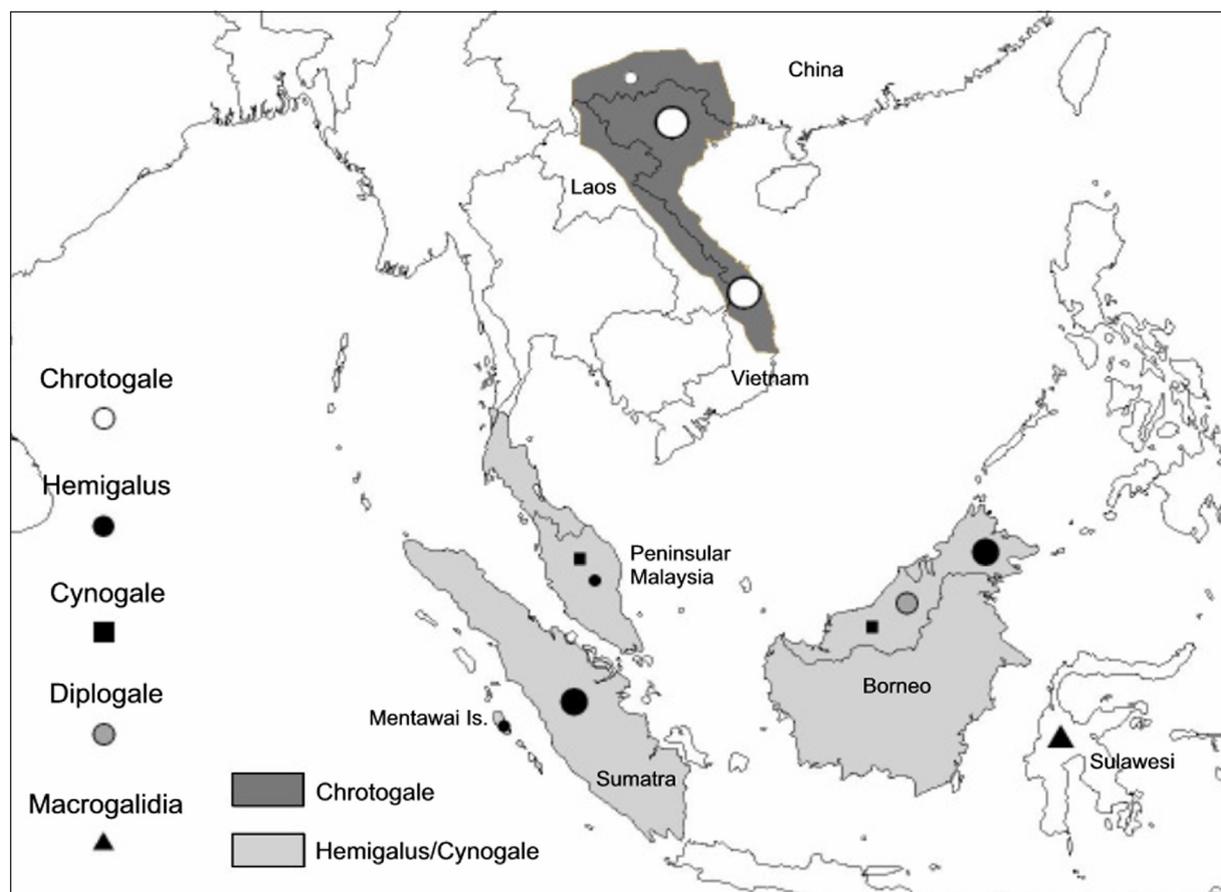


Fig. 1. Map showing the distribution of the samples of Hemigalinae used in this study. The gray shadings show the range of *Chrotogale owstoni* Thomas, 1912, *Cynogale bennettii* Gray, 1837 and *Hemigalus derbyanus* (Gray, 1837); *Diplogale hosei* (Thomas, 1892) is only found on Borneo and *Macrogalidia musschenbroekii* (Schlegel, 1879) only occurs on Sulawesi. The size of the sample symbols corresponds to the number of samples from each area (the smallest equals 1, and the largest equals 12–14).

The systematics of the Hemigalinae had previously only been assessed using morphological data (Pocock 1933; Gregory & Hellman 1939; Wozencraft 1989; Veron 1994, 1995) until Patou *et al.* (2008) proposed a molecular phylogeny of the Hemigalinae and Paradoxurinae. Patou *et al.* (2008) found that the banded civet and Owston's civet were sister species, with the otter civet as the sister taxon to these two (as also obtained later by Agnarsson *et al.* 2010). Unfortunately, Hose's civet and the Sulawesi palm civet *Macrogalidia musschenbroekii* (Schlegel, 1879) were missing from these molecular studies. Wilting & Fickel (2012) provided data for these two species; they confirmed that Hose's civet is a member of the Hemigalinae, and found that the Sulawesi palm civet grouped with this subfamily (whereas it was previously classified within the Paradoxurinae; Wozencraft 2005). However, their phylogenetic trees showed very low branch support for some taxa, and the relationships between the species of Hemigalinae were not resolved.

Very few studies have explored intraspecific variation within the species of Hemigalinae. Veron *et al.* (2004) conducted a molecular study on Owston's civet and obtained two main groups: northern and central Vietnam; however, samples from China were missing. Based on morphological features, two species for the otter civet have been proposed, *Cynogale lowei* Pocock, 1933 and *C. bennettii*, but examination of the only specimen available for *C. lowei*, and doubt about its geographic origin, led Veron *et al.* (2006) to consider *C. lowei* as a synonym of *C. bennettii*. Four subspecies of the banded civet were proposed by Wozencraft (2005): *Hemigalus derbyanus derbyanus* (Gray, 1837) (Myanmar, Peninsular Malaysia, Sumatra); *H. d. boei* Muller, 1838 (Borneo); *H. d. minor* Miller, 1903 (South Pagai Island, Mentawai Islands); and *H. d. sipora* Chasen & Kloss, 1927 (Sipora Island, Mentawai Islands). However, Pocock (1933) had previously proposed that *H. d. derbyanus* ranged from Myanmar to the Malay peninsula, Sumatra and Borneo, and that *H. d. minor* comprises both the South Pagai and Sipora Island populations. Corbet & Hill (1992) did not find any morphological support for these subspecies, and there has been no recent taxonomic revision of *H. derbyanus*. On the basis of a short mitochondrial fragment, Wilting *et al.* (2012) suggested a split of ca 2.7 million years between *H. d. derbyanus* and *H. d. minor*; unfortunately, they did not provide details about their dataset and results, and their sequences are not available in GenBank.

Tectonic movements, geographical and ecological barriers, and climatic variations across Southeast Asia have played important roles in the speciation and population structure of forest-dependent species (Meijaard 2009; Esselstyn *et al.* 2010; Shekelle *et al.* 2010; Woodruff 2010; Veron *et al.* 2014, 2015b, 2015c), and therefore, these might have affected the distribution and speciation of the Hemigalinae civets. The distinction between the Indochinese and Sundaic faunas might have arisen as a result of the rapid sea-level changes along the Thai-Malay peninsula during the last five million years, which caused local extirpations (Woodruff & Turner 2009), or it has been maintained by the ecological differences between these two subregions (Meijaard 2009). Within the Sundaic region, climate-induced sea-level changes have altered the topography repeatedly, exposing and flooding land corridors between the mainland and different islands, and ecological factors played a role in restricting movements of species across this region. For instance, during the Last Glacial Maximum (LGM), the central part of the Sundaland might have been covered by open habitat (Bird *et al.* 2005; Meijaard 2003; de Bruyn *et al.* 2014; but see also Woodruff 2010), which could have limited the exchanges of forest-dependent species between Borneo and the rest of the Sundaic region (Veron *et al.* 2014; 2015c), and this could have affected the Hemigalinae civets.

The aims of this study were to further clarify the relationships of the species within the Hemigalinae, to study the intraspecific diversity and genetic structure within the banded and Owston's civets, and to explore the role of geographical barriers and environmental fluctuations in shaping the structure between and within species. We analysed three mitochondrial fragments, Cytochrome *b*, Control Region and NADH dehydrogenase subunit 2, and two nuclear genes, Beta-fibrinogen intron 7 and inter-

photoreceptor retinoid binding protein (IPRB). Due to the elusive nature of the Hemigalinae civets and the difficulties of obtaining fresh samples, the use of museum samples was crucial for this study.

Material and methods

Sampling, extraction, PCR and sequencing

We collected fresh (hair or tissue) and museum samples (from skins and tissues taken from skulls) from 51 individuals of nine species of Hemigalinae and Paradoxurinae (Table 1, Fig. 1). Total genomic DNA was isolated following a cetyltrimethyl ammonium bromide (CTAB)-based protocol (Winnepenninckx *et al.* 1993). For museum samples, we added dithiothreitol (DTT 1M, ca 15 μ l per extract) during tissue lysis to break up disulfide bonds and we increased the lysis time (up to 72 hours).

We sequenced three mitochondrial fragments: Cytochrome *b* gene (Cytb), the control region (CR; hypervariable region 1) and NADH dehydrogenase subunit 2 (ND2), using the primers from Veron *et al.* (2004, 2014, 2015a), Patou *et al.* (2008, 2009) and Wilting & Fickel (2012). We sequenced the nuclear marker intron 7 of Beta-fibrinogen (FGB) using the primers of Yu & Zhang (2005). IRBP sequences were from previous studies (see Table 1).

Polymerase chain reactions (PCRs) were performed as in Patou *et al.* (2010), with annealing temperatures of 50°C for Cytb and ND2, 61°C for CR, and 59°C for FGB. PCR products were visualized on a 1.5% agarose gel. PCR products were then purified and sequenced in both directions on an automated DNA sequencer by Genoscope and Eurofins. Sequences obtained from DNA extracted from museum samples were amplified and sequenced twice to ensure their quality and authenticity. Sequences were edited, assembled and aligned manually using Bioedit, version 7 (Hall 1999).

Phylogenetic and haplotype network analyses

Phylogenetic analyses were performed using neighbour-joining (NJ), maximum likelihood (ML) and maximum parsimony (MP) as implemented in MEGA6 (Tamura *et al.* 2013), and Bayesian inference (BI) using MrBayes 3.2 (Ronquist *et al.* 2012). We rooted the phylogenetic analyses with three Viverrinae (*Genetta servalina* Pucheran, 1855, *Viverricula indica* (Saint-Hilaire, 1803) and *Viverra tangalunga* Gray, 1832), one species of Felidae (*Panthera leo* (Linnaeus, 1758)) and two species of Herpestidae (*Urva auropunctata* (Hodgson, 1836) and *U. javanica* (Saint-Hilaire, 1818)). Individual loci were first analysed independently and then combined.

For ML, the best-fitting model was estimated prior to the analyses using MEGA6, following the Akaike information criterion (AIC). The selected model was then implemented in the ML analyses, using the Nearest-Neighbor-Interchange heuristic method and node robustness was assessed through 1000 bootstrap replicates. For the BI analysis combining the four genes (Cytb, ND2, FGB and IRBP), jModelTest v. 2.1.7 (Darriba *et al.* 2012) was used to evaluate the models of nucleotide substitution for each of the ten partitions (FGB and the three codon-positions for Cytb, ND2 and IRBP), following the Akaike information criterion. Bayesian analyses were then conducted using the selected GTR+I+G model for Cytb-1 and Cytb-3, GTR+G model for Cytb-2 and ND2-3, GTR model for FGB, HKY+I+G model for ND2-1, HKY+G model for ND2-2, HKY model for IRBP-1 and IRBP-3, and K80 model for IRBP-2. The posterior probabilities (PP) were calculated using four independent Markov chains run for 10 000 000 Metropolis-coupled MCMC generations, with trees sampled every 1000 generations and a burn-in of 25%.

Trees were visualized and edited using FigTree v. 1.4.0 (Rambaut 2012). We compared resulting topologies and their node support; nodes were considered as supported when posterior probabilities were ≥ 0.95 and bootstrap values were $\geq 70\%$ (see Alfaro *et al.* 2003).

Table 1. List of the samples included in this study. For each sample, we report the identification number, the sample/specimen number (AHNU = Anhui Normal University, Wuhu, China; BZM = Museum für Naturkunde, Berlin, Germany; FMNH = Field Museum of Natural History, Chicago, IL, USA; ISEM = Institut des Sciences de l'Évolution, Montpellier, France; MCZ = Harvard Museum of Comparative Zoology, Cambridge, MA, USA; MNHN = Muséum national d'Histoire naturelle, Paris, France; RMNH = Rijksmuseum van Natuurlijke Historie, Naturalis, Leiden, the Netherlands), the GenBank numbers for the five genes, and locality (OCP = specimens held at the Owston's Palm Civet Conservation Program, Cuc Phuong National Park, Vietnam; ND = no data). Identification numbers in bold indicate samples used in the Cytb + ND2 + FGB + IRBP dataset for the phylogenetic analyses. GenBank numbers in bold are new sequences from this study; other sequences are from the following sources: Cracraft *et al.* 1998; Veron & Heard 2000; Yoder *et al.* 2003; Gaubert *et al.* 2004a, 2004b; Gaubert & Cordeiro-Estrela 2006; Veron *et al.* 2004; Yu *et al.* 2004; Masuda *et al.* 2008; Fang & Wu 2005 (unpubl.); Yu & Zhang 2005; Patou *et al.* 2008, 2009, 2010; Wilting & Fickel 2012; Veron *et al.* 2015b. Sequences <200 bp cannot be submitted to GenBank (available on request to GV). [continued on next two pages]

Species	Identification #	Sample/Specimen #	Cytb		CR		ND2		FGB		IRBP		Locality
			GenBank #	GenBank #	GenBank #	GenBank #	GenBank #	GenBank #	GenBank #	GenBank #			
<i>Arctictis binturong</i>	AbTC444	MNHN TC-444	KP986469	-	-	-	-	-	-	-	-	-	ND (Servion Zoo)
<i>Arctictis binturong</i>	AbTC94	MNHN TC-94	-	-	-	-	KM819558	EF680503	DQ683125	-	-	-	ND (Carnivore Preservation Trust)
<i>Arctogalidia trivirgata</i>	AfTC155	MNHN 2001-495	KM819540	-	-	-	KM819559	KM819523	-	-	-	-	ND (Parc Zoologique de Paris, MNHN)
<i>Arctogalidia trivirgata</i>	AfTC1	MNHN 1998-1970	-	-	-	-	-	-	-	-	-	-	ND (Ménagerie du Jardin des Plantes, MNHN, Paris)
<i>Chrotogale owstoni</i>	CoDQ286775	"AHNU0310"	DQ286775	-	-	-	-	-	-	-	-	-	China
<i>Chrotogale owstoni</i>	CoSH1	MNHN SH-1	AF125142	-	-	-	-	-	-	-	-	-	Vietnam, North (from traffic, OCP)
<i>Chrotogale owstoni</i>	CoSH10	MNHN SH-10	AY155248	-	-	-	-	-	-	-	-	-	Vietnam (Hô-Chi-Minh-Ville Zoo)
<i>Chrotogale owstoni</i>	CoSH11	MNHN SH-11	AY155263	-	-	-	-	-	-	-	-	-	Vietnam (Hô-Chi-Minh-Ville Zoo)
<i>Chrotogale owstoni</i>	CoSH12	MNHN SH-12	AY155269	-	-	-	-	-	-	-	-	-	Vietnam (Hô-Chi-Minh-Ville Zoo)
<i>Chrotogale owstoni</i>	CoSH13	MNHN SH-13	AY155266	-	-	-	-	-	-	-	-	-	Vietnam (Hô-Chi-Minh-Ville Zoo)
<i>Chrotogale owstoni</i>	CoSH14	MNHN SH-14	AY155252	-	-	-	-	-	-	-	-	-	Vietnam (Hô-Chi-Minh-Ville Zoo)
<i>Chrotogale owstoni</i>	CoSH15	MNHN SH-15	AY155253	-	-	-	-	-	-	-	-	-	Vietnam (Hô-Chi-Minh-Ville Zoo)
<i>Chrotogale owstoni</i>	CoSH16	MNHN SH-16	AY155259	-	-	-	-	-	-	-	-	-	Vietnam (Hô-Chi-Minh-Ville Zoo)
<i>Chrotogale owstoni</i>	CoSH3	MNHN SH-3	AY155251	-	-	-	-	-	-	-	-	-	Vietnam (OCP)
<i>Chrotogale owstoni</i>	CoSH4	MNHN SH-4	AY155258	-	-	-	-	-	-	-	-	-	Vietnam, North (OCP)
<i>Chrotogale owstoni</i>	CoSH6	MNHN SH-6	AY155264	-	-	-	-	-	-	-	-	-	Vietnam, North (OCP)
<i>Chrotogale owstoni</i>	CoSH8	MNHN SH-8	AF125144	-	-	-	-	-	-	-	-	-	Vietnam (Hô-Chi-Minh-Ville Zoo)
<i>Chrotogale owstoni</i>	CoSH9	MNHN SH-9	AY155249	-	-	-	-	-	-	-	-	-	Vietnam (Hô-Chi-Minh-Ville Zoo)

Species	Identification #	Sample/Specimen #	Cytb GenBank #	CR GenBank #	ND2 GenBank #	FGB GenBank #	IRBP GenBank #	Locality
<i>Chrotogale owstoni</i>	CoT2092	MNHN T-2092	AY155262	–	DQ683984	EF680505	DQ683127	Vietnam, North
<i>Chrotogale owstoni</i>	CoTC186	MNHN TC-186	AY155261	–	–	–	–	Vietnam, North (OCP)
<i>Chrotogale owstoni</i>	CoTC187	MNHN TC-187	AY155267	–	–	–	–	Vietnam, North (OCP)
<i>Chrotogale owstoni</i>	CoTC188	MNHN TC-188	AY155250	–	–	–	–	Vietnam, North, Kim Boi, Hoa Binh (OCP)
<i>Chrotogale owstoni</i>	CoTC189	MNHN TC-189	AY155268	–	–	–	–	Vietnam (OCP)
<i>Chrotogale owstoni</i>	CoTC190	MNHN TC-190	AY155270	–	–	–	–	Vietnam (OCP)
<i>Chrotogale owstoni</i>	CoTC191	MNHN TC-191	AY155260	–	–	–	–	Vietnam (captive born, OCP)
<i>Chrotogale owstoni</i>	CoTC193	MNHN TC-193	AY155256	–	–	–	–	Vietnam (captive born, OCP)
<i>Chrotogale owstoni</i>	CoTC197	MNHN TC-197	AY155271	–	–	–	–	Vietnam (OCP)
<i>Chrotogale owstoni</i>	CoTC204	MNHN TC-204	AY155255	–	–	–	–	Vietnam, Center, Binh Dinh (OCP)
<i>Chrotogale owstoni</i>	CoTC205	MNHN TC-205	AY155254	–	–	–	–	Vietnam, North, Nghe An (OCP)
<i>Chrotogale owstoni</i>	CoTC206	MNHN TC-206	AY155265	–	–	–	–	Vietnam, North, Nghe An (OCP)
<i>Chrotogale owstoni</i>	CoTC207	MNHN TC-207	AY155257	–	–	–	–	Vietnam, North, Van Ban, Lao Cai Province
<i>Cynogale bennettii</i>	CbM1962	MNHN 1962-170	KP986470	–	KP986485	–	–	Malaysia, Malacca
<i>Cynogale bennettii</i>	CbTC147	MNHN TC-417	DQ683992	–	DQ683983	–	–	Borneo, Sarawak (Negara Zoo, Kuala Lumpur)
<i>Diplogale hosei</i>	Dhf88298	FMNH 88298	KP986471	–	KP986486	–	–	Malaysia, Borneo, Sarawak, Kelabit Plateau, Pa Umur
<i>Diplogale hosei</i>	DhjQ219112	RMNH 34568	JQ219112	–	JQ219110	–	–	Malaysia, Borneo, Sarawak, Salekan Mt
<i>Diplogale hosei</i>	DhjQ219111	BZM 14291	–	–	JQ219111	–	–	Brunei, Marabok Mt
<i>Hemigalus derbyanus</i>	HdC38647	MCZ 38647	KP986472	–	–	–	–	Indonesia, Sumatra, East, Little Siak river
<i>Hemigalus derbyanus</i>	HdM24	MNHN 1886-24	KU696424	–	–	–	–	Indonesia, Sumatra, Palembang
<i>Hemigalus derbyanus</i>	HdM489	MNHN 1865-489	KU696425	–	–	–	–	Malaysia, peninsular Malaysia, Penang Island
<i>Hemigalus derbyanus</i>	HdR34643	RMNH 34643	KU696426	–	–	–	–	Indonesia, Borneo
<i>Hemigalus derbyanus</i>	HdR5109	RMNH 5109	KU696427	–	–	–	–	Indonesia, Sumatra, Atjeh, Rampaih
<i>Hemigalus derbyanus</i>	HdTC09	MNHN TC-09	AF125143	KP986468	AY170052	KP986482	AY170082	ND (Singapore Zoo)
<i>Hemigalus derbyanus</i>	HdTC20	MNHN TC-20	KP986473	–	–	–	–	Malaysia, Borneo, Sarawak (Cincinmati Zoo)
<i>Hemigalus derbyanus</i>	HdTC21	MNHN TC-21	<200bp	KP986463	–	–	–	Malaysia, Borneo, Sabah, Danum Valley

Species	Identification		Sample/Specimen		Cytb		CR		ND2		FGB		IRBP		Locality
	#		#		GenBank #		GenBank #		GenBank #		GenBank #	GenBank #		GenBank #	
<i>Hemigalus derbyanus</i>	HdTC22		MNHN TC-22		AY155273	-	DQ683987		KP986479		-				Malaysia, Borneo, Sabah, Danum Valley
<i>Hemigalus derbyanus</i>	HdTC23		MNHN TC-23		AY155272	KP986464		EF680508		-					Malaysia, Borneo, Sabah, Danum Valley
<i>Hemigalus derbyanus</i>	HdTC286		MNHN TC-286		KP986474	KP986465		KP986480		-					Indonesia, Siberut Is., Mentawai Is., N Muarasiberut
<i>Hemigalus derbyanus</i>	HdTC300		MNHN TC-300		KP986475	KP986466		KP986481		-					Indonesia, Borneo, W Kalimantan, Kerapa Bejali
<i>Hemigalus derbyanus</i>	HdTC411		MNHN TC-411		KP986476	KP986467		KU696429		-					Malaysia (Negara Zoo, Kuala Lumpur)
<i>Hemigalus derbyanus</i>	HdTC756		MNHN TC-756		KU696428	-	-	-	-	-	-	-	-	-	Sumatra? (Batu Secret Zoo & Maharami Zoo, Java)
<i>Macrogalidia musschenbroekii</i>	MmJQ219116		RMNH a		JQ219116	-	JQ219113		-		-				Indonesia, Sulawesi, Manado-Kimilo
<i>Macrogalidia musschenbroekii</i>	MmJQ219114		RMNH 32244		-	-	JQ219114		-		-				Indonesia, Sulawesi, Amurang
<i>Macrogalidia musschenbroekii</i>	MmJQ219115		RMNH 32243		-	-	JQ219115		-		-				Indonesia, Sulawesi, Amurang
<i>Macrogalidia musschenbroekii</i>	MmM1868		MNHN 1868-1327		KP986477	-	KP986487		-		-				Indonesia, Sulawesi
<i>Paguma larvata</i>	PIAB303959		"SE4"		AB303959	-	-		-		-				Thailand
<i>Paguma larvata</i>	PIAY525040		-		-	-	-		-		AY525040				China, Yunnan Province
<i>Paguma larvata</i>	PIC72		MNHN C-72		-	-	DQ683990		-		-				ND
<i>Paguma larvata</i>	PIL92		MNHN L-92		-	-	-		KP986483		-				China, Guangxi
<i>Paradoxurus philippinensis</i>	PhF3167		FMNH LRH 3167		AY170113	FJ881543	AY170056		EF680510		AY170086				Philippines, Leyte Island
<i>Genetta servalina</i>	Gs		ISEM T-4620		AF511053	-	AY170058		EF680507		AY170088				Gabon
<i>Viverricula indica</i>	Vi		MNHN TC-25		-	-	-		-		DQ267568				Madagascar
<i>Viverricula indica</i>	Vi		MNHN TC-177		AY241890	-	-		-		-				Taiwan
<i>Viverricula indica</i>	Vi		MNHN TC-256		-	-	DQ683991		-		-				Thailand
<i>Viverra tangalunga</i>	Vt		FMNH LRH 4121		AY170112	-	AY170055		-		AY170085				Philippines
<i>Viverra tangalunga</i>	Vt		MNHN TC-534		-	-	-		EF680512		-				Malaysia
<i>Panthera leo</i>	Pleo		-		AF053052	-	AY170043		AY634374		AY170073				ND
<i>Urva auropunctata</i>	Ua		"Nellis"		AY170108	-	AY170051		-		AY170081				Caribbean islands
<i>Urva auropunctata</i>	Ua		MNHN TC-340		-	-	-		FJ391194		-				Croatia, Korcula Island
<i>Urva javanica</i>	Uj		MNHN TC-258		KP986478	-	FJ391234		KP986484		-				Thailand

We used DnaSP v. 5.10 (Librado & Rosas 2009) to define haplotypes and to compute genetic diversity (haplotype and nucleotide diversity), and NETWORK v. 4.6 (www.fluxus-engineering.com) to construct haplotype median-joining networks (Bandelt *et al.* 1999).

We computed genetic distances (within and between groups) and genetic diversity (haplotype and nucleotide diversity) using MEGA6 and DnaSP v. 5.10.

Results

All new sequences were deposited in GenBank (accession numbers: KP986463 to KP986487 and KU696424 to KU696429; Table 1). Due to the degraded nature of DNA retrieved from samples taken from museum specimens and poorly preserved tissue, only partial sequences could be obtained from some samples and nuclear sequences were not retrieved from museum specimens. For the *Diplogale hosei* Cytb sequence from GenBank (JQ219112; Wilting & Fickel 2012), we replaced the nucleotides in position 327 to 344 by ‘N’, as we strongly suspected that these nucleotides were those of the primer sequence (their primer CytBViv0323f), based on a comparison within the alignment.

The Cytb and ND2 fragments that we obtained from a *D. hosei* specimen (FMNH 88298) differed by 0.5% and 1.5% to the two individuals sequenced by Wilting & Fickel (2012). The Cytb sequence of a specimen of *Cynogale bennettii* (MNHN 1962-170) did not differ from the sequence of the individual sequenced by Patou *et al.* (2008), while the ND2 sequence differed by 0.7%. The Cytb fragment of a *Macrogalidia musschenbroekii* specimen (MNHN 1868-1327) did not differ from the three sequences obtained by Wilting & Fickel (2012), while its ND2 sequence differed by 0.0–0.6%. Any differences we found may reflect sequencing errors, which can happen with ancient DNA, or were due to individual variations (and these differences were not higher than the intraspecific variations observed within other species of Viverridae).

All gene fragments were analysed both individually and combined, with the different phylogenetic methods. The phylogenetic analyses of the dataset combining Cytb, ND2, FGB, and IRBP (length of the alignment, number of variable positions and number of parsimony-informative sites: 3342/1226/801, $n = 15$, including 6 outgroups) confirmed the monophyly of the Hemigalinae and Paradoxurinae (Fig. 2). Within the Hemigalinae, *Hemigalus* and *Chrotogale* are sister species (with a Bayesian posterior probability (bpp) of 0.91; ML bootstrap = 96%), and *Diplogale* is sister to these two species in the BI tree (bpp = 1; Fig. 2), as well as in the MP tree (MP bootstrap > 50%), while in the ML tree, the position of *Diplogale* within this subfamily was unresolved (Fig. 2). *Macrogalidia* clusters within the Hemigalinae in all analyses (bpp = 1; ML bootstrap = 99%; Fig. 2); it is sister to *Cynogale* in the BI tree (bpp = 0.90), but its position (and that of *Cynogale*) within this subfamily were unresolved in the ML and MP trees.

For the complete Cytb (1140 bp, $n = 46$), the distances between the two subfamilies (as previously defined) for Hemigalinae (without *Macrogalidia*) and Paradoxurinae (including *Macrogalidia*) ranged from 12.5% to 17.6%. The average Cytb distance between the two clades obtained in our study, Hemigalinae including *Macrogalidia* and Paradoxurinae without *Macrogalidia*, was 15.9%, and the mean within group distances were 7.2% and 12.3%, respectively. The distances between *Macrogalidia* and the species of Hemigalinae ranged from 12.0% to 14.9%, and to the species of Paradoxurinae from 14.4% to 15.9%. The mean distances between the remaining four species of the Hemigalinae clade ranged from 11.9% to 16.7%; the most distant species to the other three was *Cynogale*, and the smallest mean distance was between *Hemigalus* and *Chrotogale*.

We analysed a fragment of Cytb (895 bp, positions 123–1015 in complete Cytb alignment) for *H. derbyanus* and *C. owstoni* in order to search for geographical structure within these two species (895 / 241 / 142; $n = 39$; model GTR + I + G; Fig. 3). *H. derbyanus* was structured into two main clades:

one containing an individual from Siberut Island (Mentawai Islands) and a second clade that comprised all other individuals (Fig. 3). The overall mean distance within *H. derbyanus* was 1.6%; the mean distances of the Siberut Island individual to those from Sumatra and Borneo were 4.7% and 5.5%, respectively, whereas it ranged from 1.0% to 1.3% between Sumatra, Borneo and Peninsular Malaysia. *C. owstoni* formed one group from northern Vietnam (although its monophyly was poorly supported or not retrieved in some analyses), that is sister group to another from central Vietnam, whereas the individual from China was distant to these two (Fig. 3). The overall mean distance within *C. owstoni* was 1.1%; the mean distance between the two Vietnam groups was 1.4%, while the Chinese individual was separated from the latter groups by a mean distance of 2.1% to 3.4%.

A fragment of CR was obtained for a few individuals of *H. derbyanus* (592 / 18 / 0, $n = 6$) and provided a similar phylogenetic structure (not shown) as Cytb, with the same two main clades; the mean distance between the Siberut Island individual and the others was 4.7%. We obtained four CR haplotypes (195 bp excluding missing data; haplotype diversity, Hd: 0.8; nucleotide diversity, Pi: 0.01880; average number of nucleotide differences, k: 3.667), with the Siberut Island individual separated by eight to ten mutations to any other haplotype.

We also used a Cytb fragment (834 bp, positions 129–962 in Cytb alignment) to compute haplotype networks for *H. derbyanus* and *C. owstoni*. For *H. derbyanus*, we obtained eight haplotypes (Hd: 0.972; Pi: 0.01952; k: 16.278; $n=9$; Fig. 4), with the Siberut Island haplotype (H6) separated by 39 mutations from the other individuals. One Sumatra individual (H1) was separated from a haplogroup of Borneo and zoo individuals. For *C. owstoni*, we obtained 19 haplotypes (Hd: 0.9692; Pi: 0.00886; k: 7.345;

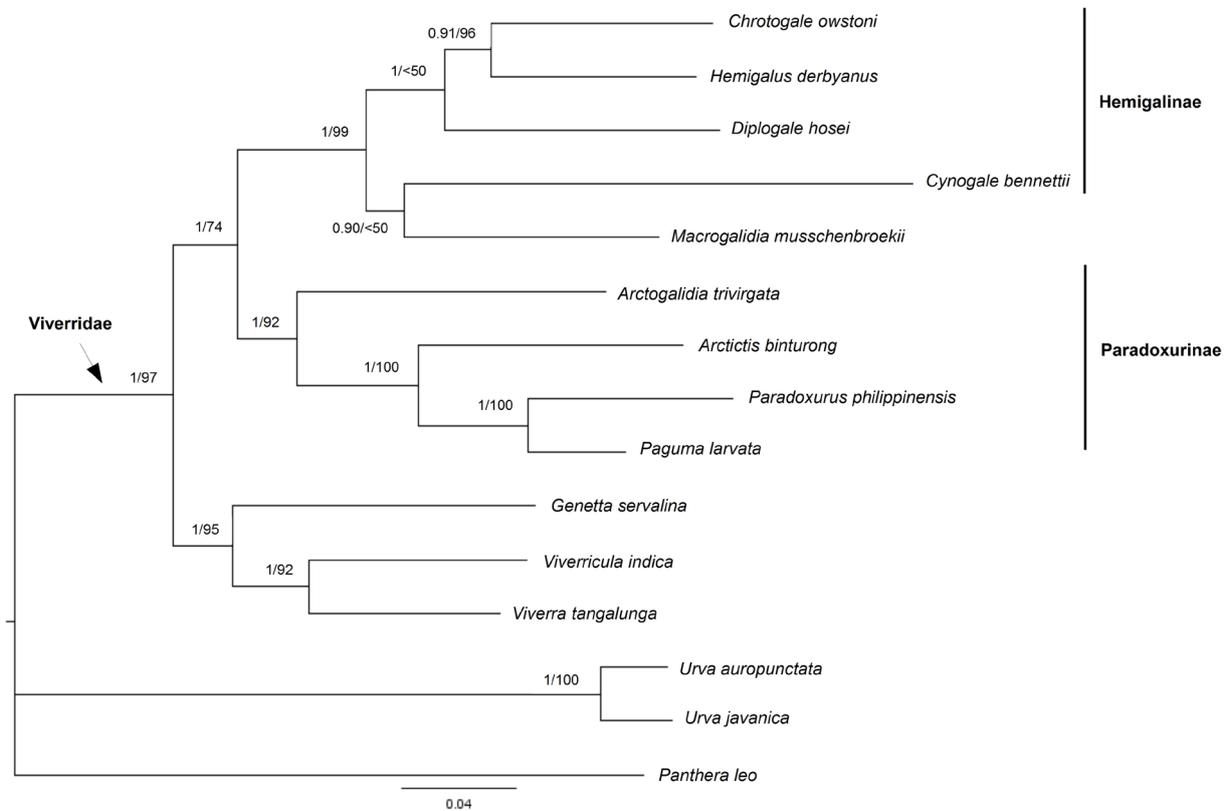


Fig. 2. Bayesian tree reconstructed from a combined dataset of Cytb + ND2 + FGB + IRBP (3342 bp). The values on the branches are bayesian posterior probabilities for the partitioned analysis (see text for models) and bootstrap proportions obtained from ML analysis (model: GTR + I + G).

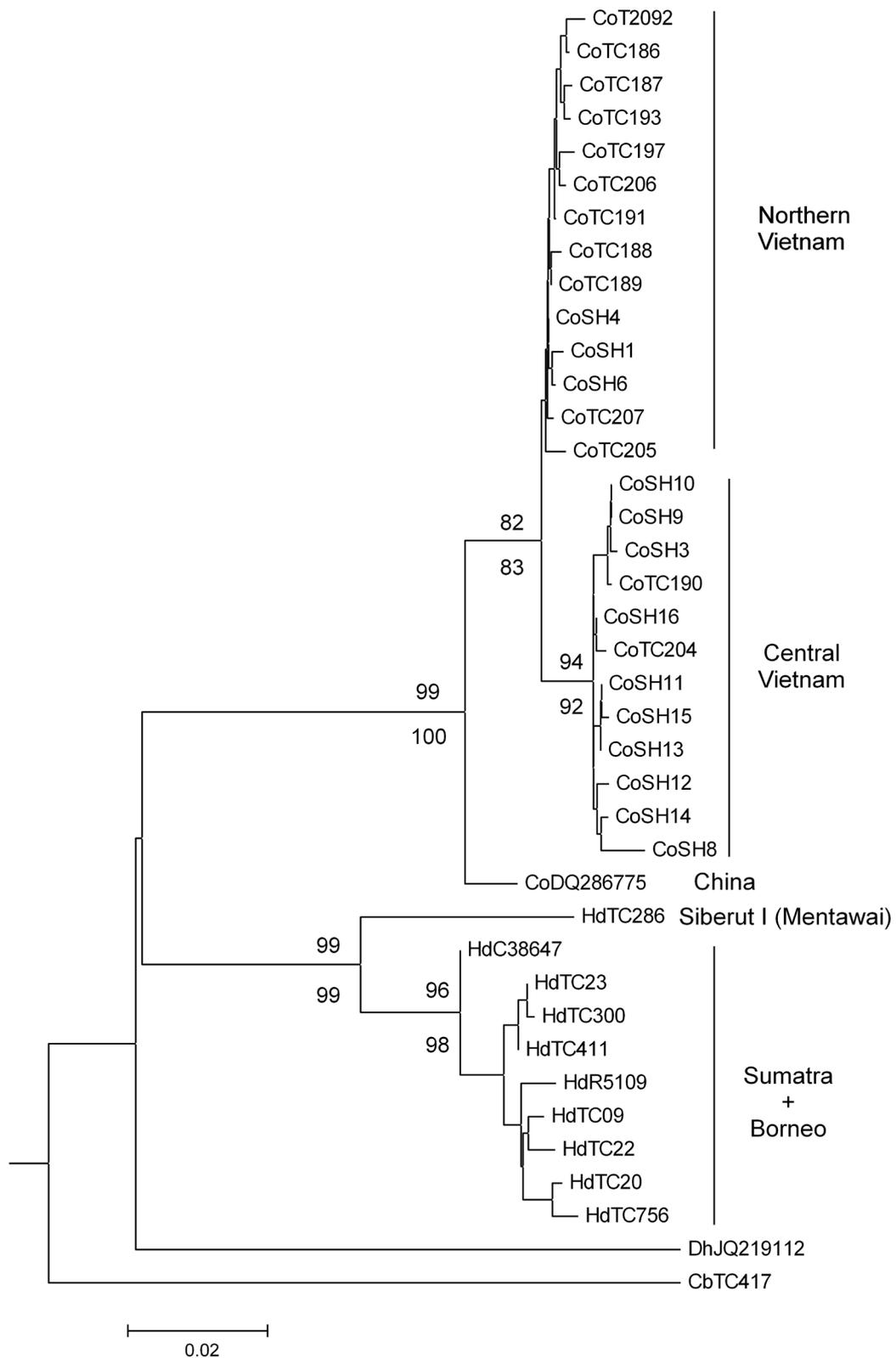


Fig. 3. Phylogenetic tree obtained with NJ for a fragment of Cytb (893 bp). The values over the branches are the bootstrap proportions for NJ, and below the branches are those for ML. Co = *Chrotogale owstoni* Thomas, 1912; Hd = *Hemigalus derbyanus* (Gray, 1837); Dh = *Diplogale hosei* (Thomas, 1892); Cb = *Cynogale bennettii* Gray, 1837.

n = 26; Fig. 5), forming two groups for northern and southern Vietnam, separated by eight mutations (the Chinese individual could not be used in this analysis due to missing data).

We also computed haplotypes using smaller Cytb fragments in order to include additional individuals of various origins. For *H. derbyanus*, using a 253 bp fragment in the 3' region (positions 768–1020 in the Cytb alignment), we obtained six haplotypes (Hd: 0.8030; Pi: 0.01509; k: 3.818; n = 12; Figure 4), organized in a star-like structure, with a central haplotype (H5) from Borneo (and also zoo individuals); the Siberut Island (Mentawai) individual (H6) was separated by 13 mutations from the two Sumatra haplotypes (H2 and H4), which were separated from the Borneo haplotype (H5) by two mutations; the individual from Peninsula Malaysia (H3) was separated by one mutation from the Borneo haplotype; another haplotype (H1) comprising individuals from Borneo and Sumatra was three mutations distant from the Borneo haplotype (H5). For *C. owstoni*, using another 253 bp fragment in the 5' region (positions 123–375 in Cytb alignment), we obtained six haplotypes (Hd: 0.7000; Pi: 0.00901; k: 2.280; n = 25; Fig. 5); northern Vietnam individuals formed a haplogroup of three haplotypes (H2, H5, H6), while central Vietnam individuals formed a haplogroup of two haplotypes (H3, H4); the Chinese individual (H1) was separated from these groups by a minimum of five and eight mutations, respectively; the northern and central Vietnam groups were separated by a minimum of three mutations.

We also computed haplotypes for the *H. derbyanus* FGB dataset (321bp), and we obtained three haplotypes (Hd: 0.6000; Pi: 0.00415; k: 1.333; n = 6); the Siberut Island (Mentawai Islands) individual was separated by three and four mutations from the other two haplotypes (not shown).

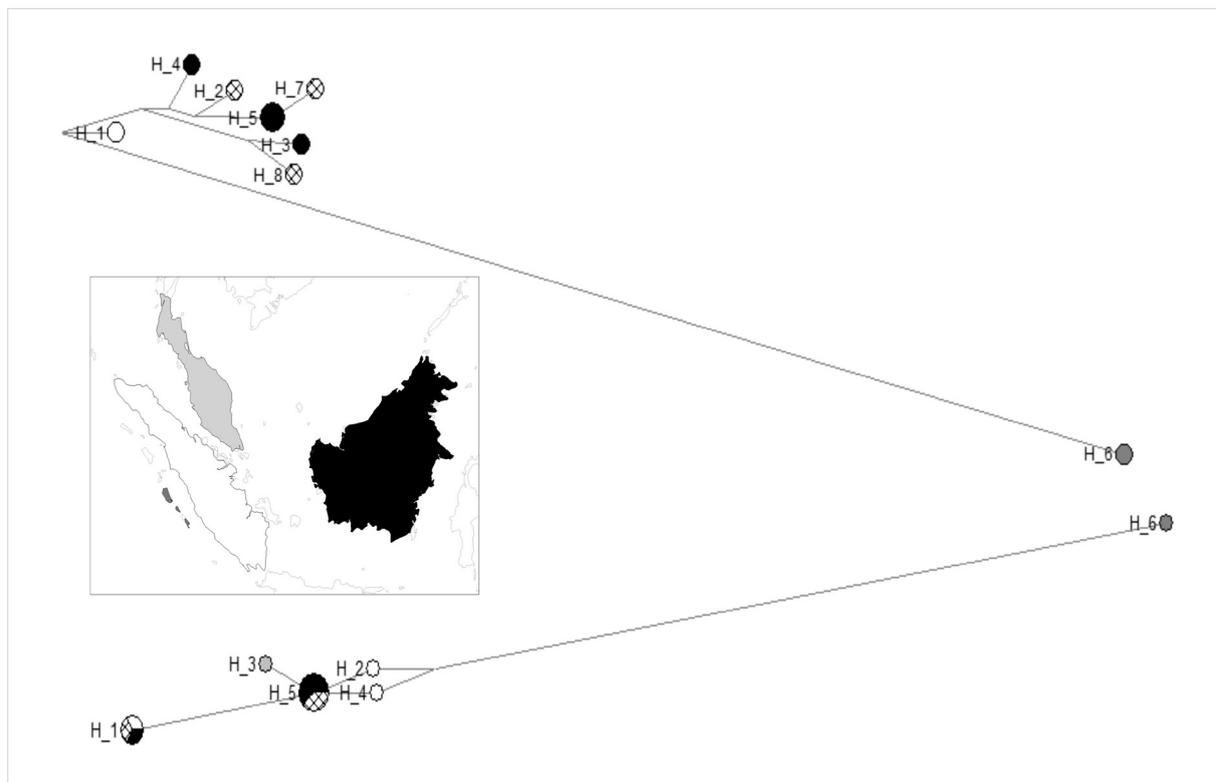


Fig. 4. Median-joining haplotype network for *Hemigalus derbyanus* (Gray, 1837) Cytb haplotypes (top: 837 bp, bottom: 253bp). The size of each circle is proportional to the haplotype frequency. The colours of the haplotypes correspond to those on the map: black = Borneo; dark grey = Siberut Island (Mentawai Islands); light grey = Penang Island (Peninsular Malaysia); white = Sumatra; hatched = Zoo samples (on top network: Singapore Zoo (H2), Negara Zoo, Kuala Lumpur (H7) and Batu Secret Zoo & Maharani Zoo, Java (H8)).

Our results suggest that the *H. derbyanus* individuals from the Singapore Zoo (HdTC09), the Negara Zoo in Kuala Lumpur (TC-411), and the Batu Secret Zoo & Maharani Zoo in Java (TC-756) all come from Borneo, despite the fact that the latter individual was supposed to come from Sumatra. The individual from the Cincinnati Zoo (TC-20) was supposed to come from Borneo and our results agree with this.

Discussion

While Wilting & Fickel (2012) did not obtain a resolution for the banded, Hose and Owston's civets relationships, our study found that the banded and Owston's civets are sister species, and also suggested that Hose's civet might be the sister species to these two.

Similar to Wilting & Fickel (2012), the Sulawesi palm civet was found within the Hemigalinae. It either clustered with the otter civet (although this was weakly supported) or its position was unresolved. These two species had missing data (nuclear genes) and long branches (in particular the otter civet), which could have affected their phylogenetic position; long branch attraction is a commonly recognized artefact in phylogenetic reconstruction that can produce misleading (but sometimes strongly supported) relationships (Felsenstein 1978; Simmons 2012). Also, the use of only mitochondrial data can lead to misleading relationships at ordinal and also lower taxonomic levels (e.g., for carnivores, Sato *et al.* 2003). For example, prior to the addition of nuclear data, the small-toothed palm civet *Arctogalidia trivirgata* was not retrieved within the Paradoxurinae (Patou *et al.* 2008). Morphological features support the inclusion of the Sulawesi palm civet in the Paradoxurinae (Gaubert *et al.* 2005), which either invalidates

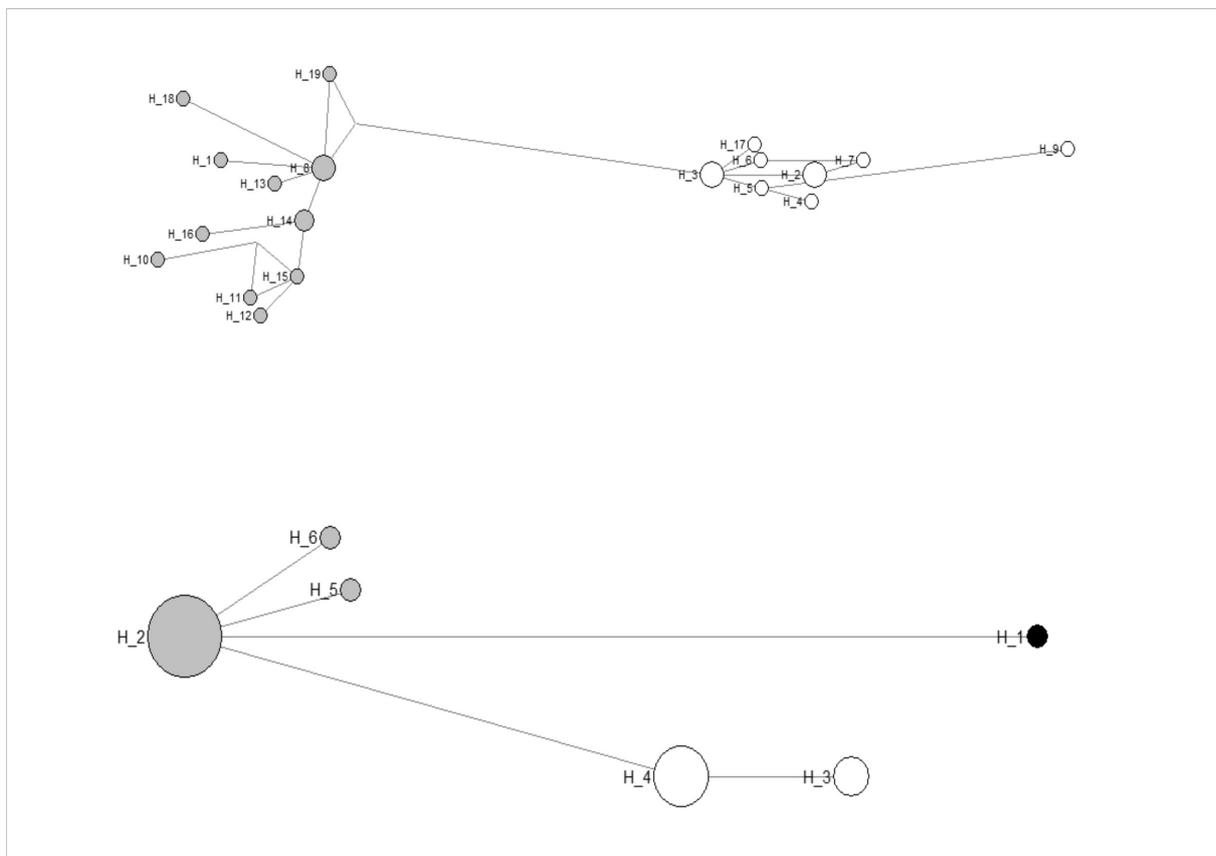


Fig. 5. Median-joining haplotype network for *Chrotogale owstoni* Thomas, 1912 Cytb haplotypes (top: 837 bp, bottom: 235 bp). The size of each circle is proportional to the haplotype frequency. White = central Vietnam clade; grey = northern Vietnam clade, black = China.

the molecular results, or indicates homoplasy in the morphological features. Further genetic studies, with additional samples and data (nuclear genes) are needed to clarify further the phylogenetic position of the Sulawesi palm civet. We advocate that further studies be conducted before moving *Macrogalidia* to the Hemigalinae. The Sulawesi palm civet is a threatened species endemic to Sulawesi (Jennings & Veron 2009; IUCN 2015), and is the only native carnivore found east of Wallace's Line (Veron 2001). Hall (2001) found evidence of a land bridge west of Sulawesi ca 20 million years ago (Mya), and suggested faunal exchanges between Sulawesi and the rest of Southeast Asia occurred ca 10 Mya. More recently, it has been suggested that colonisations of Sulawesi started during the early Miocene, and that speciation events happened as early as 20 Mya (Stelbrink *et al.* 2012). Patou *et al.* (2008) proposed that the Hemigalinae diverged 15.4–8.4 Mya, which corresponds to the dates of origin of several Sulawesi taxa (Stelbrink *et al.* 2012). These findings suggest that the Sulawesi palm civet diverged from the other species more than 10 Mya, which is supported by its high Cytb divergence (12.0–14.9%) from its relatives. This ancient speciation explains why the analysis of only mitochondrial sequences has not fully resolved its phylogenetic relationships.

The northern distribution limit of the banded civet is close to the Isthmus of Kra, along the Thai-Malay Peninsula (Jennings *et al.* 2013), which is a transitional region between the Indochinese and Sundaic faunas (Woodruff & Turner 2009; Meijaard 2009). The range of Owston's civet is restricted to southern China, Laos, and Vietnam (Jennings & Veron 2009). Eustatic and climatic events in this region may have caused the speciation of these two civet species (with subsequent range restrictions due to habitat changes that occurred during the Plio-Pleistocene and more recently to human-induced modifications). Hose's civet is found only on Borneo, where it is sympatric with the banded civet (although there is a tendency for these two species to separate spatially along an elevation gradient; Jennings *et al.* 2013). However, we do not know if Hose's civet might have had a wider distribution in the past and was then restricted to forest refugia in the mountains of Borneo during Plio-Pleistocene climatic variations, or if it speciated on Borneo from an ancestor of *Hemigalus* + *Chrotogale*. The otter civet is a specialised viverrid that is adapted to aquatic life (with webbed feet, and nostrils and ears that can be closed by flaps) that ranges across the Sundaic region (Veron *et al.* 2006), and it could have diverged first within the subfamily.

We found a strong geographical genetic structure in the banded and Owston's civets. Within the banded civet, the individual from Siberut Island (Mentawai Islands) was very distant from the populations from both Sumatra and Borneo (for both Cytb and FGB), and according to our haplotype networks it is closer to Sumatra individuals. In contrast, the Mentawai population of the common palm civet (*Paradoxurus* sp.) was found to be closer to those from Borneo and the Philippines (*Paradoxurus philippinensis*) than to the nearby Sumatran populations (*Paradoxurus musangus*) (Patou *et al.* 2010; Veron *et al.* 2015c). Although the four Mentawai Islands (Siberut, Sipora, North and South Pagai) are close to Sumatra, they are separated by a deep sea channel, the Mentawai Strait, which has isolated populations and explains the high level of species endemism on these islands (Wilting *et al.* 2012). Their strong divergence from Sumatran populations might also be explained by local extinctions during the Pleistocene (Patou *et al.* 2010; Wilting *et al.* 2012) and the Mentawai Islands might have served as a forest refuge during glaciations. The divergence time of Mentawai taxa has been estimated from 1.1 to 3.5 Mya in mammals (Patou *et al.* 2010; Wilting *et al.* 2012). The Mentawai Islands have been separated from Sumatra at least since the Mid-Pleistocene and might have remained separated despite the sea level fluctuations of the Late Pleistocene (Voris 2000; Wilting *et al.* 2012). The Cytb distance of the Siberut Island individual to other banded civet populations ranged from 4.7 to 5.5%, which is close to the divergence found between other small carnivore species (Veron *et al.* 2007, 2015a, 2015c); our nuclear data also confirmed this strong divergence. Two subspecies have been described from the Mentawai Islands: *Hemigalus derbyanus minor* Miller, 1903 (South Pagai Island) and *H. d. sipora* Chasen & Kloss, 1927 (Sipora Island). Very little is known about the population from Siberut Island, which has not been attributed to

any subspecies (Jennings *et al.* 2013). The four Mentawai Islands were likely connected during periods of lower sea levels (Sathiamurthy & Voris 2006), and there does not seem to be any endemism on each island, as several species occur on all or several of the four islands (Sargis *et al.* 2014). It is therefore likely that banded civets from the islands of Siberut, Sipora and South Pagai belong to the same taxon, which would be *Hemigalus derbyanus minor*.

Banded civet individuals from Sumatra were not strongly divergent from those from Borneo, whereas a strong divergence between Sumatran and Borneo populations has been found in other forest species (Veron *et al.* 2015a). Borneo has been isolated from Sumatra for ca 20 000 years, at the end of the Last Glacial Maximum, and even when land connections existed between Borneo and the rest of the Sundaic region, open habitat might have restricted the movements of some forest animals (Meijaard 2003; Bird *et al.* 2005; Cannon *et al.* 2009). Our results suggest that there have been independent connections between Borneo and Sumatran populations, and between Borneo and Peninsular Malaysian populations (in this study represented by an individual from Penang Island, which is very close and connected to the NW coast of Peninsular Malaysia). Although Peninsular Malaysia and Sumatra have been connected frequently during glacial periods, the banded civet individuals from these two areas did not form a monophyletic group in our analyses, whereas a close relationship and low differentiation of populations from Sumatra and Peninsular Malaysia have been found in many other mammals, such as rodents, macaques, palm civets and mongooses (Gorog *et al.* 2004; Ziegler *et al.* 2007; Patou *et al.* 2010; Veron *et al.* 2015a). Possible explanations for these findings would be independent dispersals during periods of lower sea levels (e.g., Last Glacial Maximum), or that banded civets were transported from one area to another, as has been suggested for some other civet species (Veron *et al.* 2014, 2015c), although there is no evidence that this has ever occurred for the banded civet. With regards to the structure obtained and the low divergences observed, we would suggest that the populations from Sumatra, Peninsular Malaysia and Borneo are placed in the same subspecies *Hemigalus derbyanus derbyanus* (Gray, 1837).

Within Owston's civet, we obtained two main groups in Vietnam, which confirms the finding of Veron *et al.* (2004), and we found a third group from China, quite distant from the northern Vietnam group. This might have resulted from either geographic barriers or Pleistocene climatic fluctuations (as suggested for bats, see Tu *et al.* 2017) that shaped the population structure of this species. However, only one sequence was available for China (and it came from GenBank so we cannot confirm its validity), and thus, additional data would be needed to confirm this finding. These three groups could have been maintained due to limited exchanges between isolated populations as a result of habitat destruction (see IUCN 2015). To assess whether these populations should be considered subspecies would require further investigations, as the origin of several individuals was uncertain and samples from Laos were missing in our dataset. This is a very poorly known, endangered civet species that is severely threatened by forest loss, hunting and the wildlife trade (Willcox *et al.* 2011; Coudrat *et al.* 2014).

Further studies are needed on the intraspecific diversity and genetic structure of the Hemigalinae civets, and for the designation of conservation units, in particular, for island endemic species and subspecies. Unfortunately, due to their elusive nature, these civet species have rarely been studied in the wild and are very rarely trapped, so obtaining fresh samples is extremely difficult. Finally, ecological studies are urgently needed in order to better understand and assess the conservation status of these threatened species.

Acknowledgements

We thank the following people and institutions for their contribution to this study: F. Catzeffis (Institut des Sciences de L'Evolution, Université de Montpellier), C.P. Colon (Fordham University), R. Debryne (UMS CNRS 2700, MNHN, Paris), A. Erman & E. Meijaard (People & Nature Consulting International), M.F. Gorra (Carnivore Preservation Trust), L. Grassman (Texas A&M University

– Kingsville), L.L. Lee (Taiwan University), B. Long (World Wildlife Fund), P. Martelli (Singapore Zoological Gardens), J. Patton (Museum of Vertebrate Zoology, Berkeley, CA), M.L. Patou (Biotope), S. Robertson (FFI, Owston’s Palm Civet Conservation Program), T.L. Roth (Cincinnati Zoo), S. Vellayan (Zoo Negara, Kuala Lumpur), Siew Te Wong (Borneo Sun Bear Conservation Center), Servion Zoo, D. Boussarie, and S. Heard. We thank the following curators and museums for access to specimens and samples: N. Duncan, E. Westwig, E. Hoeger (American Museum of Natural History, New York), L.R. Heaney, J.D. Phelps, the late W.T. Stanley (Field Museum of Natural History, Chicago), M. Omura, B. Zimkus, J. Chupasko (Harvard Museum of Comparative Zoology, Cambridge, MA), S. van der Mije, P. Kamminga (Naturalis, Leiden, the Netherlands) and K.K.P. Lim (Raffles Museum of Biodiversity Research, Singapore). Thanks are due to the Forest Protection Department of Vietnam’s Ministry of Agriculture & Rural Development for their permission to export samples. We thank the EPU and PERHILITAN for permission to conduct research in Malaysia, and S. Ellagupillay (PERHILITAN) and Z. Akbar (University Kebangsaan Malaysia) for their support; funding for the Malaysian Carnivore Project is acknowledged at www.smallcarnivores.org. Molecular work was undertaken at the ‘Service de Systématique Moléculaire’ (UMS CNRS 2700, MNHN, Paris), and we thank the staff of the lab for their help. The sequencing was supported by the network “Bibliothèque du Vivant” funded by CNRS, MNHN, INRA and CEA (Genoscope, www.genoscope.fr). G.V. received financial support from MNHN, CNRS, and from the “Action Transversale du Muséum, Biodiversité actuelle et fossile” (MNHN, French Ministry of Research). We thank the Associate Editor and anonymous reviewers for their useful suggestions on an earlier version of this paper.

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Manuscript received: 16 February 2016

Manuscript accepted: 5 September 2016

Published on: 23 February 2017

Guest editors: Line Le Gall, Frédéric Delsuc, Stéphane Hourdez, Guillaume Lecointre and Jean-Yves Rasplus

Desk editor: Danny Eibye-Jacobsen

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