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Genetic diversity and structure of the binturong *Arctictis binturong* (Carnivora: Viverridae) – status of the elusive Palawan binturong and implications for conservation

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Abstract

The binturong is a forest mesocarnivore ranging from Nepal to Indonesia and the Philippines. Several subspecies of binturongs are recognized but a revision is needed. The binturong from Palawan was described as a species and is now considered a subspecies, but its status has never been checked using molecular approaches. Owing to its restricted range and the pressure on its habitat, the Palawan binturong may be endangered, and so it is crucial to clarify its taxonomic status. Such information is important for the management of captive populations. We sequenced one nuclear and two mitochondrial markers for binturongs from locations over the species range, and from zoos. Our results provided an assessment of the

genetic polymorphism and structure within the binturong, resulting in two groups, corresponding to the Indochinese and the Sundaic regions. Within the latter were found the Palawan binturongs on one side, and an individual from Sulu archipelago (a locality not reported before) on the other side. The Palawan binturongs formed a monophyletic group, genetically very close to Bornean binturongs, which suggests that they may have dispersed from Borneo, and may represent a lineage to preserve, but which is not a separate species nor a separate subspecies.

Keywords: Asia – Carnivora - mitochondrial – phylogeography - taxonomy

Introduction

Although carnivoran mammals seem well studied and include many flagship species, most small carnivoran species receive very little attention and so their systematics, distribution and conservation status remain poorly known. This is the case for the binturong (*Arctictis binturong* Raffles, 1921), a Southeast Asian carnivoran belonging to the Family Viverridae. This is one of the largest members of the family, weighing 6 to 20 kg, and with a body length reaching over 90 cm, and a long tail of similar length; it is one of the only two carnivoran species with a prehensile tail (Jennings & Veron 2009). The binturong is a forest species, strongly arboreal, feeding on invertebrates, small vertebrates, and fruits; it may be predominantly frugivorous and feeds largely on various species of figs (Jennings & Veron 2009; Nakabayashi *et al.* 2016, 2017; Nakabayashi & Ahmad 2018), and seems to contribute to seed dispersal (Colon & Campos-Arceiz 2013). The binturong is classified as Vulnerable by the IUCN; the main threats it faces are destruction and degradation of primary rainforest, hunting for meat, use in traditional medicines and as pets, as well as accidental or intentional snaring, which are exacerbated by negligible penalties for hunting and trade in some countries (The IUCN Red List of Threatened Species 2016; Sanggin *et al.* 2016; Gray *et al.* 2017). In addition, like the common palm civets (*Paradoxurus* spp.), binturongs are live trapped and kept in farms for the production of civet coffee (Kopi Luwak) in Indonesia, with poor housing conditions, resulting in high mortality (D’Cruze *et al.* 2014).

The distribution of the binturong ranges from Nepal to Indonesia and the Philippines; it is known to occur in the following countries: Bangladesh, Bhutan, Brunei, Cambodia, South China, West India, Indonesia (Java, Kalimantan, Sumatra), Laos, Malaysia (Peninsular Malaysia, Sarawak, Sabah), Myanmar, Nepal, Philippines (Palawan Island), Thailand and Vietnam.

Several subspecies of binturongs are recognized, but a taxonomic revision is needed (Jennings & Veron 2009). Pocock (1933) recognized four subspecies: *A. b. albifrons* (F. Cuvier, 1822) from Nepal to northern Indochinese region, *A. b. binturong* (Raffles, 1822) in the Malay-Thai peninsula and Sumatra, *A. b. penicillatus* (Temminck, 1835), on Java and Borneo, and *A. b. whitei* (Allen, 1910) on Palawan. No recent systematic revision has been done, but a study based on Control Region sequences suggested the presence of a main divergence between the Indochinese and Sundaic regions (Cosson *et al.* 2007). However, populations from several parts of the range were missing in this former study, in particular, binturongs from the Philippines.

In the Philippines, the binturong is said to occur only on the island of Palawan (Corbet & Hill, 1992; Wozencraft 1993; Jennings & Veron 2009). However, we discovered that it also occurs (or occurred) in the archipelago of Sulu, where Hombron and Jacquinot collected one specimen during the expedition on the French ship *Astrolabe* in 1837-1840 (specimen MNHN-ZM-MO 1962-328; Oustalet 1901; GV pers. obs.). To our knowledge, this is the only specimen from the Sulu Islands, and the presence of the binturong in the Philippine Islands other than Palawan has been overlooked so far. Its presence in the Sulu Islands was not mentioned by Musser & Heaney (1985) who provided a list of mammals occurring in the archipelago (while they mentioned the presence of another viverrid, the common palm civet).

The Palawan binturong *Arctictis whitei* Allen, 1910 was described on the basis of a female specimen collected in 1909 together with three other specimens by J. R. White, after whom it was named. Allen (1910) mentioned some differences in the morphology of the teeth and pelage colour of the head, when compared to specimens from Sumatra and India. Unfortunately, this author apparently did not compare the Palawan binturong to Borneo specimens, to which it is geographically closer. The Palawan binturong is considered a separate species by Taylor (1934) and Goodwin (1953). Pocock (1933) did not find much morphological evidence for distinguishing the Palawan binturong from Borneo and Java

specimens, and he recognized it as a subspecies, close to *A. b. penicillatus* (Borneo and Java). Already earlier, Oustalet (1901), reviewing the specimens from various origins, suggested that there was only one species of binturong, and that the coloration may vary with age. Corbet & Hill (1992) listed the name of the Palawan taxa without mentioning if they recognized the subspecies as valid. The subspecies is listed by Wozencraft (2005).

The Palawan binturong has a very small distribution and thus may be of conservation concern. Owing to its dependence on forest, it is threatened by deforestation, which is important in Palawan (11% of forest has been lost between 2000 and 2017, www.globalforestwatch.org). Moreover, Palawan is a hotspot of illegal wildlife trade and Palawan binturongs have been seized regularly (Cruz *et al.* 2007).

The binturong is part of a European Endangered Species Program (EEP), in which 193 zoological parks participate. The number of binturongs included in the program in 2018 was 148 individuals, but only 23.2% of the individuals have a known pedigree (AB pers. info.). One of the concerns of the captive breeding program is to maintain the main lineages (see Cosson *et al.* 2007) and in particular, that of the Palawan binturong. Recently, binturongs from Ailon Zoo (formerly known as Ailon Montalban Zoological Park), in the Philippines, were brought to several zoos in Europe to contribute to the captive breeding of this population.

The main purpose of this study was to investigate the systematic status of the Palawan binturong, which has sometimes been recognized as a species (Allen 1910; Taylor 1934; Goodwin 1953). This investigation has been recognized as a priority by the IUCN/SSC Small Carnivores Specialist Group (Schreiber *et al.* 1989). For this purpose, we sequenced one nuclear and two mitochondrial markers for binturong individuals from various locations over the species range, in order to investigate the genetic diversity and structure of the species. The paucity of fresh samples required us to use museum specimens including one specimen of the type series of *A. b. whitei* (AMNH 29741), collected by White in 1909. We also included the only known specimen from Sulu archipelago in the Philippines (MNHN-ZM-MO 1962-328), collected between 1837 and 1840. We included zoo individuals, among which some were said to be Palawan binturongs. Our aim is to help to clarify the taxonomic status of the binturongs from the Philippines, both from Palawan and the Sulu archipelago, but we also investigated

the structure of the populations within the rest of the range. Such studies are crucial for setting conservation priorities and for helping captive breeding programs.

Material and methods

Sampling, extraction, PCR and sequencing

We analyzed 73 samples (tissues and hair samples, and dry tissues from museum specimens) of *Arctictis binturong* (Table 1, Figure 1). DNA was isolated following a cetyl trimethyl ammonium bromide (CTAB)-based protocol (Winnepenninckx *et al.* 1993). For museum samples, dithiothreitol (DTT 1M, ca 8-15 μ L per extract) was added during tissue lysis to break up disulfide bonds, and lysis time was increased (up to 72 hours).

We sequenced two mitochondrial fragments: Cytochrome b (Cytb), and the hypervariable region 1 of the Control Region (CR), using previously described primers (Cytb: Veron and Heard 2000; Veron *et al.* 2004, 2014; CR: Palomares *et al.* 2002; Cosson *et al.* 2007). To provide an evolutionary assessment independent from mitochondrial markers, we amplified the nuclear marker Beta-fibrinogen intron 7 (FGB), using primers from Yu & Zhang (2005).

Polymerase chain reactions (PCRs) were performed as in Veron *et al.* (2014), with annealing temperatures of 50°C for Cytb, 61°C for CR, and 59°C for FGB. PCR products were sent to Eurofins Genomics (Ebersberg, Germany) for purification and sequencing (on Applied Biosystem® 3730XL DNA Analyzer). Sequences were edited and aligned manually using Bioedit (version 7; Hall 1999).

Phylogenetic and haplotypic network analyses

Phylogenetic analyses for each marker were performed using Maximum Likelihood (ML) method, 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 representatives of two other genera of Viverridae (another species of Paradoxurinae, *Arctogalidia trivirgata* and one species of Hemigalinae, *Chrotogale owstoni*). For ML, the best-fitting model was estimated using MEGA6, following the Akaike information criterion (AIC). The selected model was implemented in the ML analyses and node robustness was assessed through 1,000

bootstrap replicates. For BI, we used Reversible Jump Markov Chain, to sample across the 201 substitution models, and gamma distribution (Lset nst = mixed rates = gamma option) to sample the posterior distribution of trees and take into account the substitution model uncertainty. We used default priors for branch lengths and ran the chains for 10,000,000 Metropolis-coupled MCMC generations, with trees sampled every 1,000 generations, and a burn-in of 25%. Two Bayesian runs were performed, and the posterior probabilities were checked to ascertain that the chains had reached stationarity.

We compared resulting topologies and node support; nodes were considered as supported when posterior probabilities were ≥ 0.95 and bootstrap values were $\geq 70\%$.

We employed DNAsp 5.10 (Librado & Rosas 2009) for defining haplotypes, and Network (v 4.6, www.fluxus-engineering.com) to construct haplotype median-joining networks (Bandelt *et al.* 1999) for each of the fragments. We computed genetic distances (p-distances within and between groups) and genetic diversity (haplotype and nucleotide diversity) using MEGA6 and DNAsp5.10.

Results

We obtained sequences from 73 individuals of *Arctictis binturong* (GenBank numbers MK680970 to MK681110; Table 1), and with previously sequenced individuals, we analyzed a total of 105 individuals, covering the range of the species in Southeast Asia (Figure 1). None of the museum samples or poorly preserved samples provided nuclear fragments.

The ML and BI analyses of Cytb (length of the Cytb fragment = 1140 bp; number of variable sites = 66; number of parsimony informative sites = 45; n = 67; Figure S 1) provided trees with one well supported clade comprising Indochinese region individuals, and two clades with Sundaic region individuals. Within one of those Sundaic clades was nested a well-supported clade grouping all the Palawan individuals.

The Cytb fragment analyzed provided an overall mean distance of 1.5% (range = 0 to 4.3%) within the species. The Cytb divergence between the Sundaic and Indochinese regions was 2.6%. Within those regions, the mean distance was 0.6% for the Sundaic region, and 0.2% within the Indochinese region. Between the Palawan and Indonesia-Malaysia

individuals, the mean distance was 0.65%, while it was 2.78% between the Palawan clade and the Indochinese region.

Between localities, the Cytb mean distances ranged from 0.09% between Vietnam and Myanmar to 1.95% between Palawan and Thailand (Table 2). The lowest mean Cytb distances of Palawan individuals were those to Indonesian and Malaysian individuals (with no precise localities) and to Bornean individuals (0.19 to 0.38%). Within localities, Cytb mean distances are provided in Table 2.

The Cytb haplotype network based on the whole sequence (length = 1140 bp; Number of haplotypes, $h = 22$; Haplotype diversity, $Hd = 0.9145$; Nucleotide diversity, $Pi = 0.01466$; Number of polymorphic sites, $S = 52$; Average number of nucleotide differences, $k = 15.398$; $n = 51$; Figure S 2) displayed two main haplogroups, separated by 21 mutations, and corresponding to the Indochinese region and Sundaic region. Within the latter is nested the Palawan haplogroup, separated by three mutations to the closest Sundaic individuals.

Another Cytb haplotype network was constructed based on a shorter fragment in order to include most museum specimens which had missing data (length = 538 bp, excluding 323-767 and 1021-1140 on complete Cytb alignment; Number of Haplotypes, $h = 18$; Haplotype diversity, $Hd = 0.8234$; Nucleotide diversity, $Pi = 0.01462$; Number of polymorphic sites, $S = 25$; Average number of nucleotide differences, $k = 7.867$; $n = 62$). The network (Figure 2) showed two main haplogroups separated by 11 mutations, one comprising individuals from the Indochinese region and the other comprising individuals from the Sundaic region. Within the latter were found the individuals from Palawan (3 haplotypes, separated by one mutation), which clustered together. The structure was not strong within the Sundaic region, but the Palawan group was close to one Bornean haplotype, to which they were separated by one mutation (Figure 2).

To account for missing data in the Sulu individual, the Cytb haplotype network was also constructed with another fragment (length = 567 bp located at 425-1020 on complete Cytb alignment; Number of Haplotypes, $h = 18$; Haplotype diversity, $Hd = 0.8656$; Nucleotide diversity, $Pi = 0.01401$; Number of polymorphic sites, $S = 29$; Average number of nucleotide differences, $k = 7.946$; $n = 59$). The results (Figure 3) were similar to those obtained with the other Cytb fragment. The Sulu individual did not cluster with the other individuals

from the Philippines (which were all from Palawan); it was close (separated by one mutation) to the same Bornean haplotype which was closest to the Palawan individuals.

The CR fragment (length = 593 bp; number of variable sites = 77; number of parsimony informative sites = 39; n = 85) showed an overall mean distance of 2.1% (range from 0 to 5.5%) across the species. Between localities, the lowest CR distances were between Myanmar and Laos individuals (0.58%), and the highest between those from Thailand and Borneo (4.04%). The lowest CR distances to Palawan individuals were those from Malaysia (with no precise localities) and Borneo (1.10% to 1.43%).

The CR haplotype network (length = 451 bp; length excluding gaps = 246 bp; Number of haplotypes, h = 30; Haplotype diversity, Hd = 0.8731; Nucleotide diversity, Pi = 0.02192; Number of polymorphic sites, S = 31; Average number of nucleotide differences, k = 5.392; n = 80) showed again two main haplogroups for the two main regions; within the Sundaic haplogroup, Palawan individuals were represented by two close haplotypes separated by two mutations (Figure 4). Within the Indochinese region, Laos was represented by three haplotypes (separated by one to two mutations), one of which was shared with Myanmar individuals, Thailand was represented by two haplotypes (separated by four mutations), and Vietnam by one haplotype.

The FGB fragment (length = 651 bp; number of variable sites = 11; number of parsimony informative sites = 5; n = 48) showed an overall mean distance of 0.2% (range from 0 to 1.2%) across the species. Between localities, the FGB distances ranged between 0 and 0.5%. The phylogenetic analyses failed to provide any well supported clades due to the low number of informative sites. Most variable sites were heterozygous.

Discussion

The results of this study provide a better overview on the genetic polymorphism and structure within the binturong. The overall diversity (e.g. Cytb: 1.5%, and pairwise distances ranging from 0 to 4.3%) tends to be similar to (e.g. within *Paradoxurus* spp., Veron et al. 2015c) or lower than (e.g. within the small-toothed palm civet *Arctogalidia trivirgata*: overall diversity: 11% for Cytb, Veron et al. 2015b) that of other Paradoxurinae species studied previously. We obtained two quite distant main haplogroups, one for the Indochinese region

and one for the Sundaic region, which correspond to a well-known biogeographical split, likely related to repeated sea-level variations and local extinctions around the Isthmus of Kra (Woodruff & Turner 2009; Meijaard 2009). A similar subdivision between these two biogeographical regions has been observed in many other mammal species (e.g. common palm civet, Patou *et al.* 2010; felids, Luo *et al.* 2014; long-tailed macaque, *Macaca fascicularis*, Abdul-Latiff *et al.* 2014; red muntjacs, *Muntiacus* spp., Martins *et al.* 2017).

Surprisingly, we found no strong structure within the Sundaic region, while a strong divergence for Bornean populations has been observed in other viverrids (e.g. small-toothed palm civet, Veron *et al.* 2015b; masked palm civet *Paguma larvata*, Patou *et al.* 2009), other carnivorans (e.g. short-tailed mongoose *Urva brachyura*, Veron *et al.* 2015a), as well as in other mammals (e.g. rodents, Gorog *et al.* 2004; colugos and mouse deers, Mason *et al.* 2019). This could be explained by a more recent dispersal of the binturong within the Sundaic region, and/or by the larger dispersal capacity of this species, which may have been capable of using forest corridors that may have been present over the Sunda Shelf during low sea levels and wet periods (Sheldon *et al.* 2015). Or this could also be explained by a lower rate of evolution of the markers in this species compared to the carnivoran species studied previously. Also, except for some museum samples with precise localities, many of the samples were from zoos, and although some clearly fall within the Sundaic region haplogroup, we cannot assess more precisely their origin. Anyway, overall, the divergences between individuals from the Sundaic region were quite low.

Our results suggested that the Palawan binturongs, including one individual from the type series of *A. b. whitei* (AMNH 29741), form a distinct haplogroup, closely related to Bornean individuals, but no haplotypes were shared with Bornean individuals, and, despite a quite low divergence to them, the Palawan binturongs form a monophyletic group. Despite our low sample size, this suggests that there may have been one colonization event, very likely from Borneo. Landscape reconstructions by Robles *et al.* (2015) suggested that the last land-bridge connection between Borneo and Palawan occurred at ca. 440 Ky (or even earlier at ca. 630Ky), which may explain the absence of shared haplotypes between Palawan and other localities. Also, our results suggest a low polymorphism within the Palawan binturongs (see Table 2), which could be an impediment to the long term survival of the population. To investigate whether this could be due to a bottleneck or a founder effect, or a consequence of

our sampling (with many individuals coming from the same wildlife rescue center in the Philippines) would require more samples. However, the museum individual collected in 1901 in Palawan (AMNH 29741), shared its haplotype with some of the recent samples from this wildlife rescue center, suggesting that the low polymorphism observed is not solely related to our sampling.

The individual from the Sulu archipelago did not group with the other Philippine individuals (which were all from Palawan), but it was closer to one Borneo haplotype, which geographically makes sense as the archipelago is closer to Borneo than to Palawan. This archipelago is thought to have comprised fewer but larger islands during the Pleistocene, almost connecting them to Borneo and Mindanao; the Sulu fauna includes species occurring in the Sundaic region (but not in the rest of the Philippines), and a few endemics (Heaney 1986). Musser & Heaney (1985) mentioned only one carnivoran present in two islands of the Sulu archipelago, the common palm civet, but not the binturong. Unfortunately, there is no information about the precise island of origin of the only binturong specimen within the archipelago. Also, we did not find any other mention of the species in this archipelago (beside Oustalet 1901, and this MNHN specimen collected in 1837-1840), and thus, we do not know in which islands of the archipelago the species may be present. Further investigation of the binturong population in this archipelago is needed. It cannot be totally excluded that the presence of the binturong in this archipelago might have resulted from introductions, as occurred frequently for other viverrid species (common palm civet, Patou *et al.* 2010; Malay civet, Veron *et al.* 2014).

Our results tend to suggest the presence of at least two subspecies, one in the Indochinese region, *A. b. albifrons*, and one in the Sundaic region, *A. b. binturong*. Whether the latter may have to be split into two or three subspecies (*A. b. binturong* in the Thai-Malay peninsula; *A. b. penicillatus*, on Borneo and Java, and *A. b. whitei* on Palawan) would require further investigations, although the low structure and low divergence for the three sequenced markers would tend to be consistent with having only one subspecies for the Sundaic region, including Palawan and Sulu. However, more individuals with a known origin would be needed to confirm whether there is any geographical structure within the Sundaic region. Further information from more variable nuclear markers would also be needed. Anyway, the

Palawan binturong is now isolated from the Bornean population; it may represent an important conservation entity, which needs attention.

Within the Indochinese region, more samples with a known geographic origin, including samples from the western part of the range of the species (the Himalaya region) would be needed to investigate further the geographic structure.

Morphologically, the pelage of the binturong is of little use to define subspecies or geographical variations, having no specific pattern or marks. The color varies from black to blackish, and with some greyish areas in particular on the head (with whitish hair tips), but no geographical pattern can be clearly identified from our observations of museum specimens, or of individuals in the wild and in captivity. No obvious diagnostic characters on the skulls for the subspecies/genetic groups could be found on the series of specimens observed (95 specimens from 10 museums, GV pers. obs.), however the use of morphometric geometrics analyses may reveal some differences. From preliminary analyses of the body measurements from museum specimens, wild individuals from rescue centers, and zoo individuals with known origins (with a total of 69 individuals), we observed that the individuals north the Isthmus of Kra (Indochinese region) seem significantly larger than the ones from the south (Sundaic region). The individuals from Palawan do not differ significantly in size from the ones from the Sundaic region, although they are significantly larger than the ones from Borneo (Data S 1 and Table S 1). Owing to the low number of specimens, we were not able to test for size differences between males and females, so these results remain preliminary. Further morphological investigations should be done on binturongs with a larger sample size and appropriate methods to look for geographical variations.

From our genetic data, all the zoo individuals which were said to originate in Palawan clustered with known specimens from Palawan. One individual from Parken Zoo (Sweden) obtained from a private collection, also grouped with the Palawan individuals. Thus, the following zoos outside the Philippines have the Palawan binturong, including Parken Zoo in Sweden, and City of Belfast Zoo in the UK (and also previously Sandwich Zoo, UK), likely all coming from the same facility, Avilon Zoo in the Philippines, which seemed to have obtained them from a rescue center (DF pers. obs.).

A few zoo individuals were said to be from Borneo, in particular in Singapore Zoo. One of them (TC13, sampled in 1997) seems to be from Borneo, while for another one, this

origin appeared to be unlikely (TC465, sampled in 2005), as it clustered with the Indochinese region haplogroup (see Table S 2). Another one (TC627, sampled in 2010) said to be from Borneo, clustered with the Sundaic region individuals, but it could not be confirmed that its origin was indeed Borneo. So it appears that individuals from Singapore Zoo have various origins or have been crossed with individuals from various origins. Berlin Zoo individuals (TC653 to TC655, sampled in 2010) were said to be from Malaysia and did cluster with the Sundaic region individuals.

According to the genealogy based on the studbook (AB pers. info.), a series of individuals that we sampled (TC-331, 332, 333, 336, 337, 338, 371, 376, 381, 382, 393, 399, 761) were all derived from the same pair (EEP#107 and EEP#108, not sampled) which was said to be from the Malay archipelago. However, our results attribute them all to the Indochinese region group. Thus, our results suggest that the geographical origin of zoo individuals has to be taken with extreme caution. Crossing of individuals from different regions has also likely occurred frequently.

The zoos in Singapore, Taiwan, and Malaysia have only individuals from the Sundaic region (with the one exception mentioned above). The binturongs in French zoos belong only to the Indochinese haplogroup. The zoos in the Indochinese region seem to have binturongs only from this region (Vietnam, Myanmar and Laos). Other zoos which provided samples have binturongs from various origins.

For the captive breeding program, according to our results, it is possible to maintain separate management of the Palawan binturongs; also populations from the Sundaic and Indochinese regions should be kept separately, as they appear to be two distinct lineages, but it appears that some mixing has already occurred.

In the absence of any signal in the nuclear marker used here, these results are based only on the maternal lineages, and therefore should be taken with caution.

Conclusion

This study has provided a better assessment of the genetic polymorphism and structure within the binturong, with two main groups, corresponding to the Indochinese region and the Sundaic region. Within the latter, are found the Palawan binturongs on one side, and the Sulu

individual on the other side. The Palawan binturongs appear to be very close to the Bornean binturongs, and should not be considered a separate species nor a separate subspecies. However, they form a separate monophyletic group, which may result from one dispersal event from Borneo during lower sea levels. Palawan binturongs do not share their haplotypes with binturongs from any other localities and are now geographically separated from Bornean binturongs, and thus may represent an important conservation entity. Due to anthropogenic pressures on their populations and habitat, conservation attention is needed. In the latest Philippines' Department of Environment and Natural Resources list of threatened terrestrial species, binturongs are listed under the Other Threatened Species category, granting them legal protection in the Philippines (Gonzalez et al. 2018). A program is currently underway (see <http://en.abconservation.org/our-current-and-future-projects/>) to study the Palawan binturong and is already providing the first information on this population, which has never been studied before. Over its whole range, the binturong remains the victim of many threats according to the IUCN, and research and conservation actions are urgently needed for this threatened forest species.

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Tables

Table 1: List of the samples included in this study. For each sample, we report: the identification number, the specimen/sample number (AMNH=American Museum of Natural History, New York, USA; ISEM= Institut des Science de l'Evolution, Montpellier, France; MNHN=Museum National d'Histoire Naturelle, Paris, France), the GenBank (Gbk) number, locality (OCP=Owston's civet Conservation Program; RSCC=Rare Species Conservation Center; WS: Wildlife Sanctuary), and studbook number (EEP=European Endangered Species Programme). GenBank numbers in bold represent new sequences produced in this study; others from GenBank, with references: Albert R., unpublished; Dang T.T., Nguyen G.S., Ho T.L., and Le X.C., unpublished; Cosson et al. (2007); Ouitavon K., Karinthanyakit W., Phetkhong J., Marcheaw B., and Penchart K., unpublished; Patou et al. (2008); Veron et al.

(2004, 2015b,c, 2017). Identification numbers in bold correspond to samples from historical museum specimens.

Species	Id #	Sample #	Cytb	CR	BFG	Origin	Studbook # / Zoo Id #
<i>A. binturong</i>	AbA103996	AMNH 103996	MK680970			Indonesia: Borneo, Kalimantan, Pelebon, Sungai Kajan	
<i>A. binturong</i>	AbA103997	AMNH 103997	MK680971			Indonesia: Borneo, Kalimantan, Pelebon, Sungai Kajan	
<i>A. binturong</i>	AbA106767	AMNH 106767	MK680972			Indonesia: Borneo, Kalimantan, Landak River, Perboeah	
<i>A. binturong</i>	AbA107134	AMNH 107134	MK680973			Indonesia: Borneo, Kalimantan, Landak River, Perboeah	
<i>A. binturong</i>	AbA29741	AMNH 29741	MK680974			Philippines: Palawan, Iwahig	
<i>A. binturong</i>	AbAY048793	AB3	AY048793			ND	
<i>A. binturong</i>	AbJN709947	CaymucB12	JN709947			Vietnam	
<i>A. binturong</i>	AbJX310330	Abin01	JX310330			Thailand	
<i>A. binturong</i>	AbM328	MNHN-ZMO-1962-328	MK680975			Philippines: Sulu archipelago	
<i>A. binturong</i>	AbSH23	MNHN SH23	MK680976	DQ302037	MK681067	Vietnam: Hô-Chi-Minh-Ville Zoo	
<i>A. binturong</i>	AbTC013	MNHN TC013	KJ852005	DQ302073	KJ852001	ND: Singapore Zoological Gardens	
<i>A. binturong</i>	AbTC028	MNHN RL78/97	MK680977	MK681034	MK681068	ND: Southport Zoo, UK	
<i>A. binturong</i>	AbTC029	MNHN RL77/97	MK680978	MK681069	MK681069	ND: Southport Zoo, UK	
<i>A. binturong</i>	AbTC094	MNHN TC094	MK680979	DQ302067	EF680503	ND: Carnivore Preservation Trust, Pittsboro, USA	ISIS #01035
<i>A. binturong</i>	AbTC095	MNHN TC095	MK680980	DQ302068	MK681070	ND: Carnivore Preservation Trust, Pittsboro, USA	ISIS #01027
<i>A. binturong</i>	AbTC117	MNHN TC117	MK680981	DQ302034	MK681071	Thailand: Chaiyaphum Province, Phu Khieo WS	
<i>A. binturong</i>	AbTC118	MNHN TC118		DQ302035		Thailand: Chaiyaphum Province, Phu Khieo WS	
<i>A. binturong</i>	AbTC119	MNHN TC119		DQ302035	MK681035	Thailand: Chaiyaphum Province, Phu Khieo WS	
<i>A. binturong</i>	AbTC212	MNHN TC212	MK680982	DQ302040	MK681072	Myanmar: Yangoo Zoo	
<i>A. binturong</i>	AbTC213	MNHN TC213	MK680983	DQ302039	KM819522	Myanmar: Yangoo Zoo	
<i>A. binturong</i>	AbTC328	MNHN TC328	KM819539	DQ302036	MK681073	ND: Servion Zoo, France	EEP #402 ou 403
<i>A. binturong</i>	AbTC329	MNHN TC329		DQ302042		ND: Darmstadt Zoo, Germany, then Servion Zoo, France	EEP #407?
<i>A. binturong</i>	AbTC330	MNHN TC330		DQ302043		ND: La Barben Zoo, France	
<i>A. binturong</i>	AbTC331	MNHN TC331		DQ302051		ND: St Martin La Plaine Zoo, France	EEP #675 / SA 0096
<i>A. binturong</i>	AbTC332	MNHN TC332		DQ302050		ND: St Martin La Plaine Zoo, France	EEP #578 / S 96086
<i>A. binturong</i>	AbTC333	MNHN TC333		DQ302049		ND: St Martin La Plaine Zoo, France	EEP #674 / SA 0095
<i>A. binturong</i>	AbTC335	MNHN TC335		DQ302053		ND: St Martin La Plaine Zoo, France	EEP #584 / S 98003
<i>A. binturong</i>	AbTC336	MNHN TC336		DQ302048		ND: St Martin La Plaine Zoo, France	EEP #621 / S 98111
<i>A. binturong</i>	AbTC337	MNHN TC337/TC394		DQ302047		ND: St Martin La Plaine Zoo, then Dierenpark Wissel, NL	EEP #645 / SA 0025
<i>A. binturong</i>	AbTC338	MNHN TC338	MK680984	DQ302046	MK681074	ND: Servion Zoo, then St Martin La Plaine Zoo, France	EEP #505 / S 91149
<i>A. binturong</i>	AbTC367	MNHN TC367	MK680985	DQ302071	MK681075	ND: Taipei Zoo, Taiwan	
<i>A. binturong</i>	AbTC368	MNHN TC368		DQ302057		ND: Ostrava Zoo, CZ	EEP #504 / Schon
<i>A. binturong</i>	AbTC369	MNHN TC369		DQ302070		ND: Ostrava Zoo, CZ	EEP #641 / Sabah
<i>A. binturong</i>	AbTC371	MNHN TC371		DQ302088		ND: Ostrava Zoo, CZ	EEP #582 / Klaus
<i>A. binturong</i>	AbTC372	MNHN TC372		DQ302075		ND: Conservator's Center, Mebane, USA	Sabk #507
<i>A. binturong</i>	AbTC375	MNHN TC375		DQ302061		ND: Conservator's Center, Mebane, USA	Yogi
<i>A. binturong</i>	AbTC376	MNHN TC376		DQ302041		ND: Southport Zoo, then Linton Zoo, UK	EEP #173
<i>A. binturong</i>	AbTC378	MNHN TC378	MK680986	DQ302076	MK681076	ND: Artis Zoo, Amsterdam, NL	EEP #707 / M03059
<i>A. binturong</i>	AbTC381	MNHN TC381		DQ302062		ND: Paignton Zoo, UK	EEP #207 / 1376
<i>A. binturong</i>	AbTC382	MNHN TC382	MK680987	DQ302055	MK681077	ND: Banham Zoo, then Colchester Zoo, UK	EEP #212 / 1728
<i>A. binturong</i>	AbTC384	MNHN TC384	MK680988	DQ302059	MK681078	ND: Lille Zoo, France	EEP #656 / 1531
<i>A. binturong</i>	AbTC385	MNHN TC385/TC767	MK681027	DQ302063		ND: Lille Zoo, then Zoo Pont Scorf, France	EEP #658 / 1533
<i>A. binturong</i>	AbTC386	MNHN TC386		DQ302044		ND: Lille Zoo, France	EEP #664 / 1822
<i>A. binturong</i>	AbTC387	MNHN TC387	MK680989	DQ302058	MK681079	ND: Darmstadt, Germany, then Lille Zoo, France	EEP #422 / 781
<i>A. binturong</i>	AbTC388	MNHN TC388	MK680990	DQ302045	MK681080	ND: Darmstadt, Germany, then Lille Zoo, France	EEP #431 / 782
<i>A. binturong</i>	AbTC389	MNHN TC389	MK680991	DQ302056	MK681081	ND: Darmstadt, Germany, then Lille Zoo, France	EEP #438 / 783
<i>A. binturong</i>	AbTC390	MNHN TC390		DQ302054		ND: St Martin La Plaine Zoo, then Olmoucou Zoo, CZ	EEP #509 / 4990
<i>A. binturong</i>	AbTC391	MNHN TC391		DQ302052		ND: St Martin La Plaine Zoo, then Olmoucou Zoo, CZ	EEP #514 / 4981
<i>A. binturong</i>	AbTC392	MNHN TC392		DQ302072		ND: Olmoucou Zoo, CZ	EEP #401 / 5000
<i>A. binturong</i>	AbTC393	MNHN TC393	MK680992			ND: St Martin La Plaine Zoo, then Aquazoo Friesland, NL	EEP #647 / 500218
<i>A. binturong</i>	AbTC396	MNHN TC396		DQ302064		ND: Lille Zoo, France, then Aquazoo Friesland, NL	EEP #657 / 500217
<i>A. binturong</i>	AbTC397	MNHN TC397		DQ302065		ND: Dierenpark Wissel, NL	EEP #624 / 100036
<i>A. binturong</i>	AbTC398	MNHN TC398		DQ302066		ND: Overloon Zoo, NL	EEP #623 / 300039
<i>A. binturong</i>	AbTC399	MNHN TC399		DQ302089		ND: St Martin La Plaine Zoo, then Overloon Zoo, NL	EEP #508 / 300567
<i>A. binturong</i>	AbTC404	MNHN TC404	MK680993	DQ302081		Malaysia: Kuala Lumpur Zoo	
<i>A. binturong</i>	AbTC405	MNHN TC405	MK680994	MK681036	MK681082	Malaysia: Kuala Lumpur Zoo	
<i>A. binturong</i>	AbTC406	MNHN TC406	MK680995			Malaysia: Kuala Lumpur Zoo	
<i>A. binturong</i>	AbTC407	MNHN TC407		DQ302082		Malaysia: Kuala Lumpur Zoo	
<i>A. binturong</i>	AbTC408	MNHN TC408	MK680996	MK681037		Malaysia: Kuala Lumpur Zoo	
<i>A. binturong</i>	AbTC420	MNHN TC420	MK680997	MK681038	MK681083	Malaysia: Kuala Lumpur Zoo	
<i>A. binturong</i>	AbTC421	MNHN TC421	MK680998	DQ302083	MK681084	Malaysia: Kuala Lumpur Zoo	
<i>A. binturong</i>	AbTC422	MNHN TC422		DQ302086		Malaysia: Kuala Lumpur Zoo	
<i>A. binturong</i>	AbTC427	MNHN TC427	MK680999	DQ302079	MK681085	Malaysia: Temerloh Zoo, Pahang	
<i>A. binturong</i>	AbTC428	MNHN TC428	<200bp			Malaysia: Temerloh Zoo, Pahang	
<i>A. binturong</i>	AbTC439	MNHN TC439	MK681000	DQ302080	MK681086	ND: Eberswalde Zoo, Germany	EEP #429
<i>A. binturong</i>	AbTC443	MNHN TC443	MK681001	DQ302038	MK681087	ND: Servion Zoo, France	EEP #405
<i>A. binturong</i>	AbTC444	MNHN TC444	KP986469			ND: Darmstadt, Germany, then Servion Zoo, France	EEP #427
<i>A. binturong</i>	AbTC465	MNHN TC465	MK681002	DQ302090	<200 bp	ND: Singapore Zoo, then Artis Zoo, Amsterdam, NL	EEP #648 / M00139
<i>A. binturong</i>	AbTC466	MNHN TC466		DQ302078		ND: Singapore Zoo, then Artis Zoo, Amsterdam, NL	EEP #651 / M02001
<i>A. binturong</i>	AbTC468	MNHN TC468		DQ302077		ND: Artis Zoo, Amsterdam, NL	EEP #687 / M04023
<i>A. binturong</i>	AbTC547	MNHN TC547	MK681003	MK681039	MK681089	ND: Halle Zoo, Germany, then Madrid Zoo, Spain	EEP #627 / 994052
<i>A. binturong</i>	AbTC627	MNHN TC627	MK681004	MK681040	MK681090	ND: Singapore Zoo	Theresa
<i>A. binturong</i>	AbTC628	MNHN TC628	MK681005	MK681041	MK681091	ND: Singapore Zoo	G10532, Hiam
<i>A. binturong</i>	AbTC630	MNHN TC630/TC370	MK681006	MK681042	MK681092	ND: Halle Zoo, then Dortmund Zoo, Germany	EEP #642 / Henry
<i>A. binturong</i>	AbTC631	MNHN TC631	MK681007	MK681043	MK681093	ND: Darmstadt Zoo, then Dortmund Zoo, Germany	EEP #716
<i>A. binturong</i>	AbTC653	MNHN TC653	MK681008	MK681044	MK681094	ND: Halle Zoo then Berlin Zoo, Germany	EEP #640 / Vincent
<i>A. binturong</i>	AbTC654	MNHN TC654	MK681009	<200bp		ND: Berlin Zoo, Germany	EEP #758
<i>A. binturong</i>	AbTC655	MNHN TC655	MK681010	<200bp		ND: Berlin Zoo, Germany	EEP #757
<i>A. binturong</i>	AbTC679	MNHN TC679	MK681011	MK681045	MK681095	Philippines: Palawan	
<i>A. binturong</i>	AbTC680	MNHN TC680	MK681012	MK681046	MK681096	Philippines: Palawan	
<i>A. binturong</i>	AbTC681	MNHN TC681	MK681013	MK681047	MK681097	Philippines: Palawan	
<i>A. binturong</i>	AbTC732	MNHN TC732	MK681014	MK681048	MK681098	Philippines: Palawan, Avilon Zoo, then RSCC, Sandwich, UK	
<i>A. binturong</i>	AbTC733	MNHN TC733	MK681015	MK681049	MK681099	Philippines: Palawan, Avilon Zoo, then RSCC, Sandwich, UK	
<i>A. binturong</i>	AbTC734	MNHN TC734	MK681016			Philippines: Palawan, Avilon Zoo, then RSCC, Sandwich, UK	
<i>A. binturong</i>	AbTC735	MNHN TC735	MK681017	MK681050	MK681100	Philippines: Palawan, Avilon Zoo, then RSCC, Sandwich, UK	
<i>A. binturong</i>	AbTC736	MNHN TC736	MK681018	MK681051	MK681101	Philippines: Palawan, Avilon Zoo, then RSCC, Sandwich, UK	Kervul
<i>A. binturong</i>	AbTC737	MNHN TC737	MK681019	MK681052	MK681102	Philippines: Palawan, then Prague Zoo, CZ	
<i>A. binturong</i>	AbTC738	MNHN TC738		MK681053		ND: Madrid Zoo, Spain	EEP # 684 / B16
<i>A. binturong</i>	AbTC742	MNHN TC742		MK681054	MK681103	ND: Parken Zoo, Eskilstuna, Sweden	EEP #774 / Henri
<i>A. binturong</i>	AbTC743	MNHN TC743		MK681055		ND: Avilon Zoo, Philippines, then Belfast Zoos, UK	EEP #740 / ID 9424
<i>A. binturong</i>	AbTC744	MNHN TC744	MK681020	MK681056		ND: Avilon Zoo, Philippines, then Belfast Zoo, UK	EEP #738 / ID 9425
<i>A. binturong</i>	AbTC751	MNHN TC751	MK681021			Indonesia: Batu Secret Zoo, Indonesia	
<i>A. binturong</i>	AbTC759	MNHN TC759	MK681022	MK681057	MK681104	ND: ménagerie du Jardin des Plantes, MNHN, Paris	EEP #654
<i>A. binturong</i>	AbTC761	MNHN TC761	MK681023		MK681105	ND: ménagerie du Jardin des Plantes, MNHN, Paris	EEP #648
<i>A. binturong</i>	AbTC762	MNHN TC762	MK681024			ND: Downtown Aquarium Denver, USA	AB092414
<i>A. binturong</i>	AbTC764	MNHN TC764	MK681025			ND: Ostrava Zoo, CZ	EEP #767 / Luang
<i>A. binturong</i>	AbTC765	MNHN TC765/TC437	MK681026	MK681058		ND: Hall Zoo, then Ostrava Zoo, CZ	EEP #639 / Momo
<i>A. binturong</i>	AbTC794	MNHN TC794		MK681059		Laos: Laos Wildlife Rescue Center/ Lao Zoo	Hary
<i>A. binturong</i>	AbTC796	MNHN TC796		MK681060		Laos: Laos Wildlife Rescue Center/ Lao Zoo	Lee
<i>A. binturong</i>	AbTC797	MNHN TC797	MK681028	MK681061	MK681106	Laos: Laos Wildlife Rescue Center/ Lao Zoo	Kate
<i>A. binturong</i>	AbTC800	MNHN TC800	MK681029	MK681062	MK681107	Laos: Laos Wildlife Rescue Center/ Lao Zoo	Mike
<i>A. binturong</i>	AbTC801	MNHN TC801	MK681030	MK681063	MK681108	Laos: Laos Wildlife Rescue Center/ Lao Zoo	Rachel
<i>A. binturong</i>	AbTC803	MNHN TC803	MK681031	MK681064	MK681109	Laos: Laos Wildlife Rescue Center/ Lao Zoo	Melissa
<i>A. binturong</i>	AbTC806	MNHN TC806	MK681032	MK681065		Laos: Laos Wildlife Rescue Center/ Lao Zoo	Phant
<i>A. binturong</i>	AbTC807	MNHN TC807	MK681033	MK681066		Laos: Lao Zoo	Dao
<i>A. trivirgata</i>	AbC155	MNHN-ZMO-2001-495	KM819540			ND: Parc Zoologique de Paris, MNHN	
<i>C. owstoni</i>	CoSH4	MNHN SH-4	AY155258			Vietnam: North, then OCP	
<i>C. owstoni</i>	CoT2092	ISEM T-2092			EF680505	Vietnam: North	

Table 2: Estimates of evolutionary divergence over sequence pairs between localities (below the diagonal) and within localities (on the diagonal). Borneo individuals were separated from Malaysia and Indonesia individuals from other localities.

	Borneo	Indonesia	Malaysia	Palawan	Laos	Myanmar	Thailand	Vietnam
Borneo (n=4)	0.41%							
Indonesia (n=1)	0.32%	NA						
Malaysia (n=7)	0.28%	0.24%	0.23%					
Palawan (n=11)	0.38%	0.19%	0.31%	0.04%				
Laos (n=6)	1.73%	1.70%	1.61%	1.79%	0.09%			
Myanmar (n=2)	1.48%	1.54%	1.43%	1.60%	0.10%	0.00%		
Thailand (n=2)	1.80%	1.79%	1.76%	1.95%	0.20%	0.26%	0.60%	
Vietnam (n=2)	1.80%	1.78%	1.66%	1.74%	0.14%	0.09%	0.32%	0.17%

Figure legends

Figure 1: Distribution of *Arctictis binturong* based on IUCN data in grey, and localities of samples (colour dots) used in this study. Samples from the Indochinese region are indicated in blue, those from the Sundaic region in pink, and those from the Philippines in red.

Figure 2: Median-joining network of Cytb haplotypes for the fragment of 538 bp. The size of each circle is proportional to the haplotype frequency; the shortest link corresponds to one mutation (the number of mutations between the two main haplogroups is indicated above the link). Indochinese region: blue; Sundaic region: pink; the Philippines: red; unknown (zoo individuals with no origin indicated): white. Box: focus on the Sundaic region and the Philippines. Colours: The Philippines: red; Borneo: dark pink; peninsular Malaysia: light pink; Malaysia (with locality unknown): very light pink; unknown (zoo individuals with no origin indicated): white.

Figure 3: Median-joining network of Cytb haplotypes for the fragment of 567 bp focusing on the Sundaic region and the Philippines. The size of each circle is proportional to the haplotype frequency; the shortest link corresponds to one mutation. Colours: The Philippines: red; Borneo: dark pink; peninsular Malaysia: light pink; Malaysia (with locality unknown): very light pink; unknown (zoo individuals with no origin indicated): white.

Figure 4: Median-joining network of CR haplotypes. The size of each circle is proportional to the haplotype frequency; the shortest link corresponds to one mutation. Indochinese region: blue; Sundaic region: pink; the Philippines: red; unknown (zoo individuals with no origin indicated): white.

Supporting Information

Figure S 1: ML tree of *Arctictis binturong* obtained with Cytb (1140 bp, model GTR+G+I). BI posterior probabilities and bootstrap proportions are provided for the main nodes.

Figure S 2: Median-joining network of Cytb haplotypes for the fragment of 1140 bp. The size of each circle is proportional to the haplotype frequency; the shortest link corresponds to one mutation. Indochinese region: blue; Sundaic region: pink; the Philippines: red.

Table S 1: Individuals used in the morphometric analyses, with their origin, source of the data (and references), and measurements (TotL: Total length; HB: Head and body length; T: Tail length; W: weight).

Table S 2: Assignment of zoo individuals to the main haplogroups. The supposed origin is based on the information provided by the zoos, or is based on the genealogy from the studbook (AB, pers. info.). The haplogroup is in bold when it contradicts the supposed origin.

Data S 1: Preliminary results on size variations in *Arctictis binturong*.