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Heavily exploited but poorly known: systematics and biogeography of commercially harvested pythons (*Python curtus* group) in Southeast Asia

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More than 100 000 blood pythons (*brongersmai*) and short-tailed pythons (*curtus* and *breitensteini*) are taken from Borneo and Sumatra each year for the commercial leather trade. Traditionally, all have been treated as a single polytypic species (*Python curtus*), with three subspecies differing in colour, size and geographic distribution. Analyses of DNA sequences and morphological data clarify the phylogenetic relationships, taxonomy and biogeography of this group. The lineage is monophyletic, and each of the three subspecies differs from the other two both morphologically and genetically. Given the morphological and genetic distinctiveness of each taxon, we here elevate the three subspecies to full species status. *Python brongersmai* is the most distinctive in terms of colour (of the three, only *brongersmai* has colour-morphs that are red or orange), size (it grows to 2.6 m, vs. approx. 2.0 m for the other taxa), and scalation (e.g. *brongersmai* has >166 ventral scales, vs. <166 in the other taxa and has two supralabials over each orbit, vs. one supralabial for the other two taxa). In terms of cytochrome *b* mitochondrial DNA sequence data, *brongersmai* is almost as distant genetically from the short-tailed pythons (8.9% divergence) as is the reticulated python (*P. reticulatus*: 10.3% divergence). The other two taxa (*P. breitensteini* from Kalimantan and *P. curtus* from western and southern Sumatra) are closely related (3% divergence), despite their disjunct distribution (separated by *P. brongersmai*). Sea-level fluctuations provide a plausible biogeographic scenario to explain phylogenetic divergence within this lineage. Given the distinctiveness of the component taxa, and the ease with which even dried skins can be identified to species level (based on ventral counts), the managers of this important commercial resource should no longer treat the *P. curtus* group as a single biological taxon.

ADDITIONAL KEYWORDS: snake – Borneo – Sumatra – Kalimantan – Malaysia – cytochrome *b* – molecular phylogenetics – biogeography – taxonomy.

INTRODUCTION

An accurate taxonomy is an essential first step towards the conservation, management, or sustainable exploitation of any biological resource. If we do not know how many species we are dealing with, it is easy to establish dangerously flawed priorities (Daugherty *et al.*, 1990). The most robust basis for taxonomic decisions involves information on phylogenetic relationships among the biological entities under study (Christoffersen, 1995; Keogh, 1995, 1998; Lee, 1996). Such information also may clarify the biogeographic basis for interspecific and intraspecific divergences (Morrone & Crisci, 1995; Ronquist, 1998; Keogh, Scott & Scanlon, 2000). Data on phylogeny and systematics are available for many major lineages of mammals and birds (e.g. Sibley & Ahlquist, 1990; Mindell, 1997; Bininda-Emonds, Gittleman & Purvis, 1999; Liu & Miyamoto, 1999), but studies on most other types of organisms lag far behind. In some cases, this ignorance extends even to organisms that are of substantial conservation concern (e.g. Daugherty *et al.*, 1990) or that are important in commercial trade – sometimes in very large volumes (King, 1995). The latter situation is particularly worrying, because managers who mistakenly treat multi-species lineages as a single taxon may thereby fail to regulate harvesting levels to the

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appropriate degree for each component species (King, 1995; Crozier, 1997; Vazquez & Gittleman, 1998; Bininda-Emonds, Vazquez & Manne, 2000). In this paper, we provide the first detailed phylogenetic, taxonomic, and biogeographic analysis of an Indonesian python 'species' that supports a major international trade in leather goods.

The commercial trade in Indonesian snakes involves capturing animals from the wild, killing them, and selling their skins and other products (notably, meat and medicinal items such as gall bladders). The primary focus of the trade is the reticulated python (*P. reticulatus*), with an average of >500 000 specimens taken from Sumatra and Borneo each year (Groombridge & Luxmoore, 1991). The only other Asian python species harvested in large numbers are the blood and short-tailed pythons (*P. curtus*), of which approximately 70 000 to 200 000 are taken per annum (Groombridge & Luxmoore, 1991). Remarkably, these species have attracted very little scientific attention. Recent studies on both taxa have clarified ecological traits and attempted to evaluate the overall sustainability of the offtake (Shine *et al.*, 1998a–d, 1999a, b). However, the taxonomy of these 'species' remains virtually unstudied, despite substantial geographic variation in body size and morphology across their broad ranges and insular distributions. Both taxa may actually consist of multiple species. If so, we need to understand patterns of phylogenetic divergence so that we can adequately manage these valuable resources.

As well as providing a basis for conservation and management of these large tropical predators, information on the phylogeny of blood and short-tailed pythons is of considerable interest in terms of biogeography. *Python curtus* occur on Sumatra, Borneo, and smaller associated islands, but they do not occur on Java nor east of Wallace's line. Recent advances in our understanding of the geological history of this important biogeographic region – and especially, the timing and sequence of divisions and connections between landmasses (Hall, 1998; Metcalfe, 1999) – offer the opportunity to interpret pythonine phylogeny in terms of vicariance and dispersal events through evolutionary time. With these issues in mind, we gathered genetic and morphological data to clarify phylogenetic relationships and biogeography within the *Python curtus* group.

MATERIAL AND METHODS

STUDY TAXA

Historically, three subspecies of *Python curtus* have been recognized based on differences in colour, adult body size, meristic scale traits and geographic distributions (Brongersma, 1947; Stimson, 1969). *Python curtus brongersmai* is a large snake (to over 2 m) and the only *P. curtus* subspecies to extend into mainland Southeast Asia (McDiarmid, Campbell & Touré, 1999). Its range also includes the eastern side of Sumatra and islands in the Strait of Malacca between Sumatra and Peninsular Malaysia. This taxon is highly polymorphic in colour with individual snakes being various shades of red, yellow, brown or black (Shine *et al.*, 1998a). Although snakes of different colour morphs have been reported to hatch from a single clutch of eggs, detailed analysis of wild-caught snakes has revealed significant differences between morphs (even within a single geographic area) in traits such as body sizes, relative tail lengths, food habits, parasite loads and clutch sizes (Shine *et al.*, 1998a). Hence, the possibility that the different morphs represent divergent phylogenetic lineages within *P. c. brongersmai* deserves attention. *Python curtus curtus* and *Python curtus breitensteini* are smaller than *P. c. brongersma*. Both are dark in coloration and neither displays the extreme colour polymorphism of *P. c. brongersmai*. Both taxa are found only on islands in the Indonesian archipelago; *P. c. curtus* is found in western and southern Sumatra, whereas *P. c. breitensteini* is found on Borneo, including the geopolitical areas of Kalimantan, Sarawak, Sabah and Brunei.

MOLECULAR DATA

A total of 36 tissue samples was assembled from representatives of each of the three putative *Python curtus* subspecies and each of the *P. curtus brongersmai* colour morphs (Fig. 1). Most of our tissue samples were obtained from specimens collected for the reptile skinning industry in the Palembang, Medan and Bengkulu areas of Sumatra and the Pontianak area of Kalimantan on the island of Borneo. Other samples were obtained from live animals exported for the pet industry. For these individuals plus outgroups *Morelia viridis* and *Python reticulatus*, a portion of the cytochrome *b* mitochondrial gene was sequenced following standard procedures described elsewhere for other snake groups (Keogh, 1998; Keogh, Shine & Donnellan, 1998, Keogh *et al.*, 2000).

Sequences were aligned by eye and the resulting data matrix analysed by maximum parsimony (MP) and maximum likelihood (ML) methods with the computer program PAUP* 4.0 (Swofford, 2000). The *Morelia viridis* sequence was designated the outgroup in all analyses and two *Python reticulatus* samples were included in all analyses as a second outgroup. The actual transition/transversion (ti/tv) ratio was estimated by ML analyses of alternative reduced data sets (i.e. single representatives of unique haplotypes). Alternative data sets differed by inclusion/exclusion of outgroup haplotypes. This ti/tv ratio then was used in subsequent ML analyses on this reduced data set.

Branch and bound MP analyses were performed on the full data set with all variable sites weighted equally and with ti/tv ratios of two, three, four, five and six to approximate and flank the actual ratio. The amount of phylogenetic information in the data set was estimated with the g_1 statistic (Hillis, 1991; Hillis & Huelsenbeck, 1992) calculated by examining the tree length distribution of 10 000 randomly generated parsimony trees using the random trees function of PAUP* with outgroups excluded. Relative branch support in each phylogenetic analysis was evaluated with 2000 bootstrap pseudoreplicates for MP analyses. The ability of our sequence data set to reject alternative phylogenetic hypotheses was examined further with non-parametric Templeton Tests (Wilcoxon signed-rank test) (Templeton, 1983) in PAUP*. This test examines if there is a significant difference between the most parsimonious tree and an alternative topology.

MORPHOLOGICAL DATA

The three currently recognized *Python curtus* taxa have been poorly described and diagnosed. Our morphological data and descriptions are based on the examination of 95 preserved specimens and a large number of live and photographed specimens as there are relatively few specimens held in museums. Vida Preciosa International, Inc. (VPI) of Boerne, TX currently houses more than 100 live specimens of these pythons with locality data. Additionally, over the past 21 years, one of us (DGB) has amassed a collection of detailed photographs of more than 150 specimens. Data on characters of lepidosis already in the literature were incorporated into our study.

Characteristics of scutellation and pattern were noted on the 95 preserved specimens. Eighteen lepidotic characters were examined as follows: supraoculars; postoculars; suboculars; preoculars; large loreal scales not in the naso-preocular loreal series; the naso-preocular series of loreal scales; supralabials; infralabials; the number of pitted anterior infralabials; the number of pitted posterior infralabials; the number of parietal scales contacting the midline suture; the presence or absence of broad contact between the anterior pair of parietals; the number of scales in the ventral series; the number of scales in the subcaudal series; the number of dorsal scales in a series around the anterior body one-head-length posterior to the nape of the neck; the number of dorsal scales in a series around the body at midbody; and the number of dorsal scales in a series around the posterior body one-head-length anterior to the vent. All possible data were recorded for each specimen, but a complete count of all lepidotic characters often could not be made on a specimen as many of the specimens available for our study were heads only.

The colour pattern of these pythons is among the most variable of all pythonine snakes and we found it difficult to quantify. Subjective notes were taken on all examined specimens. Additional data were recorded from live and photographed specimens. Likewise, colour is highly variable within this lineage. Data on colour were taken from live specimens in the VPI collection and from the photographic collection. Fifty photographs of living specimens of all three taxa were scanned and stored as TIFF images. In order to make these images available to other researchers, a CD with the images has been deposited in each of the ancillary photography collections of the Australian National University, University of Texas at Arlington, and the University of Sydney. These photos are intended to illustrate the range of variation in appearance and in characters of scalation that we observed in the living specimens.

RESULTS

MOLECULAR DATA

In total the cytochrome *b* mitochondrial DNA sequence data set comprised 322 base pairs. Sequences will be deposited on GenBank after publication. Jukes–Cantor (1969) interspecific genetic distances between mitochondrial haplotypes are presented in Table 1. Out of the 36 samples, only eight mitochondrial haplotypes were detected among the three taxa (Fig. 1, Table 1). Intrataxon sequence divergence was very low, all less than 1%: 0.3–0.9% among *brongersmai*, 0.3–0.6% among *breitensteini*, and 0.1% among *curtus* haplotypes. Among the ingroup taxa sequence divergence ranged from 7.8–9.0% between *brongersmai* and *breitensteini*, 7.9–8.2% between *brongersmai* and *curtus*, and 2.5–3.2% between *breitensteini* and *curtus*. Differences between the outgroups and ingroup ranged from 12.6–15.2% for the outgroup *Morelia viridis* and 10.3–12.4% for the outgroup *Python reticulatus*.

When the outgroups *M. viridis* and *P. reticulatus* are included there are 61 variable sites (8 first, 2 second, 51 third codon position changes) of which 46 are parsimony informative. When only ingroup sequences are considered there are 33 variable sites (4 first, 1 second, 28 third codon position changes), 30 of which are parsimony informative. The distribution of 10 000 randomly generated trees was highly left-skewed ($g_1 = -0.203$, $P<0.01$) indicating strong phylogenetic signal in the data (Hillis, 1991; Hillis & Huelsenbeck, 1992). Maximum likelihood estimates of the actual transition/transversion ratio were 2.82 and 4.20 including and excluding outgroup sequences respectively. The unweighted MP analyses as well as the ti/tv ratios of two, four, six and the ML estimated ratios all resulted in a single identical most parsimonious tree (Fig. 1:

Table 1. Jukes–Cantor (1969) genetic distances between mitochondrial haplotypes. Numbers correspond to haplotype numbers used in Table 1 and Figures 1 and 4

	1	2	3	4	5	6	7	8	9	10
1	—		within *brongersmai*							
2	0.10135	—		↓						
3	0.14245	0.11380	—		between *brongersmai* and *breitensteini*					
4	0.14365	0.12409	0.00689	—		within *breitensteini*				
5	0.13812	0.11020	0.00938	0.00332	↙ —					
6	0.12185	0.11020	0.08196	0.08577	0.08543	—	↓			
7	0.12598	0.11380	0.07850	0.08200	0.08196	0.00311	—			
8	0.12636	0.11020	0.08543	0.08963	0.08892	0.00311	0.00624	—	within *curtus*	
9	0.15156	0.11380	0.07850	0.08192	0.08196	0.02848	0.03172	0.03172	↓ —	
10	0.14833	0.10304	0.07850	0.08200	0.08196	0.02848	0.03172	0.02527	0.01253	—
				↑			↑			
			between *brongersmai* and *curtus*			between *breitensteini* and *curtus*				

length = 77 steps, CI = 0.870, RC = 0.852 in the unweighted analysis). ML analyses using the estimated ti/tv ratio also resulted in the same topology.

The topology of the single MP tree strongly supports the monophyly of the three taxa with high bootstrap values (Hillis & Bull, 1993) (Fig. 1). The taxon *brongersmai* is strongly supported by bootstrap values of 99–100%, *breitensteini* by values of 90–97% and *curtus* by values 82–89%. The variation in bootstrap values reflects results obtained for analyses of unweighted and ti/tv ratio = 2.8 data. In all three taxa there is evidence for phylogeographic substructure.

Within the polymorphic *brongersmai* there is no evidence to support the notion that the colour morphs correspond to phylogenetic lineages. Rather, mitochondrial haplotypes were identical for representatives of all *brongersmai* colour morphs from both the Medan area of northeastern Sumatra and Bangka Island in southeastern Sumatra. Other *brongersmai* haplotypes from Malaysia differed from these Sumatran animals by only single base pair changes.

The phylogenetic tree presented in Figure 1 shows that the dark coloured *breitensteini* and *curtus* are more closely related to each other than either is to the colour polymorphic *brongersmai*. The tree also shows that the 'black' *breitensteini* and *curtus* are not closely related to the 'black' or 'brown' colour morphs of *brongersmai*. Templeton tests of alternative topologies strongly support these hypotheses. When *breitensteini* snakes are made the sister group to *brongersmai* the resulting tree is 83 steps long, six steps longer than the most parsimonious tree ($z = 2.4495$, $P < 0.015$). Thus our data allow us to reject the hypothesis that *breitensteini* and *brongersmai* are more closely related to each other than *brongersmai* is to *curtus* and that the 'black' and 'brown' colour morphs of *brongersmai* might instead actually be members of the other clades.

MORPHOLOGICAL DATA AND SYSTEMATIC DESCRIPTION

Blood pythons and short-tailed pythons have long flat heads, thick muscular necks, large heavyset bodies, and short tails. The centre of the back is ridged. Females are slightly larger than males. Both sexes have prominent cloacal spurs. The spurs of adult males are more strongly hooked inward and thicker than those of females. Typically the spurs of adult males are more worn; they may be rounded and blunt and shorter than those of females.

Blood python and short-tailed pythons can be differentiated from all other pythons by the presence of a naso-preocular groove, a diagonal division that passes between the large facial scales from the upper posterior margin of the nasal scale posterior to the lower prefrontals (Fig. 2). The groove is bounded above by the prefrontals and upper preocular and below by 1–3 large loreals and the upper margins of supralabial scales. The groove itself is scaled with a series of small-to-granular loreal scales. Blood pythons and short-tailed pythons also have significantly shorter than all other pythons with an average ratio of tail-length/head-length of only1.6 (see character 74, Kluge, 1993).

SYNONYMY OF *PYTHON CURTUS* SCHLEGEL, 1872

Python curtus Schlegel, 1872, Dier. Koink. Zool. Genoot. Nat. art. Mag. Amsterdam, 64 pages [54]. Holotype RMNH 3782. Type-locality: 'Sumatra'.

Aspidoboa curtus Sauvage, 1884, Bull. Soc. Philomath. Paris (7)8:142–147[143] [placed in synonymy by Boulenger (1890:433).] *Python breitensteini* Steindachner, 1880, Sitzungsber. Akad. Wiss. Wien, Math. Naturwiss. KL. 82:267–268 [267]. Holotype NMW 13287: 1. Type-locality: 'Tewah, Borneo' [now Muarateweh, at the junction of the Barito and Teweh Rivers in

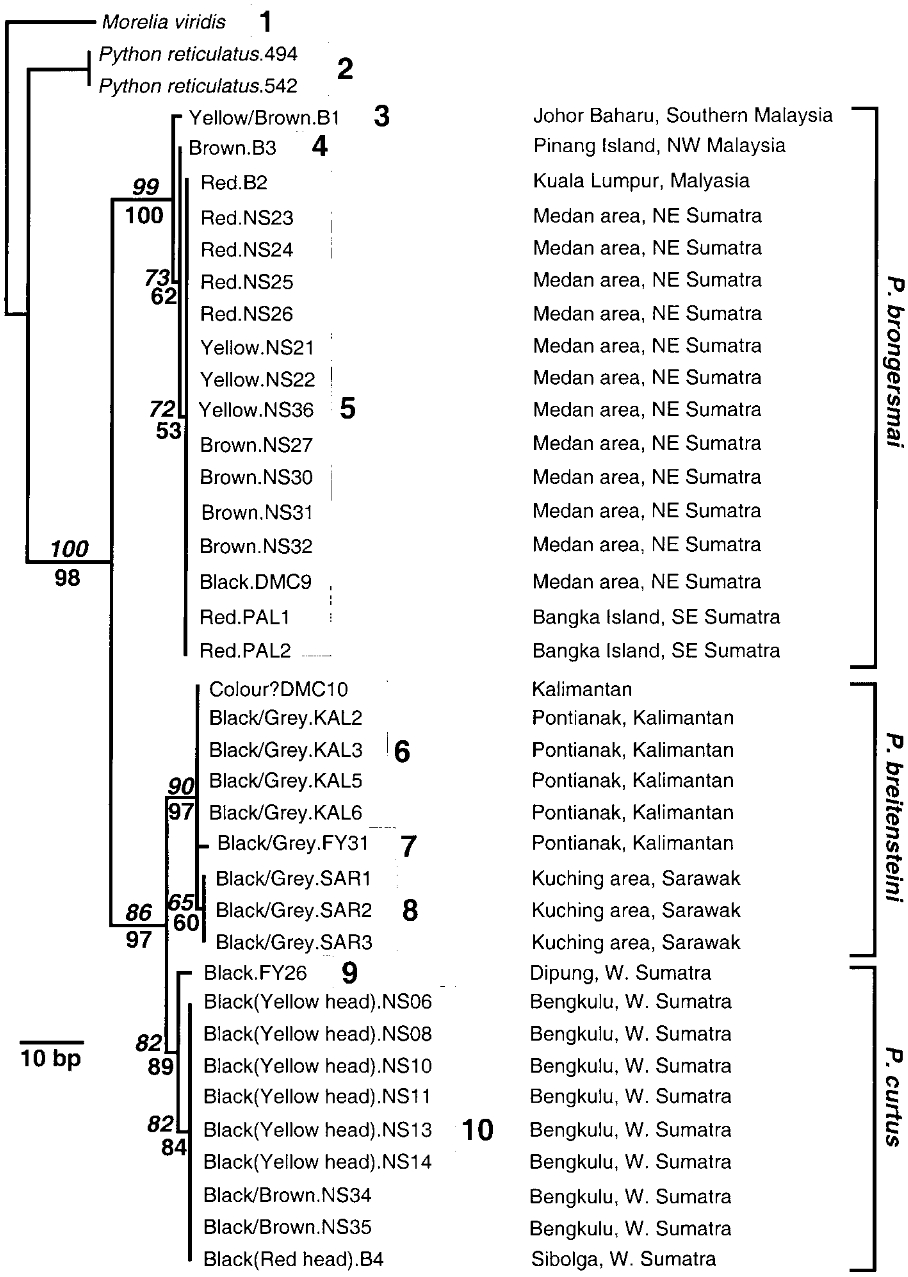

Figure 1. Phylogram showing relationships among the three *Python curtus* group taxa derived from an unweighted maximum parsimony analysis. The colour, specimen number and locality data of each specimen included in our study is noted. Numbers after brackets represent the haplotype number and correspond to the haplotype numbers used in Table 1 and Fig. 4. Numbers on branches represent bootstrap values for an unweighted parsimony analysis (italics) and a transition/transversion ratio of 2.0. See text for details of other analyses.

Kalimantan, Indonesia] [provisionally placed in synonymy by Boulenger (1893:433).]

Python curtus Boulenger, 1893, Cat. Snakes Brit, Mus. 1: 448 [pp 89–90] [listed *Python breitensteini* in synonymy on page 89].

Python curtus curtus Stull, 1935, Proc. Boston. Soc. Nat. Hist. 40:387–408 [393].

Python curtus breitensteini Stull, 1935, Proc. Boston. Soc. Nat. Hist. 40:387–408 [387, 393].

Python curtus brongersmai Stull, 1938, Occas. Pap.

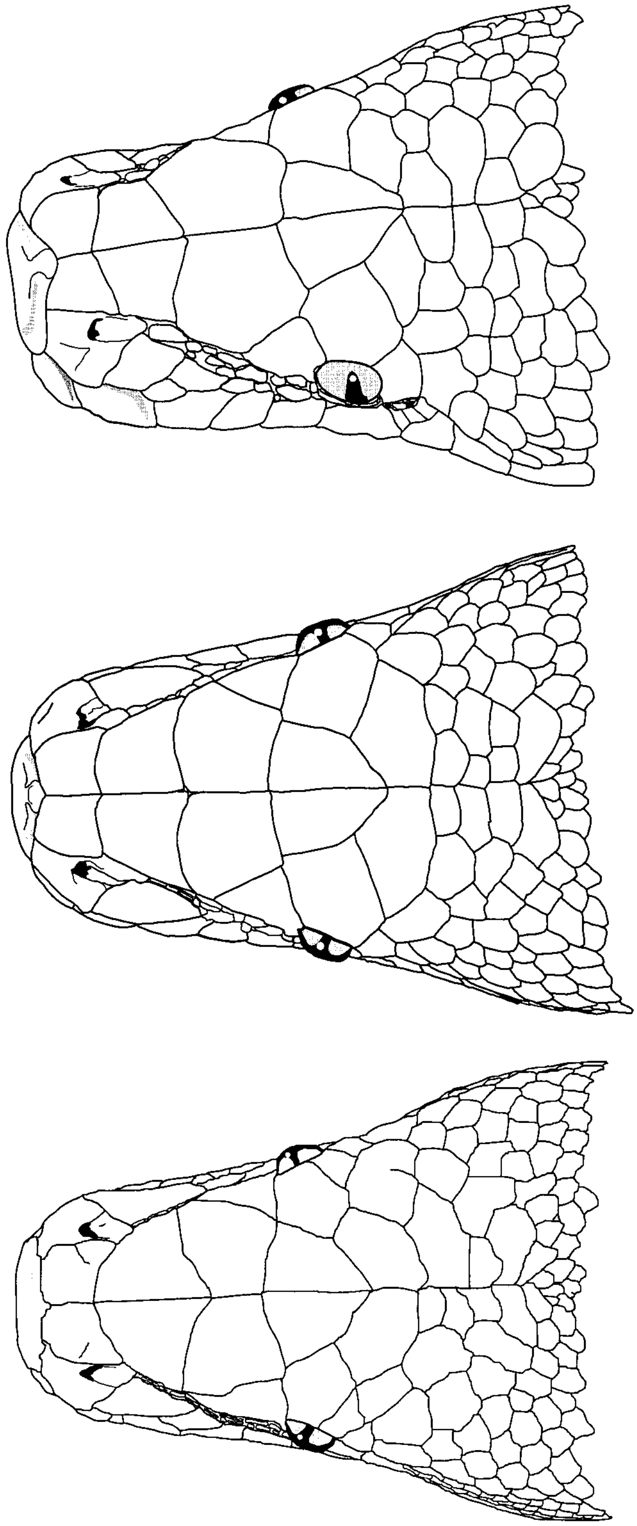

Figure 2. Head scalation of the three taxa within the *Python curtus* lineage: *Python curtus* (top), *Python breitensteini* (middle), *Python brongersmai* (bottom).

Boston Soc. Nat Hist. 8:297—300 [297]. Type-specimen MCZ 29779. Type-Locality: 'Singapore, Malay Peninsula'.

Python curtus curtus Stimson, 1969, Das Tierreich 89: 1–49 [29].

Python curtus breitensteini Stimson, 1969, Das Tierreich 89:1–49 [29].

Python curtus brongersmai Stimson, 1969, Das Tierreich 89:1–49 [29].

Python curtus Stuebing, 1991, Raffles Bull. Zool. 39: 323–362 [328].

DESCRIPTION OF TAXA

We elevate all three traditionally recognized subspecies to full species status, as follows.

PYTHON BRONGERSMAI STULL, 1938
BLOOD PYTHON

Holotype. MCZ 29779.

Type Locality. Singapore, Malay Peninsula.

Etymology. Named in honor of Dr Brongersma.

Diagnosis. *P. brongersmai* has 167 or more ventral scales, while *P. curtus* has 165 or less. *Python brongersmai* does not have suboculars and the lower margin of the orbit is in broad contact with the adjacent supralabials, while *P. curtus* has a series of small subocular scales that separate the supralabials from contacting the lower margin of the orbit. *Python brongersmai* has two supraoculars over each eye, while *P. curtus* typically has one. Normal colour phases for adult *P. brongersmai* include a predominantly red dark red appearance; no *P. curtus* have been observed with a predominantly red or dark red appearance.

Description

Body size. Maximum length for the taxon approaches 2.6 m. Large females weigh 14–22 kg. In the sample of wild-caught snakes studied by Shine *et al.* (1999a), 1037 adult males averaged 132.4 cm snout–vent length (SD = 11.95) and 732 adult females averaged 143.9-- cm SVL (SD = 11.82).

Pattern variation. This taxon displays a variable pattern. The top of the head is dark charcoal grey, pale grey, brown, or reddish brown. Excepting specimens with the darkest heads, there is a faint thin dark stripe on the midline from the rostral to the occiput. Most specimens display a thin pale line from the occiput posterior to the nape of the neck, ending where it contacts the dark pattern on the upper surface of the neck. Usually the side of the head from the first supralabial to beneath the eye is dark and unmarked. On some specimens, the sides of the snout are pale gray or brown with a dark mark on the lower portion of the upper preocular. There is a thin pale postocular stripe from behind the eye to the angle of the jaw. There is a black postocular blotch on the side of the head. The anterior point of this blotch contacts the posterior margin of the eye, from whence it widens and extends posteriorly on the side of the head onto neck. The chin is white and immaculate.

The upper surface of the neck and back is dark, with small pale vertebral spots centred along the vertebral line. The vertebral spots are either widely spaced or are numerous and in places coalesce to become elongated blotches or stripes. The lateral surfaces of the anterior body are pale with a longitudinal series of dark lateral blotches on the lower sides. Each blotch originates at the ventral surface and rises to about halfway up the sides. On the posterior half of the body these dark lateral blotches become taller and some or all contact and coalesce with the dark dorsal surface. Rounded black blotches 2–6 scales long occur on the lateral surfaces of the body, centred in pale areas of pattern. These black blotches may occur in every pale area on the sides (thus appearing as a longitudinal series of lateral black blotches) or alternatively, only a few lateral black blotches may be scattered along the body.

The upper surface of the tail is dark. The pale vertebral blotches may continue onto the dark upper surface of the tail or the upper surface of the tail may be uniformly dark. The lower sides of the tail are pale and the subcaudal surface is dark. The chin and ventral surface of the neck is immaculate white. The venter becomes progressively darker down the length of the body with increasing numbers of grey smudges and indistinct blotches.

Colour variation. Blood pythons can change the intensity or darkness of their head colour over a period of several hours; a black-headed specimen can change the head colour to pale silver grey and then back to black in a day's time. We are unable to determine why or how this change occurs, nor have we been able to understand how to elicit this change, but we have observed it repeatedly.

Colour varies substantially within this taxon. As mentioned, there are a wide variety of head colours. The pale postocular stripe is pale grey, sometimes with pale reddish margins. The eyes are pale at the top and shade to dark grey or black at the bottom. The pupil of the eye appears wider at the bottom than the top at all degrees of dilation. The tongue is dark.

The dark pattern elements on the body are all of similar colour within a single specimen. However, different individuals range from rich yellow to medium brown to orange-red to red to dark oxblood and, rarely, to very dark grey. In most blood pythons, the dark pattern elements are some shade of red and are not bounded by discrete black margins. The pale pattern elements on the back are typically yellowish. The pale pattern on the sides is usually a pale grey with tiny black flecks.

Although the pattern does not change with age, there is an ontogenetic colour change. The head and dark areas of pattern of hatchlings are typically pale brown to brownish-orange to brown. Blood pythons gradually darken with age. The juvenile colours of the dark body pattern may dramatically transform to red in the first 2–3 years of life. At that age, some blood pythons appear as blood-red snakes, the only pythonine taxa that could be described as bright red in adulthood. By 5–7 years of age, red coloration has darkened to oxblood, or dark reddish brown.

Scalation. There is an uninterrupted straight midline suture from the rostral posterior to the occiput. There are large paired head plates in broad contact along this suture, including the internasals, anterior prefrontals, posterior prefrontals, frontals, anterior parietals, and two or three smaller pairs of parietals. The nostril is located on the medio-posterior corner of the large nasal; the medial wall of the nostril is in contact with the adjacent internasals; the nostril opens upward and is directed slightly to the posterior. The nasal may show a well-defined suture from the nostril to the posterior margin, or in some cases, the area of the nasal scale posterior to the nostril appears to be divided into several small granular scales. The naso-preocular groove contains 4–14 small loreal scales (mean = 8.39, SD = 2.41, N = 28). The anterior portion of the groove is bounded along its lower side by 1–2 larger loreal scales (mean = 1.29, SD = 0.46, N = 28) that are positioned above and in contact with the second, third and fourth supralabials; the posterior portion of the naso-preocular groove is in contact with the preoculars and the supralabial in front of the orbit. The upper preocular is large, extends medially onto the top of the head and may be in slight contact with the anterior lateral margin of the frontal scale. Bordering the orbit below the upper preocular are 1–3 considerably smaller lower preoculars (mean = 2.14, SD = 0.48, N = 28). Most specimens have two supraoculars over each eye (mean = 1.77, SD = 0.48, N = 44); there is a large anterior supraocular in broad contact with the frontal, and most specimens have a small posterior supraocular. There are 1–3 postocular scales (mean = 2.07, SD = 0.48, N = 30). The subocular scales in the circumocular series are absent and in all cases (N = 44) the orbit is bounded along its lower margin by supralabials. The exact supralabial to contact the orbit varies; in 24 specimens the sixth and seventh supralabials contact the orbit; in 13 specimens the fifth and sixth contact, in three specimens the sixth is in contact; in two specimens the seventh supralabial is in contact.

The rostral is wider than high and has a pair of deep transverse pits. The first and second supralabials are deeply pitted. There are 9–13 supralabials (mean = 11.43, SD = 0.93, *N* = 47) and 17–22 infralabials (mean = 19, SD = 1.31, *N* = 32). There are 3–6 pitted anterior infralabials (mean = 4.21, SD = 0.69, *N* = 28). The series of 3–7 pitted posterior infralabials (mean = 4.93, SD = 0.81, *N* = 28) begins on the 10th–14th infralabials (mean = 12.04, SD = 0.79, *N* = 28).

There are 167–178 ventral scales (mean = 171.85, SD = 2.86, *N* = 34) and 24–36 subcaudal scales (mean = 29.86, SD = 2.64, *N* = 22). There are 45–53 anterior dorsal scale rows (mean = 49.65, SD = 2.21, *N* = 17) approximately one head-length from the nape, 53–61 dorsal scale rows around midbody (mean = 56.74, SD = 1.82, *N* = 19) and 32–38 dorsal scale rows on the posterior body (mean = 33.71, SD = 1.72, *N* = 17) approximately one head-length anterior to the vent.

Specimens examined

The data from specimens denoted by asterisk were taken from the literature. Sumatra, Indonesia: the vicinity of Rantauprapat: AM-R-51001, 51002, 51005, 51007, 51014, 51031, 51033, 51039, 41040, 51045, 51056, 51059, 51068, 51069, 51073, 51075, 51076, 51079, 51082, 51084, 51085, 51121–27, 51130–32, 51136, 51137; the vicinity of Palembang: VPI-R-079, 080; Medan: [no number]* (reported in Werner, 1925), RMNH-5427* (reported in Brongersma, 1947), ZMA-a-g* (reported in Brongersma, 1947); N. E. Sumatra: ZMA-h,i* (reported in Brongersma, 1947); Tinjoang, S. Bedjangkar, Assahan, N. E. Sumatra: ZMA-j* (reported in Brongersma, 1947); Kuala Simpang, S. E. Atchin, Sumatra: ZMA-k* (reported in Brongersma, 1947); Serbo Dolok: [no number]* (reported in Werner, 1900); Siolak Daras: [no number]* (cited as a communication from Dr O. S. Davis in Brongersma, 1947—O'Shea (pers. comm.) identifies this locality as Siolak Doiras, Korinchi); Sumatra (no other locality): RMNH 8457* (reported in Brongersma, 1947); Bangka, Indonesia: VPI-R-095. Singapore: MCZ-29779* (holotype, Stull, 1938). Peninsular Malaysia: Kuala Lumpur: USNM-53427* (paratype, Stull, 1938)); Pinang: VPI-R-092.

Our descriptions of colour and pattern also were supplemented by data from living specimens as follows. Sumatra, Indonesia: the vicinity of Rantauprapat: 20 specimens; the vicinity of Medan: 10 specimens; Bangka, Indonesia: 20 specimens; Bintan, Kepulauan Riau, Indonesia: one specimen. Peninsular Malaysia: Kuala Lumpur: 2 specimens; Johor Province, the vicinity of Johor Baharu: 20 specimens; Pinang: 6 specimens. Thailand: (no other locality): 10 specimens.

PYTHON CURTUS SCHLEGEL, 1872
SUMATRAN SHORT-TAILED PYTHON

Holotype. RMNH 3782.

Type locality. Sumatra.

Etymology. 'curtus' means shortened.

Diagnosis. Python curtus can be definitively differentiated from *P. brongersmai* by having fewer than 166 ventral scales, while *P. brongersmai* has 167 or more ventral scales. In most cases, *P. curtus* is distinguished from *P. breitensteini* in that the anterior pair of parietal scales are not in contact or are in slight contact, while in all examined specimens of *P. breitensteini*, the anterior pair of parietal scales are in broad contact at the midline suture. The bodies of adult *P. curtus* are always melanistic, while melanism is rarely seen in *P. breitensteini*. The pale markings on the bodies of *P. curtus* tend to be white or grey, while the pale markings on the bodies of *P. breitensteini* are typically pale yellow or tan. In most *P. curtus*, the fundi of the labial pits on the rostral and supralabials are darkly pigmented, while in *P. brongersmai* and *P. breitensteini* the fundi of these labial pits are typically pale in colour.

Description

Body size. Maximum length slightly exceeds 2 m. Large females weigh 15–18 kg. In the sample of wild-caught snakes studied by Shine *et al.* (1999a), 99 adult males averaged 120.7 cm snout–vent length (SD = 10.09) and 54 adult females averaged 130.1 cm SVL (SD = 7.35).

Pattern variation. This taxon is essentially a melanistic form; adult *curtus* become increasingly dark with age until much of the dorsal pattern of older specimens is obscured. The heads of adult specimens from Bandar Lampung District in southern Sumatra are black; the tops of the heads of specimens from central Sumatra are pale. On young specimens and pale-headed specimens there is a thin dark stripe on the midline of the top of the head from the internasals posterior to the occiput. Posterior to the occiput, the line expands in width and coalesces with the dark pattern on the neck. There may be a thin pale blotch centred in the line on the temporal region of the head and the nape of the neck. On 6 of 36 pale-headed adult specimens we have examined from the vicinity of Rantauprapat, Sumatra there is a transverse line across the temporal region of the head, similar in colour and thickness to the longitudinal midline stripe in the frontal region of the head. The sides of the snout are darkly stippled or uniformly black. Behind the eye there is a black triangular postocular blotch that originates on the postoculars and widens to become 4–6 scale rows in height at the level of the rictus. At the angle of the jaw this marking coalesces with the anterior lateral blotch on the neck that continues posteriorly approximately one head-length along the lower side of the anterior neck. There is a well-defined pale postocular stripe suffused with dark smudges and stipples from the lower postocular, crossing the line of the mouth 2–3 scales anterior to the rictus. There is a pale blotch on each side of the rostral, lateral to the tongue groove. There is a pale blotch on the anterior margin of the first supralabial. Some specimens may have a pale blotch on the second supralabial. The fundi of the rostral and supralabial pits are typically darkly pigmented (versus unpigmented in *breitensteini* and *brongersmai*). The lower margins of the supralabials are without dark flecking and appear pale. The infralabials anterior to the level of the eye appear as barred; each is white with a dark blotch along its anterior margin. The pitted posterior infralabials are evenly pigmented with dark stippling. The chin is white and immaculate.

The dorsal pattern of *curtus* generally comprises a series of longitudinal dark dorsal blotches. These blotches are irregular, subrectangular, or approximately rectangular in shape; most equal the width of the back. The pale background colour is darkest along the dorsolateral area, shading to a slightly paler colour at the midvertebral line, and becoming paler on the lower sides of the body. The background ground colour darkens with age with an increasingly dense fine stippling of black pigment. This stippling is absent immediately adjacent to the margin of the lateral blotches, forming a white halo around the lateral blotches. There is no pale halo bordering the dorsal blotches, as is typical for *breitensteini*. On the sides are a longitudinal series of large lateral blotches with black borders. The upper black borders are 2–4 scales wide. The blotches appear to be open on the bottom, and on the lower dorsal scale rows they shade to the ventral colour. Discrete black blotches may be scattered on the sides in the pale background colour. Most lateral blotches rise from the ventral surface to about halfway up the sides. Some lateral blotches may coalesce with superior dorsal blotches.

The dorsal and subcaudal surfaces of the tail of *curtus* are dark, sometimes with small irregular pale blotches. The venter is white or off-white and immaculate. Most paraventral scales are marked with a grey smudge.

Colour variation. Most adult *curtus* appear as dark, nearly black snakes. The sides of the head are dark, usually black. The tops of the heads of some specimens are pale, ranging from yellow-brown to brown to reddish brown. Other specimens have dark heads, the tops of their head appearing as charcoal grey or black. The pale postocular stripe is off-white with dark stipples or smudges. The colour of the iris of the eye ranges from yellow orange to orange to reddish-orange; the lower half of the pupil is made to appear wider than the upper half by a small black-pigmented blotch on the iris that contacts the lower half of the pupil.

The dark pattern elements on most of the body are dark grey-brown to black. On juvenile and young adults, the dark dorsal pattern may become increasingly dark progressing down the body, changing from brown to brownish black or black. The pale background colour of juvenile or young adults may be brown, grey-brown, or grey on the sides. In juvenile or young adult specimens the lateral blotches are similar in colour to the background colour. With age, the lateral blotches become darkly pigmented, heavily stippled with black. The lateral blotches have thick black upper margins and thin black sides. In some specimens the sides of the lateral blotches lack obvious borders, and the darker centre of the blotch shades evenly into background pigment on the lower sides of the body.

Although the pattern does not change with age, there is a dramatic ontogenetic colour change. Hatchling *curtus* appear as pale snakes with dark pattern. The head is pale, usually a pale tan. The dorsal blotches are typically dark brown. The background colour is a pale brown, sometimes with pink or flesh overtones. The centres of the lateral blotches are slightly more yellow than the background colour. As *curtus* age, nearly all aspects of the pattern become darker.

Scalation. There is an uninterrupted straight midline suture from the rostral to the posterior margin of the paired frontals. The suture then continues to the occipital region of the head, though not as straight as on the anterior portion of the head. The large paired head plates are in broad contact along this suture, including the internasals, anterior prefrontals, posterior prefrontals, frontals, and, in most specimens, three or four pairs of posterior parietals. The anterior pair of parietals is not in contact in 30 of 38 specimens examined. In all specimens of *brongersmai* and *breitensteini* we have examined, the anterior pairs of parietals are in broad contact at the midline suture.

The nostril is located on the medio-posterior corner of the large nasal; the nostril opens upward and is directed slightly to the posterior. There is a nasopreocular groove that is bordered with 5–27 small loreal scales (mean = 12.03, SD = 4.63, $N = 32$). The anterior portion of the groove is usually bounded along its lower side by 1–3 large loreal scales (mean = 1.16, SD = 0.45, *N* = 32) that contact the second and third supralabial; the posterior portion of the naso-preocular groove contacts the preoculars and the third, fourth, and fifth supralabials.

In most specimens circumocular scales encircle the orbit. There are 1–3 preoculars (mean = 1.53, SD = 0.65, *N* = 36); the upper preocular is large, extends dorso-medially across the canthus onto the top of the head, and but does not contact the frontal scale. One or two considerably smaller lower preoculars may border the orbit below the upper preocular. In all specimens examined (*N* = 39), there is one large supraocular in broad contact with the frontal. There are 1–3 postocular scales (mean = 1.92, SD = 0.60, *N* = 36), the upper one significantly larger than the others. There are 1–8 subocular scales (mean = 3.59, SD = 1.72, *N* = 32). Occasionally there are granular scales that separate some of the suboculars from directly contacting the supralabials.

The rostral is wider than high, and has a pair of deep transverse pits. The first and second supralabials are deeply pitted. There are 9–12 supralabials (mean = 10.46, SD = 0.65, *N* = 37) and 16–19 infralabials (mean = 17.13, SD = 0.87, *N* = 32). Usually beginning on the second infralabials there are 3–5 pitted anterior infralabials (mean = 3.94, SD = 0.56, *N* = 32). There is a series of 3–7 pitted posterior infralabials (mean = 4.84, SD = 0.77, *N* = 32) beginning below the eye on the 9th, 10th, or 11th infralabials (mean = 10.03, SD = 0.71, *N* = 31).

The ventral scales number 152–163 (mean = 158.35, SD = 2.88, *N* = 26) and subcaudal scales number 28–33 (mean = 30.71, SD = 1.70, *N* = 7). There are 47–51 dorsal scale rows around the neck (mean = 48.30, SD = 1.51, *N* = 7) at approximately one head-length from the nape, 55–61 dorsal scale rows around midbody (mean = 58.29, SD = 2.21, *N* = 7) and 31–37 dorsal scale rows around the posterior body (mean = 33.86, SD = 2.27, *N* = 7) at a distance of approximately one head-length anterior to the level of the vent.

Specimens examined

The data from specimens denoted by asterisk were taken from the literature. Sumatra, Indonesia: the vicinity west of Rantauprapat: AM-R-51006, 51012, 51013, 51015, 51025–28, 51036, 51038, 51041, 51048–50, 51052–54, 51106–19, 51128, 51129, 51133–35, VPI-R-091; Bandar Lampung: VPI-R-081, 082, 090; Sumatra (no other locality): RMNH-3782* (data from holotype reported in Brongersma, 1947); Mt Kabor, the vicinity of Padang: [no number]* (cited as a communication from Dr O. S. Davis in Brongersma, 1947); Kaba Wetan, Kepajang, Benkulen: [no number]* (cited as a communication from Dr O. S. Davis in Brongersma, 1947).

Our descriptions of colour and pattern also were supplemented by data from living specimens as follows. Sumatra, Indonesia: the vicinity of Rantauprapat: 15 specimens; Lampung Province: 20 specimens.

PYTHON BREITENSTEINI STEINDACHNER, 1880
BORNEO SHORT-TAILED PYTHON

Holotype. NMW 13287:1.

Type locality. 'Tewah, Borneo' (now Muarateweh, at the junction of the Barito and Teweh Rivers in Kalimantan, Indonesia).

Etymology. Named in honour of Dr Heinrich Breitenstein, a German regimental doctor who served with the Dutch army in the Dutch East Indies for 21 years. He made a collection of Borneo herpetofauna while stationed near the juncture of the Barito and Tewah Rivers that was purchased for the Naturhistorisches Museum Wien by Franz Steindachner.

Diagnosis. Python curtus can be definitively differentiated from *P. brongersmai* by having fewer than 166 ventral scales, while *P. brongersmai* has 167 or more ventral scales. In most cases, *P. breitensteini* can be distinguished from *P. curtus* in that the anterior pair of parietal scales are in broad contact at the midline suture, while in most cases the anterior parietals of *P. curtus* are not in contact or are in very weak contact. Melanism is rarely seen in *P. breitensteini*, while the bodies of adult *P. curtus* are always melanistic. The pale markings on the bodies of P. *curtus* tend to be white or grey, while the pale markings on the bodies of *P. breitensteini* are typically pale yellow or tan. The fundi of the rostral and supralabial pits of *P. breitensteini* are unpigmented, while on *P. curtus* the fundi of the labial pits on the rostral and supralabials are darkly pigmented.

Description

Body size. Females are slightly larger than males. Maximum length slightly exceeds 2 m. Large females weigh 15–20 kg.

Pattern variation. This taxon displays a variable pattern. The top of the head is pale. There is a prominent thin dark stripe on the midline of the top of the head from the internasals posterior to the occiput. Posterior to the occiput, the line becomes wider and coalesces with the dark pattern on the neck. There is a thin pale blotch centred in the line on the temporal region of the head and the nape of the neck. On 50% of the specimens we have examined (*N* = 20) there is a transverse line across the temporal region of the head similar in colour and thickness to the longitudinal midline stripe in the frontal region of the head. The sides of the snout appear darker than the top of the head due to an even flecking of dark pigment. The degree of flecking varies among specimens, with the sides of the snout of some specimens only slightly darker than the top of the head, while others appear as nearly black. There is a black mark in front of the eye on the lower portion of the upper preocular and the adjacent preocular. There is a black triangular postocular blotch that originates on the postoculars and widens to the area above the rictus; at the angle of the jaw this marking coalesces with a pale-centred blotch that continues posteriorly approximately one head-length onto the lower side of the anterior neck. There is a well-defined pale postocular stripe from the lower postocular, crossing the line of the mouth 2–3 scales anterior to the rictus and there contacting the white chin. The lower margins of the supralabials are without dark flecking and appear pale. The infralabials anterior to the level of the eye appear as barred; each is white with a dark blotch along its anterior margin. The pitted posterior infralabials are evenly pigmented with dark stippling. The chin is white and immaculate.

There are two general dorsal patterns seen in *breitensteini*. Most commonly, *breitensteini* is seen to have a longitudinal series of dark dorsal blotches. These blotches are irregular or approximately rectangular in shape, most equal the width of the back, and they tend to darken and coalesce on the posterior half of the body. In a second general dorsal pattern, specimens have a dark dorsum from the nape of the neck posterior to the tip of the tail. Typically the dark dorsal pattern becomes darker, even black, on the posterior half of the body. Interspersed along the vertebral line are small pale vertebral spots. On the posterior half of the body, the vertebral spots are more numerous and elongated and often are seen to coalesce to form a pale vertebral stripe that usually stops at the vent.

The ground colour of the side is pale, shaded darker with fine black stippling that is absent immediately adjacent to the dark dorsal pattern and the lateral blotches. On the sides are a longitudinal series of large lateral blotches with black borders. The upper black borders are 2–4 scales wide. The blotches appear to be open on the bottom and on the lower dorsal scale rows they shade to the ventral colour. There may be discrete black blotches scattered on the sides in the pale ground colour. On the anterior half of the body, the lateral blotches rise from the ventral surface to about halfway up the sides. On the posterior half of the body these dark lateral blotches contact and coalesce with the dark dorsal surface.

The tail of *breitensteini* is dark, sometimes with one or two small irregular pale blotches. The venter is off-white and immaculate. Most paraventral scales are marked with a grey smudge. The subcaudal surface is dark, sometimes with small pale blotches.

Colour variation. There is substantial colour variation in this taxon. The head is pale yellow-brown to brown. The sides of the snout are similar in colour to the top of the head, but are a darker hue. The pale postocular stripe ranges from a pale yellow-brown to a pale pinkish brown to pale tan. The sides of the head may have an orange or salmon blush. The colour of the iris of the eye ranges from yellow to orange to brown orange; the lower half of the pupil is made to appear wider than the upper half by a small black-pigmented blotch on the iris that contacts the lower half of the pupil.

The dark pattern elements on most of the body are chestnut to rich dark brown to black. Much of the dark pattern is bounded by a thin black margin. The dark dorsal pattern may become increasingly dark progressing down the body, becoming uniformly brownish black or black. The pale pattern elements on the centre of the back are yellow or yellow-brown becoming a pale brown, grey brown, or grey on the sides. The lateral blotches are yellow-brown, orange-brown, or a greenish-brown with thick black upper margins and thin black sides; in some specimens the sides of the lateral blotches are without apparent borders, and the pigmented area of the blotch shades evenly into the more neutrally coloured background pigment.

While the pattern does not change with age, there is an ontogenetic colour change. The head is pale, usually a pale tan. The dark areas of pattern of hatchlings are typically dark brown. The centres of the lateral blotches are orange-brown. The dark pattern of *P. breitensteini* on the anterior half of the body becomes somewhat paler with age while the background colour of the sides darkens with age. In some specimens from Sarawak, the head and body darkens with age to become quite dark, appearing as melanistic versions of *breitensteini*. At no age does *breitensteini* appear as a red snake, as do many specimens of *brongersmai*.

Scalation. There is an uninterrupted straight midline suture from the rostral to the posterior margin of the paired frontals; the suture then continues to the occiput, though not as straight as on the anterior portion of the head. There are large paired head plates in broad contact along this suture, including the internasals, anterior prefrontals, posterior prefrontals, frontals, anterior parietals, and 2–4 pairs of posterior parietals. The nostril is located on the medio-posterior corner of the large nasal; the nostril opens upward and is directed slightly to the posterior. There is a naso-preocular groove that is bordered with small loreal scales. The anterior portion of the groove is usually

Table 2. Key to the three taxa

1a.	There are 167 or more ventral scales	*P. brongersmai*
1b.	There are 165 or fewer ventral scales	2
2a.	The anterior pair of parientals are not in contact or are only weakly contacting	*P. curtus*
2b.	The anterior pair of parietals are in broad contact at the medial suture	*P. breitensteini*

bounded along its lower side usually by one large loreal, (mean = 1.22, SD = 0.44, *N* = 9); occasionally the large loreal appears to be subdivided to become a larger anterior scale and a smaller posterior loreal. The large one or two loreals are positioned above and in contact with the second and third supralabial. The posterior portion of the naso-preocular groove is in contact with the preoculars and the third, fourth, and fifth supralabials.

Circumocular scales encircle the orbit in most specimens. There are 1–3 preoculars (mean = 2.10, SD = 0.45, *N* = 20). The upper preocular is large, extends dorso-medially across the canthus onto the top of the head, and may contact the anterior lateral margin of the frontal scale. Below the upper preocular there may be one or two considerably smaller lower preoculars. There is one, rarely two supraoculars (mean = 1.13, SD = 0.34, *N* = 23); the large supraocular is in broad contact with the adjacent frontal. There are 1–4 postoculars (mean = 2.10, SD = 0.72, *N* = 20); in most specimens there is a large upper postocular and a small lower postocular. There are 0–5 suboculars (mean = 3.12, SD = 1.73, *N* = 8). In the one specimen observed to have no suboculars, the condition varied from the typical *brongersmai* condition of supralabial-orbit contact in that the adjacent supralabials were separated from contacting the lower margin of the orbit by a space of bare skin. In specimens with 1 or 2 suboculars, the scales were shaped as thin elongated subrectangles. The rostral is wider than high, and has a pair of deep transverse pits. The first and second supralabials are deeply pitted. There are 9–11 supralabials (mean = 10.00, SD = 0.88, *N* = 19) and 14–19 infralabials (mean = 15.38, SD = 1.61, *N* = 13). There are typically four pitted anterior infralabials, beginning on the second, and 5–6 pitted posterior infralabials.

The ventral scales number 154–165 (mean = 160.27, SD = 2.86, *N* = 22) and subcaudals number 27–33 (mean = 30.18, SD = 2.32, *N* = 11). There are 45–50 dorsal scale rows around the neck (mean = 48.00, SD = 1.73, *N* = 11) at approximately one head-length from the nape, 50–57 dorsal scale rows around midbody (mean = 54.55, SD = 2.62, *N* = 11) and 30–37 dorsal scale rows around the posterior body (mean = 32.91, SD = 1.87, *N* = 11) at approximately one head length anterior to the vent.

Specimens examined

The data from specimens denoted by asterisk were taken from the literature. Kalimantan, Indonesia: the vicinity of Pontianak: 10 unnumbered specimens (data collected by Shine in 1997); the vicinity of Sambas: VPI-R-083-089; Banjarmasin: VPI-R-093, 094. Additionally, data from 12 live specimens in the VPI collection (scale counts were made from photos) were incorporated in the data base, including 10 specimens from the vicinity of Sambas, one specimen from Sarawak, and one specimen from Banjarmasin.

Our descriptions of colour and pattern also were supplemented by data from living specimens as follows. Kalimantan, Indonesia: the vicinity of Sambas: 25 specimens; the vicinity of Pontianak: 20 specimens; the vicinity of Banjarmasin: 5 specimens. Sarawak, Malaysia: the vicinity of Kuching: 4 specimens; Sibu: 1 specimen.

For a key to the three taxa see Table 2.

DISCUSSION

The major results of our analysis are very straightforward. The Asian blood and short-tailed pythons comprise a reciprocally monophyletic group. Three taxa are recognizable within this group, and are easily distinguished from each other both genetically and phenotypically. Although criteria for recognizing taxa as species versus subspecies are necessarily subjective, the patterns of divergence represented in our data clearly express the morphological and genetic distinctiveness of each taxon and show that each taxon is on its own unique evolutionary trajectory. Thus, under the phylogenetic species concept (Cracraft, 1983), we believe the species level rank is the most appropriate for each of these three taxa. *Python curtus* and *P. breitensteini* are similar to each other in many respects, while *P. brongersmai* is much more distinctive. Phylogenetic analyses reveal that this latter taxon is the sister-group to the other two (Fig. 1). The maximum sequence divergence between *brongersmai* and both *breitensteini* and *curtus* (8.9%) is only slightly smaller than the minimum sequence divergence (10.3%) between all three ingroup taxa and the outgroup species *Python reticulatus*.

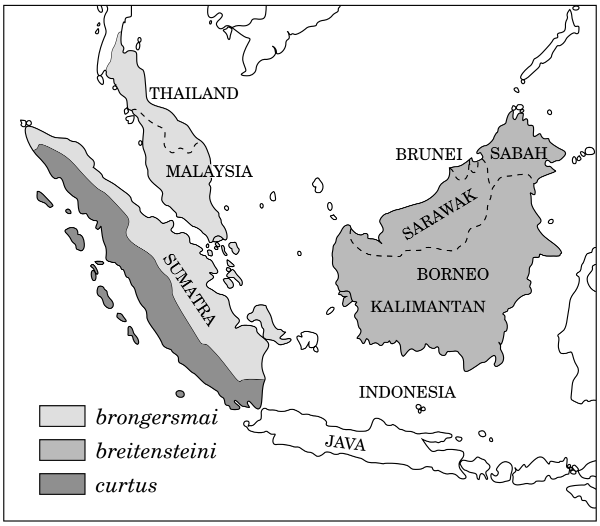

Figure 3. Geographic distributions of the three taxa within the *Python curtus* lineage. In Sumatra, *P. brongersmai* and *P. curtus* are allopatric as far as we know. The geographic division between these two taxa on the map runs along the mountain range that extends the length of Sumatra, but neither species is known to occur above approximately 2000 m on either side of the mountain range. They may overlap in the foothills is the south-eastern portion of their range, but very little is known of their distribution in this area.

Two aspects of our results are striking: the strong divergence between *brongersmai* versus the other taxa, and the lack of divergence within each of the three terminal taxa, even when comparing among specimens from very widely separated localities. In the case of *brongersmai,* this overall genetic similarity means that the divergent colour morphs within this species are so closely related to each other as to be indistinguishable in our data (Fig. 1; Table 1). Thus, although superficial examination might suggest that the darker morphs of *brongersmai* are more closely related to *curtus,* this hypothesis can be rejected from our study. The substantial ecological differences among snakes of each colour morph, even when collected in sympatry (Shine *et al.,* 1998a), thus remain an intriguing biological puzzle.

Our phylogenetic hypothesis has strong implications for the biogeographic processes involved in the evolutionary history of these animals (Figs 3 and 4). The area around Wallace's Line has been a classic research topic for geologists and biogeographers, and substantial information is available both on the geological history of the region, and the degree of biotic similarity among different parts of this region (e.g. Hall, 1998; Metcalfe, 1999). At first sight, this pattern seems paradoxical in the case of the *Python curtus* lineage (compare Figs 3 and 4). Because they both occur on Sumatra, we would expect *brongersmai* and *curtus* to be more closely related to each other than either is to the Borneo form (*breitensteini*). Instead, *curtus* and *breitensteini* are each other's closest relatives: a Templeton Test shows that forcing *curtus* to be the sister group to *brongersmai* yields a tree of 96 steps, 19 steps longer than the most parsimonious tree ($z = 4.1461$, $P<0.0001$). Thus, two closely related taxa occur at either edge of the geographic range of the lineage, in Borneo to the east (*breitensteini*) and western Sumatra to the west (*curtus*). A taxon (*brongersmai*) that is only distantly related to the other groups extends through the central area of the range (eastern Sumatra). Such a pattern could be generated by interspecific interactions, with one taxon (*brongersmai*) extending its range by competing with and thereby eliminating its relatives from eastern Sumatra. However, a model based on sea-level fluctuations is more consistent with our sequence data.

From about 20 to 10 million years ago (Mya), most of Sumatra was under water (Hall, 1998; Metcalfe, 1999). The low-lying areas of eastern Sumatra remained covered by oceans until 5 Mya, by which time the higher areas of western Sumatra had been emergent for several million years. Throughout much of this latter period, a land bridge existed between southern Kalimantan and southern Sumatra (Hall, 1998). With more recent falls in sea level, the eastern side of Sumatra emerged from the sea. Our phylogenetic hypothesis (Figs 1, 4) suggests that ancestral populations of the *Python curtus* lineage were separated into two groups by rising sea levels: one lineage (proto-*brongersmai*) on continental south-east Asia and the other (proto-*curtus*) in Borneo. The two groups were sometimes linked by direct landbridges (i.e. from Borneo to Malaysia, not via Sumatra) but habitat barriers may have discouraged gene flow. Because migration from Borneo to western Sumatra remained possible (at least intermittently), these groups remained relatively similar and ultimately achieved subspecific differentiation (*curtus* vs. *breitensteini*). These two taxa show a 3% divergence in cytochrome *b* sequences. A very conservative mitochondrial DNA calibration of approximately 2% sequence divergence/million years (Brown, George & Wilson, 1979; Wilson *et al.,* 1985) suggests that they shared a common ancestor about 1.5 Mya. But they could have diverged much earlier as several more recent studies on reptiles have suggested considerably lesser rates than 2%/million years (e.g. Zamudio & Greene, 1997).

As sea levels fell more recently (<5 Mya), vast low-lying areas of eastern Sumatra became available for colonization by pythons. Although *curtus* was presumably widespread along western Sumatra, it had no easy access to these areas because the high central

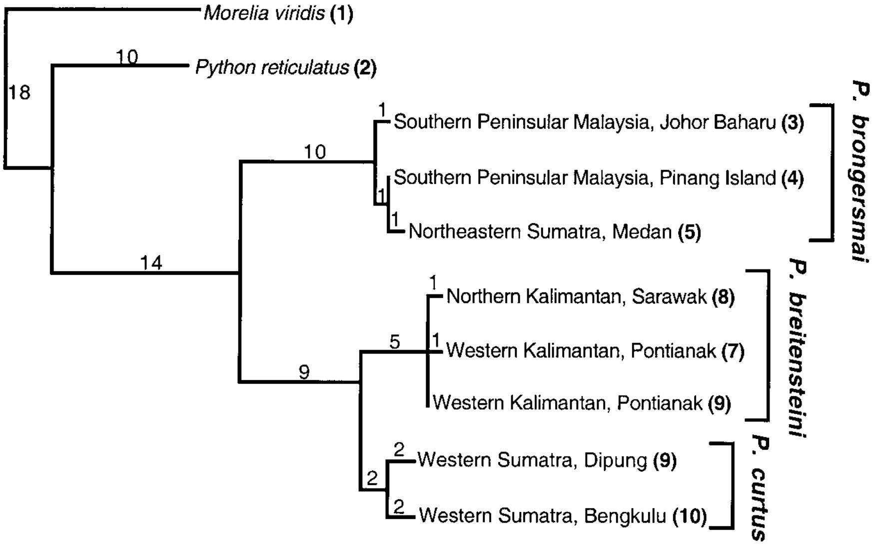

Figure 4. Phylogram showing relationships among the two outgroup and eight ingroup haplotypes. Haplotype numbers are noted in parentheses and taxon names have been replaced with locality information. Phylogeographic substructure is evident among populations of each taxon.

mountain range that runs the length of Sumatra does not provide suitable habitat for these animals. Immigration from Borneo to Sumatra was precluded by the oceans. Thus, the taxon that moved into the newly emergent area was *brongersmai*, from the adjacent mainland of Southeast Asia. The distance between eastern Sumatra and Malaysia is very small (<50 km; see Fig. 3) and these snakes presumably moved southwards along the Malay Peninsula as the land emerged from the sea. None of the lineages could spread further south into Java, because it was already isolated as an island by 5 Mya (Hall, 1998).

This biogeographical hypothesis is supported by several lines of evidence. First, reconstructions of land areas over the last 20 Myr provide robust support for the main geological assumptions behind the model (Hall, 1998; Metcalfe, 1999). Second, analyses of area cladograms of other organisms in this general region reveal similar kinds of associations as are evident in our own analyses. For example, the snake species *Naja sumatrana*, *Tropidolaemus wagleri* and *Trimeresurus sumatranus* are found on Malaysia, Borneo and Sumatra, but not on Java (Wüster & Thorpe, 1989; McDiarmid *et al.*, 1999). The plant species of Malaysia and eastern Sumatra share many affinities (note that this covers the range of *brongersmai*), with the floras of Kalimantan and northwestern Sumatra (the range of *curtus*) more similar to each other, and more distant from the eastern Sumatran-Malaysian flora (Ridder-Numan, 1998). Faunal groups such as orang-utans and freshwater fishes also reveal strong affinities between southern Borneo and Sumatra (Van Oosterzee, 1997). Morphological divergence among Indonesian reptiles correlates well with landmass connectivity during Pleistocene sea-level fluctuations (How, Schmitt & Suyanto, 1996; How & Kitchener, 1997). Third, the virtual lack of genetic substructuring within each python taxon, despite the long distances involved across their respective ranges (e.g. northern to southern Sumatra) strongly suggests recent dispersal into these areas.

Undoubtedly, other factors also have affected the distribution of this group of snakes. Climatic conditions have changed considerably through time, and events such as cold dry glacial periods 190 000 years ago, and again at 80 000 years ago, may well have modified habitats sufficiently to affect python distributions (Brandon-Jones, 1988). Another important influence on habitats is human activity. The natural habitats of the Indonesia islands have been substantially modified during the long course of human habitation. Recent studies suggest that *P. brongersmai* in northern Sumatra are much more abundant in palm-oil plantations than in natural forests, presumably because of the enhanced availability of commensal rodents as prey (Shine *et al.*, 1999a). Skin-dealers in the Rantauprapat area report that numbers of *P. brongersmai* have increased markedly (with a simultaneous decline in *P. reticulatus*) as plantations have expanded in size. There is also a strong possibility of range modification due to escape, because snakes collected for the commercial trade are often moved long distances for the point of collection to the slaughterhouses. For example, slaughterhouses in the Medan area (within the range of *P. brongersmai*) often receive shipments of live *P. curtus* from the west coast (Shine *et al.*, 1998a, 1999a).

As well as clarifying taxonomic levels and suggesting biogeographic histories, our data on the *P. curtus* lineage have significant implications for the conservation and management of these pythons. Present harvesting quotas are based on the presumption that *'Python curtus'* comprises a single biological entity (e.g. Groombridge & Luxmoore, 1991). Clearly, this is not the case. Our taxonomic revision does not affect the harvest of short-tailed pythons in Borneo, because these all belong to the subspecies *P. c. breitensteini*, and already are managed as a separate resource (Groombridge & Luxmoore, 1991; Erdelen, 1997). However, the situation in Sumatra is more worrying. Based on examination of specimens at slaughterhouses, the commercial trade is based primarily on *brongersmai* rather than *curtus* (approx. 92% *brongersmai*: Shine *et al.*, 1999a). However, the exact proportion of each species that is harvested differs among slaughterhouses and varies through time (Shine *et al.*, 1999a).

Because both of the Sumatran species of blood and short-tailed pythons feed primarily upon commensal rodents and readily exploit anthropogenically disturbed habitats, current levels of commercial offtake may well prove to be sustainable (Shine *et al.*, 1998d, 1999a,b). Nonetheless, it is difficult to evaluate the effects of the commercial trade. An approximate constancy through time in harvest levels and in average body sizes of harvested snakes may be used as an indirect indication that the populations are not being substantially altered by commercial activities (Shine *et al.*, 1998d). However, our analysis raises the possibility that such constancy overall (i.e. in the total sample) might mask substantial changes in such attributes within one of the two species involved. The obvious solution is to monitor these attributes separately for each taxon, so that (1) we have an idea of the relative harvest of each species, and (2) biological attributes can be examined at a species-specific level. In practice, distinguishing the two species is unlikely to be problematical. Even after the skins are removed and bleached, significant interspecific differences in ventral scale counts (>166 in *brongersmai*, <164 in *curtus*: see above) allow unequivocal identification of dried skins. We thus recommend that future management of this resource should involve not only regular monitoring of the numbers and sizes of skins at commercial premises, but also that a statistically robust sample of those skins should be identified to species level by counting ventral scale numbers.

More generally, there is an urgent need for further studies on the systematics of commercially exploited Asian reptiles. We doubt that blood and short-tailed pythons are unique in containing genetically and morphologically distinctive 'populations' that warrant full species status. For example, recent work has identified undescribed species within the Indonesian scrub pythons (*Morelia amethistina*: Harvey *et al.*, 2000) and freckled pythons (*Liasis mackloti*: Barker and Barker, in prep). It is entirely likely that the most intensively harvested Indonesian python, *P. reticulatus*, similarly contains an undescribed diversity of species-level taxa. Given the high rates of commercial exploitation of Indonesian reptiles, and the potential ecological role of these species (including their importance as predators of agriculturally important rodents: Lim, 1974), the current lack of understanding in this area warrants urgent attention. Without reliable, well-based taxonomies for such animals, we are unable to formulate rational plans for their management and conservation.

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