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Review of the reticulated python (*Python reticulatus* Schneider, 1801) with the description of new subspecies from Indonesia

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Abstract The geographically widespread *Python reticulatus*, the world's longest snake, has been largely neglected by taxonomists. Dwarfed individuals from Tanahjampea Island, Indonesia, differ strikingly in morphology. Phylogenetic relationships were analyzed using a 345-bp fragment of the cytochrome *b* gene for 12 specimens from different populations. Both genetic differences and morphological characters distinctly revealed two taxonomic subunits. The island populations of Tanahjampea and Selayar form two monophyletic lineages, supported by high bootstrap values, with distinct differences in color pattern and scalation. We consider these forms to represent two new subspecies. The Tanahjampea form is genetically related to populations of the Sunda Islands and mainland Southeast Asia, whereas the Selayar form is related to populations of Southwest Sulawesi. We conclude that, due to strong directional surface currents in this region, gene flow between Tanahjampea and Selayar is prevented. Sea-level changes during the Pleistocene probably contributed to the isolation of the two taxa described. Aspects of ecology and conservation status are briefly discussed. Electronic supplementary material to this paper can be obtained by using the Springer LINK server located at <http://dx.doi.org/10.1007/s00114-002-0320-4>.

Introduction

The reticulated python is one of the economically most important giant reptiles worldwide (Groombridge and Luxmoore 1991; Jenkins and Broad 1994; Murphy et al.

1998; Walls 1998). It is regulated under Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and highly exploited by the leather industry (Auliya and Abel 2000a). The majority of skins originate from Indonesia, in particular from the islands of Sumatra and Borneo (Jenkins and Broad 1994; Erdelen et al. 1997; Shine et al. 1999). The Federal Agency for Nature Conservation of Germany initiated the project "Status, population biology and conservation of the water monitor (*Varanus salvator*), the reticulated python (*Python reticulatus*) and the blood python (*Python curtus*) in Sumatra and Kalimantan, Indonesia" which was conducted from 1996 to 1997 (Erdelen et al. 1997). The major objectives of this project were to examine the harvest impact on local populations, to assess long-term sustainability of current harvesting levels and to recommend conservation measures.

Despite its extensive distribution from Assam and the Nicobar islands in the west to the Philippines and eastern Indonesia, and the fact that distinct insular morphs from Indonesia have been recognized within the pet trade (Yuwono 1998), the reticulated python has not been reviewed taxonomically. Over the last decade the live reptile trade has increased steadily, with giant snakes playing a major role in the demands of many "western" herpetoculturists (Hoover 1998; Auliya 1999). Rising demands from the main importers (USA, EU and Japan) led to the exploration of remoter regions of Indonesia, revealing new taxa or island morphs. Wallacea, a bioregion denoted to the Indonesian islands, lying between the Sunda shelf and the Sahul shelf (Darlington 1957), and thus possessing a mixture of oriental and Australian faunas, is of special interest.

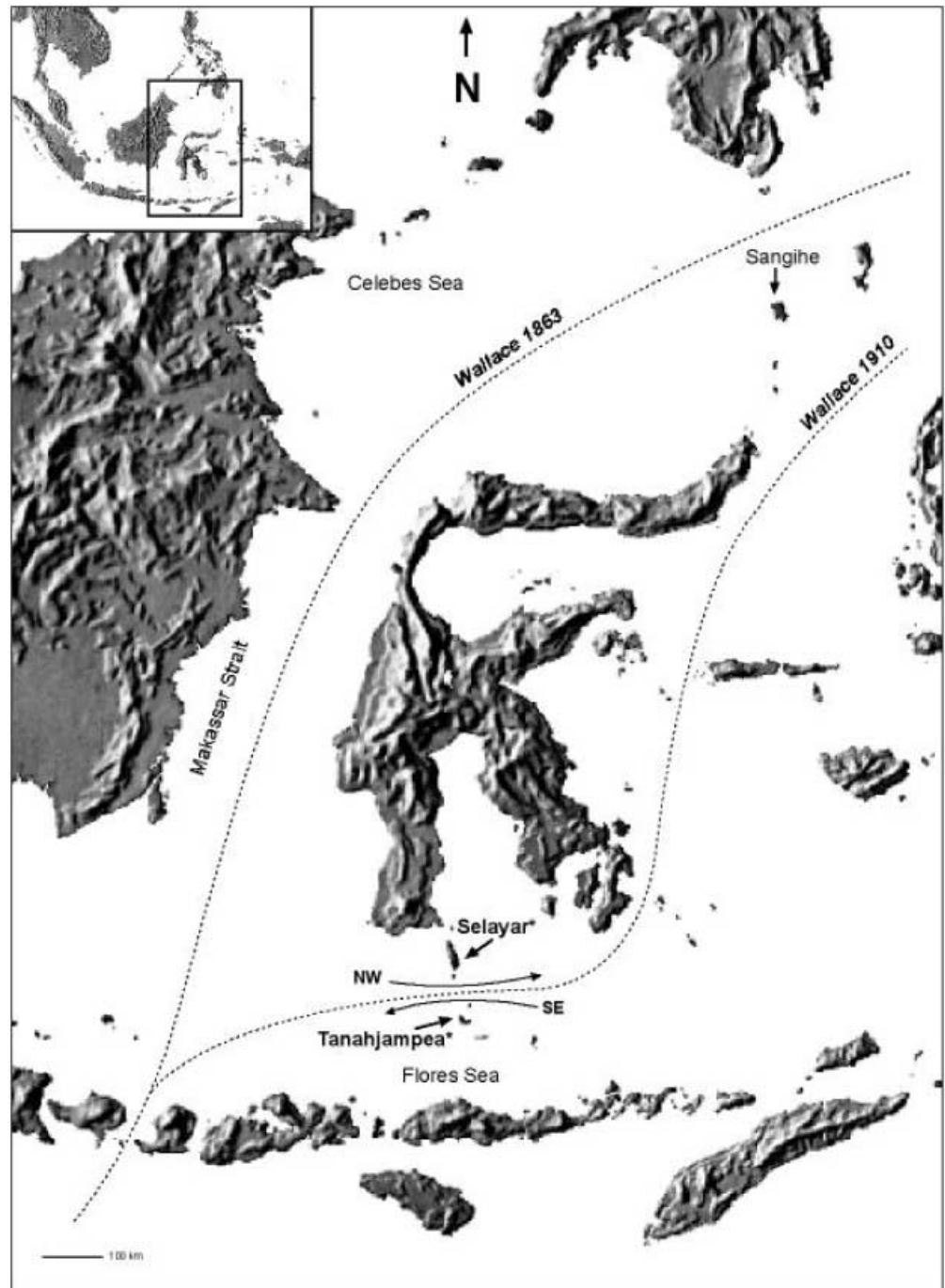
Distinct differences in morphometry and color pattern of populations originating of Tanahjampea initiated an investigation of molecular characters of *P. reticulatus*.

Mertens (1934) noted that, compared to populations of the Greater Sundas and mainland Southeast Asia, populations of smaller-sized *P. reticulatus* inhabit the Lesser Sundas. Recently reptile dealers have reported dwarf forms from the Flores Sea islands of Selayar, Kayuadi

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Fig. 1 Distribution of *Python reticulatus jampeanus* and *Python reticulatus saputrai*, also showing the location of the distinct population from Sangihe Island. Wind-forced currents generated by the monsoon winds are indicated as the northwest monsoon (NW) and the southeast monsoon (SE)



and Tanahjampea (Fig. 1). Populations of Tanahjampea reach a maximum total length of approximately 2.10 m in males and 3.35 m in females (F.B. Yuwono, D. MacRae, T. Lilley, personal communication). Compared to recorded maximum total lengths of 8–10 m elsewhere (in particular in some populations of Sulawesi), Tanahjampea pythons attain about only one-quarter of that size. Moreover, the young measure less than 30 cm in total length at birth (D. MacRae, personal communication). Field studies in Sumatra and Kalimantan document that

hatchlings measured 65–83 cm in total length (Erdelen et al. 1997; Abel 1998; Riquier 1998). Hatching sizes between 60 and 75 cm are reported from Sunda shelf populations (Van der Meer Mohr 1926; Wall 1926; Kopstein 1938; Smith 1943; Lederer 1944; Honegger 1970; Lim 1981; Murphy et al. 1994; Barker and Barker 1997). Lederer (1944) and Barker and Barker (1997) also describe newborns of 45 and 55 cm. However, the hatching size of pythons from Tanahjampea was far beyond the lowest records reported so far.

This study provides new morphological and molecular data on the taxonomy of various populations of *P. reticulatus*. We describe two new taxa and explain the distribution of these geographically isolated taxa on the basis of the region's paleogeography.

Materials and methods

Ecological fieldwork was conducted from January 1996 until February 1997, September 1999 and from 7 July until 11 August 2000 in West Kalimantan, West Java, Bali, SW Sulawesi and Selayar. In 1996, reptile slaughterhouses were visited in Sambas, Siantan and Pontianak (West Kalimantan), Medan and Rantauprapat (North Sumatra), where further taxonomic and biological data were collected. In mid-September 1999, reptile skinners were visited in North Jakarta, Tambun (West Java), and in July 2000 on Selayar Island (SW Sulawesi). Live reptile traders were visited in the years 1996, 1997, 1999 and 2000 in Jakarta, Bali, Pontianak and SW Sulawesi.

Specimens

Specimens from 12 populations of the reticulated python and one outgroup were used in our analysis (see Table 1).

Tissue samples of *P. reticulatus* (muscle, preserved in 98% ethanol) were taken from the following localities: Rengit (01°40'N; 103°08'E), West Malaysia (ZFMK 32378); Chin Xai, Vietnam (ZFMK 73478); the catchment area of Sambas (01°20'N; 109°15'E), West Kalimantan (ZFMK 70153); Cirebon (06°46'S; 108°33'E), West Java (ZFMK 73479); and Sangihe Island (Tahuna: 3°33'N, 125°33'E), off the northeastern tip of Sulawesi.

Python molurus (ZFMK 20337) from South China represents the outgroup taxon. Voucher specimens with ZFMK numbers are deposited in the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.

Blood-samples were collected from live specimens in Bali, Bira in SW Sulawesi, Selayar (ZFMK 73473, 73474), and Tanahjampea (ZFMK 73475, 73476, 73477).

In the field, blood was added to a long-term storage buffer (100 mM NaCl, 100 mM Tris-HCL pH 8.0, 100 mM EDTA, 0.5% SDS; in equal parts).

Genetic analysis

DNA was extracted using QIAmp tissue extraction kits (Qiagen). We used the primers *cytb* L14841 (light chain; 5' – AAA AAG CTT CCA TCC AAC ATC TCA GCA TGA TGA AA – 3') and *cytb* H15149 (heavy chain; 5' – AAA CTG CAG CCC CTC AGA ATG ATA TTT GTC CTC A – 3') of Kocher et al. (1989) to amplify a section of the mitochondrial cytochrome *b* ribosomal RNA gene.

PCR cycling procedure was performed following Austin (2000): (1) one cycle for 3 min at 94°C, 1 min at 47°C, 1 min at 72°C; (2) 34 cycles for 45 s at 94°C, 45 s at 57°C, 1 min at 72°C; (3) 1 cycle for 6 min at 72°C.

PCR products were purified using Qiaquick purification kits (Qiagen). Fragments were sequenced from one direction using an automatic sequencer (ABI 377). Thirteen sequences, comprising 345 bp homologous to base-pair positions 16384–16877 of the *Xenopus laevis* mitochondrial genome (Roe et al. 1985, have been submitted to GenBank (accession numbers: AY014884–AY014896) and could be unambiguously aligned (no insertions or deletions) using the computer program SEQUENCE NAVIGATOR (Applied Biosystems). The complete alignment is available from the authors on request.

Using PAUP*4.0b4a (Swofford 1998), both parsimony and likelihood phylogenetic reconstruction methods were applied. For maximum parsimony (MP) we used the branch-and-bound search

option with parsimony-uninformative characters included. When more than a single tree was found, a strict consensus tree was generated. The maximum likelihood (ML) analysis employed the HKY85 model, for which base frequencies and the transition/transversion rate ratio were estimated from the data (Hasegawa et al. 1985). The values were estimated using PAUP* and MODELTEST 3.0 (Posada and Crandall 1998). The ML tree was obtained using the heuristic search option, random addition sequences with 100 replications, and tree bisection reconnection (TBR) branch-swapping.

Relative branch support in each phylogenetic analysis was evaluated with 2,000 bootstrap pseudoreplicates for MP and 100 replicates for ML analysis. We considered bootstrap values of 80% as giving strong support to the respective node (Hillis and Bull 1993).

The program PHYSID (Wägele and Rödding 1998) was used to calculate the numbers of synapomorphies supporting monophyletic groups (with noise level reduced to 0%).

Confidence in the phylogenetic signal for this molecular dataset was assessed in two ways. The presence of a significant phylogenetic signal was estimated using the *g*1 statistic (Hillis and Huelsenbeck 1992) estimated from 100,000 randomly generated parsimony trees, and the permutation-tailed probability (PTP) test as suggested by Faith and Cranston (1991), with 100 replicates (both implemented in PAUP*).

Morphology

Morphometric measurements included total length (TOL), snout-vent length (SVL), and tail length (TL). Sexes were identified by measuring the length of the genital pockets with a probe (males have deeper pockets) and by dissection of the tail root.

Data were taken on the following scales: supralabials, infralabials, preoculars, postoculars, rostral, nasals, internasals, loreals, anterior prefrontals, posterior prefrontals, frontals, supraoculars, parietals, interparietals, ventrals, subcaudals, dorsals, and the anal shield. Subcaudal scale number 1 was defined as the first unpaired scale being distinctly wider than long, ignoring 1–2 anterior paired scales bordering the cloaca. The tail-tip was not included in the total subcaudal counts. Dorsals were counted one head length posterior to the head, at a point half of SVL minus head length, and one head length anterior to the cloaca.

In addition, infralabial, supralabial, and rostral pits were counted, as were the number of supralabials entering the orbit.

Results

Our genetic and morphological studies have resulted in the naming of two discrete subspecies with distinct genetic structure and unique characters in scalation and color pattern.

Genetic analysis

Of the 345 sequenced sites, 40 sites were variable, and 11 were parsimony-informative. For the ML analysis the following parameters were calculated by MODELTEST: transition/transversion ratio = 2.6298; base frequencies A=0.3067, C=0.3153, G=0.1068, and T=0.2717, with equal rates for all sites. The matrix for the absolute numbers of DNA-sequence differences and pairwise HKY85-corrected genetic distances for all nucleotide sites is presented in Table 1. Within *P. reticulatus*, pairwise-corrected distances were moderately large and ranged from 0.0000 to 0.03606 (Table 1). The intergeneric distances

Table 1 Summary of the absolute number of DNA-sequence differences (above the diagonal) and HKY85 corrected genetic distances below (asterisk represents holotype)

	1	2	3	4	5	6	7	8	9	10	11	12	13
1 <i>Python molurus</i> , China	-												
2 <i>Python reticulatus</i> , Vietnam	0.1394	-											
3 <i>P. reticulatus</i> , Malaysia	0.1432	0.0029	-										
4 <i>P. reticulatus</i> , Java	0.1394	0.0000	0.0029	-									
5 <i>P. reticulatus</i> , Bali	0.1341	0.0000	0.0030	0.0000	-								
6 <i>P. reticulatus</i> , W Kalimantan	0.1432	0.0029	0.0059	0.0029	0.0034	-							
7 <i>P. reticulatus</i> , Tanahjampea	0.1357	0.0029	0.0059	0.0029	0.0032	0.0059	-						
8 <i>P. reticulatus</i> , Tanahjampea	0.1357	0.0029	0.0059	0.0029	0.0032	0.0059	0.0000	-					
9 <i>P. reticulatus</i> , Tanahjampea*	0.1357	0.0029	0.0059	0.0029	0.0032	0.0058	0.0000	0.0000	-				
10 <i>P. reticulatus</i> , Sangihe	0.1509	0.0209	0.0240	0.0209	0.0202	0.0240	0.0300	0.0240	0.0238	-			
11 <i>P. reticulatus</i> , Selayar	0.1244	0.0269	0.0299	0.0269	0.0231	0.0300	0.0300	0.0300	0.0300	0.0363	-		
12 <i>P. reticulatus</i> , Selayar*	0.1244	0.0269	0.0300	0.0269	0.0232	0.0300	0.0300	0.0300	0.0299	0.0361	0.0000	-	
13 <i>P. reticulatus</i> , SW Sulawesi	0.1244	0.0269	0.0300	0.0269	0.0232	0.0300	0.0300	0.0300	0.0299	0.0361	0.0000	0.0000	-

between the outgroup *P. molurus* and the *P. reticulatus* populations varied from 0.12442 and 0.15089 (Table 1). For populations of Selayar and Tanahjampea, no sequence differences among individuals of either population were present.

The branch-and-bound search produced two equally parsimonious trees. These differed only in the positioning of the Bali specimen. The 50% majority-rule consensus tree and the single best maximum likelihood (ML) tree are presented in Fig. 2. Both MP and ML methods produced the same topology.

1. The populations of SW Sulawesi and Selayar form a distinct monophyletic clade, which is well-supported by bootstrap analysis in MP (88). In ML this clade is also evident, but it is only moderately supported by bootstrap analysis (67). The same topology was obtained using a second gene (12S rRNA) (unpublished data). For this clade we found seven supporting synapomorphies.
2. A second clade, strongly supported by bootstrap values (MP: 88; ML: 84) containing the remaining analyzed populations, supported by two synapomorphies, represents the sister lineage to the Sulawesi and Selayar clade.

Within this second clade both ML and MP analyses consistently show two more clearly differentiated populations:

3. The population from Sangihe forms a distinct lineage and stands basal within the second clade, also with moderate bootstrap support (MP: 69; ML: 79).
4. A further monophyletic group consisting of the three specimens from Tanahjampea exists, but only with a rather weak bootstrap support in MP (56), while in ML the bootstrap support is below 50%. This clade is supported by one synapomorphy.

Despite the paucity of parsimony-informative characters, we find no homoplasies between the different splits, which means that those splits are completely compatible on the reconstruction.

The *g*₁ statistic (estimated from 100,000 randomly generated trees) was -1.770 ($P < 0.01$), which according to Hillis and Huelsenbeck (1992), indicates significant phylogenetic signal. The PTP test resulted in a significant difference ($P = 0.01$) between the most parsimonious tree and trees generated from random permutations of the data matrix, which according to Faith and Cranston (1991) demonstrates the presence of significant phylogenetic signal.

Morphology

A combination of key characters easily separates the three geographic subspecies, including the nominotypic form. The taxa are characterized by specific color and pattern, body size, midbody and ventral scale counts (Ta-

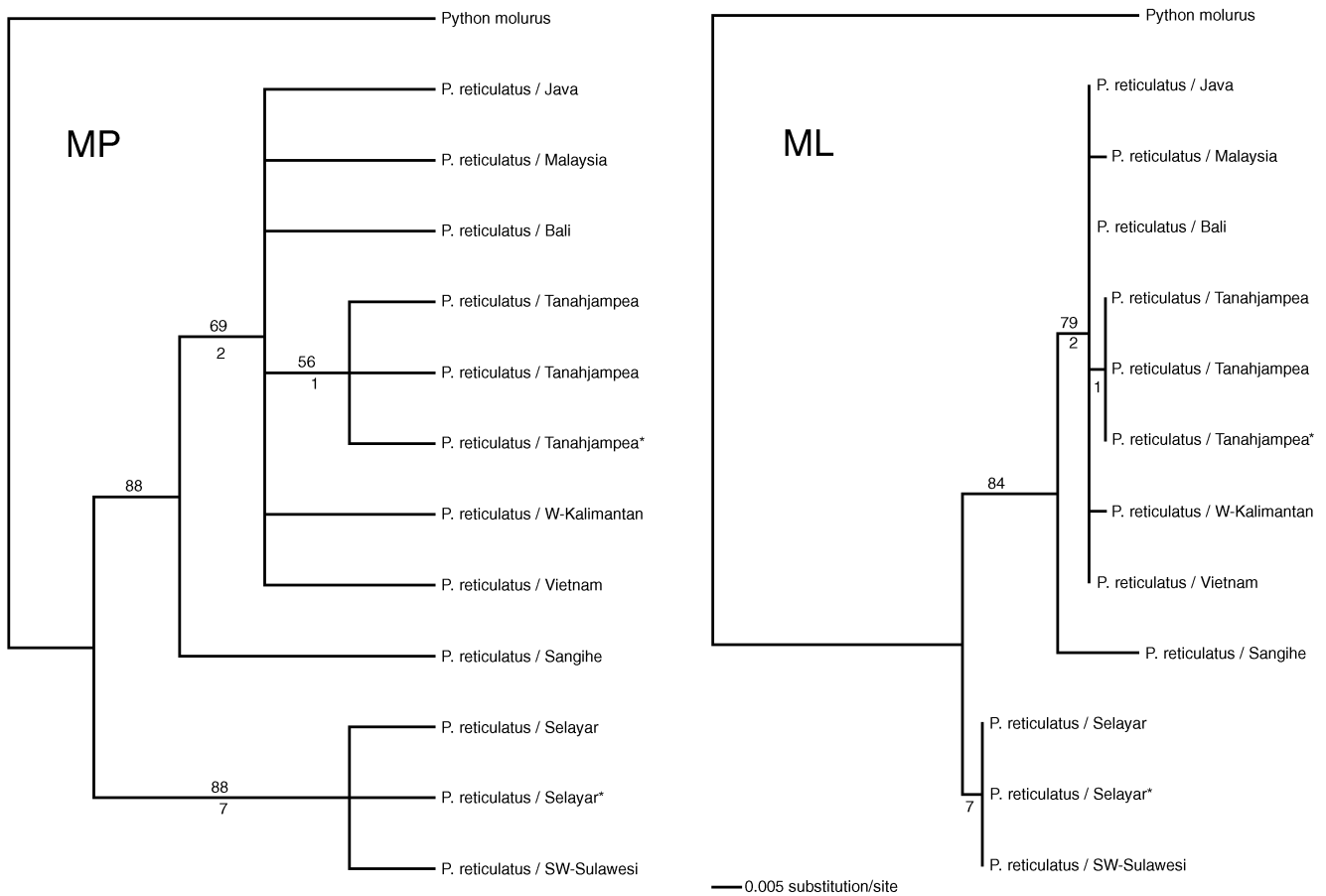


Fig. 2 Cladogram of the maximum parsimony consensus tree (MP) and phylogram of the maximum likelihood tree (ML) obtained from PAUP* searches using *Python molurus* as outgroup. Numbers above nodes represent bootstrap proportions for 2,000 and 100 pseudoreplicates for parsimony and likelihood analyses, respectively; bootstrap proportions less than 50% are not shown. Numbers below nodes represent supporting synapomorphies (*asterisk* represents the holotype)

ble 2), and dorsal head scales (Fig. 3). Morphological characters are constant within the three taxa (see below).

P. reticulatus reticulatus is distinctive in having a more vague combination of colors, a reticulation not as clearly contrasted as in Selayar pythons, lower values of ventral scale counts (304–325), as well as of midbody scales (68–78), as compared with the Selayar pythons, but higher than in Tanahjampea pythons, and having the anterior prefrontals only slightly longer than wide and two rows of posterior prefrontals (Fig. 3A).

Selayar pythons are distinctive in being colored in a bright yellow-golden pattern with a clear contrasted reticulation (see Electronic Supplementary Material S1), by having a high ventral scale count (332–334), and fairly high numbers of midbody scale rows (77–81), and having two rows of posterior prefrontals and a more elongated pair of anterior prefrontals (Fig. 3B).

In contrast, *P. reticulatus jampeanus* is distinctive in having a silvery gray and brown color pattern, almost

lacking yellow/ochre pigmentation, a reticulation dissolving particularly in the neck region and anterior dorsum (see Electronic Supplementary Material S2), the lowest body scale counts, ventrals (290–301), midbody scales (64–68), distinctly enlarged anterior prefrontals and one row of posterior prefrontals (Fig. 3C).

Taxonomy

The morphological and genetic data suggest that the populations studied merit taxonomic distinction. According to some species concepts (e.g. the evolutionary species concept), the description of allopatric populations as full species would be justified (Harvey et al. 2000). We adopt the biological species concept (Mayr and Ashlock 1991; Mayr 2000) and, as there is no evidence for potential reproductive barriers, we restrict ourselves to describe our newly identified taxa as subspecies. However, a clear definition to which population the name *reticulatus* applies to, is certainly required.

Designation of neotype

Schneider (1801) based his description of *Boa reticulata* on a specimen “Musei Goettingensis”; the same was true for his *Boa rhombeata*, described in the same publica-

Table 2 Geographic variation of midbody and ventral scales in *P. reticulatus*

	SE Asian mainland, Greater and Lesser Sundas	Tanahjampea Island	Selayar Island, SW and SE Sulawesi
Midbody scales	68–78 (<i>n</i> =91)	64–68 (<i>n</i> =4)	77–81 (<i>n</i> =5)
Ventrals	304–325 (<i>n</i> =78)	290–301 (<i>n</i> =4)	330–334 (<i>n</i> =4)
Sources	ZFMK 35529; Boulenger (1893); Mertens (1928); Taylor (1965); Auliya and Abel (2000a); This study	This study	Kopstein (1935); This study

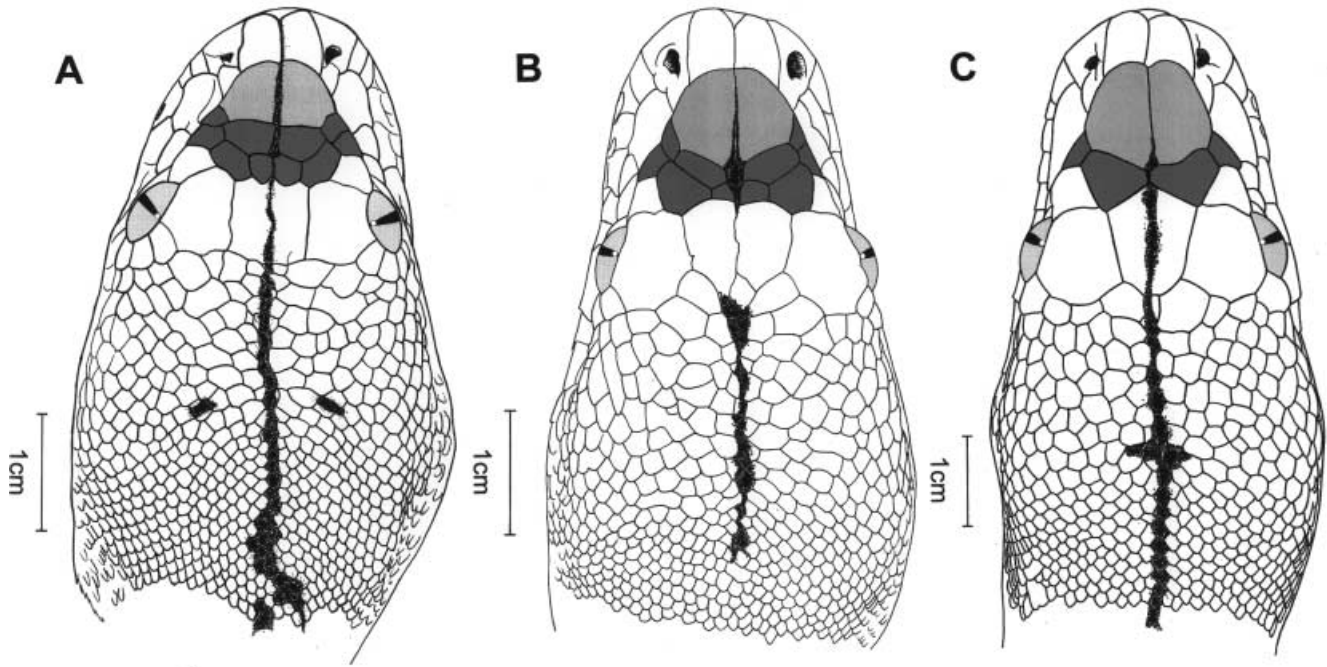


Fig. 3a–c Comparison of the dorsal head views of *Python reticulatus*. **A** *P. reticulatus reticulatus* (neotype, Malaysia), ZFMK 32378; **B** *P. reticulatus saputrai* (holotype, Selayar), ZFMK 73473; **C** *P. reticulatus jampeanus* (holotype, Tanahjampea), ZFMK 73475. Anterior prefrontals are marked light gray, posterior prefrontals dark gray

tion. For both, the respective type specimens are presumed to be lost (see Stimson 1969).

As long as *P. reticulatus* was monotypic, there was no doubt about its identity. However, our new data require a taxonomic partition of the former monotypic species, and thus the identity of the name *reticulatus* s. str. and its type locality needs to be clarified.

In 1977, the herpetological collection of the Zoological Museum of the Goettingen University was transferred to the Museum A. Koenig, Bonn (Böhme and Bischoff 1984), and several historically important type specimens previously presumed to be lost were recovered, including also another taxon described by Schneider (*Boa carinata* Schneider, 1801, currently *Candoia carinata*: Böhme et al. 1998). Unfortunately, the specimens on which Schneider based his *Boa reticulata* and *B. rhombeata*, remain untraceable and hence must be regarded as definitively lost.

Designation of a neotype is highly warranted from the following arguments (see Art. 75, ICZN 1999). (1) After partition of the formerly monotypic taxon *P. reticulatus*, an unequivocal definition of the identity of this taxon seems necessary; otherwise considerable taxonomic confusion can be expected. (2) The Latin original description by Schneider (1801) gives insufficient information to diagnose the name *reticulatus*; the diagnostic features are not highlighted in the original description. (3) This paper is the first to discuss relationships within *P. reticulatus*, which may even prove to be a species complex in the future. (4) The overwhelming majority of the literature references concerning *P. reticulatus* refer to the large-growing populations of mainland SE Asia and of the major islands of the Sunda archipelago. As we describe two taxa from relatively small islands, we think it appropriate to select a mainland specimen as the neotype, which is designated below.

Python reticulatus reticulatus (Schneider, 1801)

Neotype

ZFMK 32378, subadult.

Type locality

Rengit, West Malaysia, 1980.

Diagnosis

P. r. reticulatus is distinguished from the two newly described taxa by having the following combination of characters: (1) color pattern includes a mixture of yellow, ochre, brownish colors and black reticulation over the entire body, lacking clear contrasts, as colors are vague. In contrast, Selayar pythons show clear color contrasts, in predominantly yellow/golden/ochre colors with a clearly marked and broader reticulation pattern, whereas Tanahjampea pythons almost lack yellow colors; instead silvery/gray colors are predominant, and the reticulation is less distinct and even dissolves in the first body third; (2) iris color is bright orange, golden in Selayar pythons and golden/orange to gray/silvery in *P. r. jampeanus*; (3) tongue is blackish, pink-purple in *P. r. saputrai* and pinkish in *P. r. jampeanus*; (4) the amount of ventral scales in *P. r. reticulatus* ranges from 304–325, in *P. r. saputrai* from 330–334, in *P. r. jampeanus* from 290–301; (5) midbody scales in the nominotypic form range from 68–78, in Selayar pythons from 77–81, and in Tanahjampea pythons from 64–68; (6) the posterior prefrontals in *P. r. reticulatus* are similarly fragmented as in *P. r. saputrai*, in *P. r. jampeanus* these are distinctly reduced to a lower amount; (7) anterior prefrontals in *P. r. reticulatus* are slightly longer than wide, in *P. r. saputrai* and *P. r. jampeanus* these scales are distinctly longer than wide, particularly in the latter.

Description of neotype

TOL 130.8 cm; SVL 113.5 cm; TL 17.3 cm. Irregular black network forming squared figures dorsally; laterally white blotches framed by two black flecks; two black zigzag-lines, lower less distinct visible on flanks; ground color between lateral markings brown or gray; ventrum yellow to white, some ventrals edged dark; tail darker; head ground color brown; black median streak beginning at rostrum ending in the nape region; distinct black dot on either side of parietal region; head laterally marked with black streak on both sides (Fig. 3A).

313 ventrals; 92 subcaudals; 58 dorsals anteriorly, 72 at midbody, 37 posteriorly; anal single; rostral scale with 2 diagonal pits; 1 pair of internasals in contact with nasals; 1 pair of anterior prefrontals; 10 posterior prefrontals in two rows (Fig. 3A); 2 large supraoculars; 1 undivided frontal; 4 distinct parietals separated by 2 pairs of smaller interparietals; 13 supralabials (1–4 pitted), the 7th entering orbit; 2 preoculars and 4 postoculars on both sides; 5 loreals on left side, and 4 on right; 21 infralabials on left, 22 on right side (scales 13–18 on right side and 12–16 on left side pitted).

Python reticulatus saputrai ssp. nov*Material*

Holotype: ZFMK 73473, male, Selayar Island, Indonesia, August 2000; Paratype: ZFMK 73474, female, same data as holotype, collected by H. Lowi.

Diagnosis

P. r. saputrai can be distinguished from *P. r. reticulatus* and *P. r. jampeanus* by having the following combination of characters: (1) an overall golden-yellow color and high contrast among pattern elements on each snake (see Electronic Supplementary Material S1), while *P. r. reticulatus* is less clearly contrasted and colors are vague, whereas *P. r. jampeanus* predominantly shows silvery/gray colors; (2) iris color golden in *P. r. saputrai*, always orange in the nominotypic form, and orange/golden to silvery/gray in *P. r. jampeanus*; (3) tongue color in *P. r. saputrai* pink-purple with whitish tip, blackish in *P. r. reticulatus* and pinkish in *P. r. jampeanus*; (4) total length of *P. r. saputrai* does not exceed 4 m, specimens of *P. r. reticulatus* exceed 8 m, *P. r. jampeanus* does not exceed much more than 2 m; (5) ventrals number 332–334 in *P. r. saputrai* (*P. r. reticulatus*: 304–325; *P. r. jampeanus*: 290–301); (6) 72–81 midbody scale rows in *P. r. saputrai* (*P. r. reticulatus*: 68–78; *P. r. jampeanus*: 64–68); (7) posterior prefrontals 4–7 in more than one row, similarly to *P. r. reticulatus*, in *P. r. jampeanus* one row of predominantly 4 scales.

Description of holotype

TOL 164 cm; SVL 141 cm; TL 23 cm. Overall appearance characterized by clear, bright, contrasting colors; no distinct ground color; black network appears in distinct broad lines along total body. Dorsal pattern begins more or less with symmetrical squares, in the course these figures shift, caudally they rearrange to squares. The interior of network pattern is colored golden-orange in life, plain ochre in alcohol.

Head colored ochre-yellow in alcohol, golden-yellow in life; iris golden-orange; median streak on head irregular, rather diffuse in prefrontal area, disappearing in nape region; black streaks on lateral head sides turn to zigzag lines on lateral body parts.

332 ventrals; 95 subcaudals, which are either single and paired; 63 dorsals anteriorly, 81 at midbody and 43 posteriorly; anal entire; rostrum showing 2 diagonal slits; 1 pair of internasals, about 1.5 times as long as wide; 1 pair anterior prefrontals; 11 posterior prefrontals in two rows (Fig. 3B); frontal medially divided, between 2 large supraocular scales; 4 distinct parietals separated by 2 larger and 3 smaller interparietals.

13–14 supralabials, scales 1–4 pitted on both sides, the 7th or 8th entering orbit; 2 preoculars; 4 postoculars;

4 loreals left and 3 right; 23 infralabials, scales 15–19 on left and 13–18 on right side with pits.

Variation

ZFMK 73474 = TOL 149.5 cm. (SVL 130 cm; TL 19.5 cm).

Color pattern resembles that of holotype, but contrast less marked. Dorsal black network appears less distinct anteriorly; 334 ventrals; 93 subcaudals; 58 dorsals anteriorly, 77 at midbody, 39 posteriorly; 5 prefrontals posteriorly; 2 larger parietals separated by 4 smaller interparietals; 13 supralabials on each side, 6th and 7th entering eye on right side; 22 infralabials, scales 13–18 on left and 14–18 on right side with pits; 2 and 3 postoculars; 5 loreals.

One Selayar specimen examined in the field: TOL 167 cm; SVL 147 cm; TL 20 cm; 332 ventrals; 84 subcaudals (stub-tailed); 78 midbody scale rows; one Bira specimen examined in the field: TOL 280 cm; SVL 244 cm; TL 27 cm; 330 ventrals; 80 subcaudals (stub-tailed); 77 midbody scales (Table 2).

Etymology

The new subspecies is dedicated to George T. Saputra, chairman of the Indonesian Reptile and Amphibian Trade Association, IRATA, who generously supported this study and earlier long-term field surveys on Indonesian reptiles protected under CITES.

Distribution

Selayar (= Salayar) Island [6.10°S; 120.50°E], south of SW Sulawesi in the Flores Sea (Fig. 1) and SW Sulawesi (see below).

Python reticulatus jampeanus ssp. nov

Material

Holotype: ZFMK 73475, female, Tanahjampea Island, Indonesia, August 2000. Paratypes: ZFMK 73476, female, ZFMK 73477, female, ZFMK 73480, female, same data as holotype, collected by H. Lowi.

Diagnosis

P. r. jampeanus is distinguished from *P. r. reticulatus* and *P. r. saputrai* by the combination of following characters: (1) specimens almost lack yellow pigmentation, instead show predominantly silvery/gray and brown ground colors (see Electronic Supplementary Material S2), while color patterns of *P. r. reticulatus* contain yellow/

ochre/brown colors, *P. r. saputrai* is patterned golden/yellow; (2) black network pattern characteristically broken and diminishing in nape region and anterior dorsum, more distinct in *P. r. reticulatus*, whereas *P. r. saputrai* shows the most clearly marked contrasts; (3) eyes are orange/golden and silvery gray in *P. r. jampeanus*, orange in the nominotypic form and golden in *P. r. saputrai*; (4) tongue color pinkish, whitish on sides and tip in *P. r. jampeanus*, blackish in *P. r. reticulatus* and pink/purple in *P. r. saputrai*; (5) 60–70 midbody dorsals (*P. r. reticulatus*: 68–78; *P. r. saputrai*: 77–81); (6) 290–301 ventrals (*P. r. reticulatus*: 304–325; *P. r. saputrai*: 330–334); (7) large internasals about twice as long as wide; (8) one pair of conspicuously large anterior prefrontals, as long as frontal, in *P. r. reticulatus* almost as wide as long, in *P. r. saputrai* distinctly longer than wide; (9) reduced amount of posterior prefrontals in one row, more fragmented in two rows distinct in the *P. r. reticulatus* and *P. r. saputrai*.

Description of holotype

TOL 168.6 cm; SVL 145 cm; TL 23.6 cm. Ground color brown and gray, no yellow pigmentation; black network on anterior dorsum irregular and dissolved; caudally typical dorsal pattern apparent; laterally white blotches, framed with black; head mid-brown with black median streak beginning at posterior margin of anterior prefrontals, reaching parietal scales; lateral head streak beginning in temporal region ending at last supralabial; ventrum completely yellowish-white, except subcaudal region shaded light gray.

300 ventrals; 83 subcaudals; 54 dorsals anteriorly, 65 at midbody, 40 posteriorly; anal entire; rostral with 2 diagonal slits; 1 pair of internasals, twice as long as wide; 1 pair of large elongated anterior prefrontals, as long as frontal; 4 posterior prefrontals in one row (Fig. 3C), single frontal, with 1 large supraocular on each side; 2 median enlarged parietals, separated by a small single interparietal; 13 supralabials (scales 1–4 pitted), 6th and 7th or 8th entering orbit; 2 preoculars; 2 postoculars; 4 loreals on right and 2 on left side; 20–21 infralabials (12–16 and 11–16 with pits).

Variation

ZFMK 73476 = TOL 159.5 cm; SVL 136.5 cm; TL 23 cm. ZFMK 73477 = TOL 180 cm; SVL 152.5 cm; TL 27.5 cm. ZFMK 73480 = TOL 200.5 cm; SVL 175 cm; TL 25.5 cm. Additional live specimen: TOL 100 cm; SVL 85 cm; TL 15 cm.

ZFMK 73476 and ZFMK 73480 show weak light brown pigmentation laterally; in some specimens margins of ventrals more darkly pigmented; black flecks sometimes distinct in parietal region; ventrals 290–301; subcaudals 80–86; anterior dorsals 54; midbody dorsals 64–68; posterior dorsals 35–37. A specimen examined in

the field had 290 ventrals, 82 subcaudals (stub-tailed), and 64 midbody scales. ZFMK 73476 shows an additional posterior prefrontal. In ZFMK 73477 the frontal is fragmented into 4 scales (Table 2).

Etymology

Jampeanus is used here as an adjective for the island of Tanahjampea which is usually simply called Jampea by the inhabitants.

Distribution

With certainty only known from Tanahjampea (7°4' S; 120°41' E); possibly also on some small neighboring islands (Fig. 1).

Discussion

Distribution and taxonomy

Python reticulatus is composed of several subspecies subdivided by genetic and morphological differences. Based on our phylogenetic results, we consider the nominotypic form to be geographically restricted to mainland SE Asia, and the Greater and Lesser Sundas. *P. reticulatus saputrai* is distributed on Selayar and SW Sulawesi (Bira specimen, SW Sulawesi, genetically and morphologically conform with Selayar pythons, Fig. 2). *P. reticulatus jampeanus* is known only from Tanahjampea in the Flores Sea (Fig. 1).

According to O'Brien and Mayr (1991), a subspecies is characterized in having a "unique geographic range or habitat, a group of phylogenetically concordant phenotypic characters, and a unique natural history relative to other subdivisions of the species." Our study revealed geographically consistent morphological distinction in color and body scales in all preserved and live material examined, obtained at different periods and different localities from both islands.

Most authors who provide body scale values for *P. reticulatus* still refer to the major works of Boulenger (1893, 1912) and De Rooij (1917), the values of the latter are identical to the former. Even more recent reports cite these values (e.g. Walls 1998). Studies such as those of Wall (1926), Bourret (1936), Smith (1943), Deuve (1970), Saint-Girons (1972), Tweedie (1983) and Campden-Main (1984) partly adopt identical values. Deuve (1970) and Campden-Main (1984) mention values probably referring to populations of Laos and South Vietnam respectively. The most recent data is provided by Stuebing and Inger (1999). However, none of these works provide sample sizes.

Our data reveal that Sundaland populations have ventral scale counts ranging from 304–325 (Boulenger 1893; Mertens 1928; Taylor 1965; Campden-Main 1984;

Stuebing and Inger 1999; Auliya and Abel 2000a). Populations of Selayar and SW Sulawesi reveal the highest numbers in ventral scales (330–334). We suggest that the high ventral scale counts listed by De Rooij (1917) (up to 330), derive from Sulawesi populations. In contrast, *P. r. jampeanus* shows the lowest ventral scale counts (290), distinctly lower than the value provided by Boulenger and De Rooij, who mention 298. Consequently, our study shows that the range of ventrals must be extended to 290–334, compared to Boulenger (1893 [297–330]), Smith (1943 [297–332]), and Deuve (1970 [294–332]).

Additionally, midbody scale counts reveal higher numbers in specimens from Selayar and SW Sulawesi (76–81). A specimen examined by Kopstein (1935) from Buton Island (SE Sulawesi) falls into this range (Table 2). Sundaland populations may be characterized by 68–78 midbody scales, while Stuebing and Inger (1999) mention 70–80. Tanahjampea populations always have a lower number of midbody scales (64–68). The characteristic range of midbody scales in *P. reticulatus* is hereby extended from 69–79 (Boulenger 1893; De Rooij 1917) to 64–81.

Subcaudal counts may be biased by the inclusion of stub-tailed specimens. In addition, males have longer tails relative to the snout-vent length (Shine et al. 1998). However, we can confirm that 59 specimens with complete tails from West Kalimantan had subcaudal counts between 82 and 98.

Our results show clear differences in the number and size of anterior and posterior prefrontals in the two populations. Specimens from Tanahjampea show a reduction in the total number of upper head scales. In addition, there is an increase in size of internasals and particularly of the anterior prefrontals (Fig. 3C). In populations of Selayar Island, the posterior prefrontals are fragmented into more scales, similar to populations of the mainland and the Greater Sundas (Fig. 3A, B). Head scales such as loreals, parietals, supralabials, and infralabials are highly variable within all populations and consequently lack geographic variations.

Formerly it was believed that the frontal scale was geographically variable, being expressed as a single or divided scale (Boulenger 1893; Kopstein 1926; Mertens 1928; Taylor 1922, 1965). Underwood and Stimson (1990) finally pointed out that the frontal scale is "intraspecifically" variable. Kluge (1993) indicated that the frontal scale might show a notch anteriorly or posteriorly or even on both sides. Of 33 examined heads collected in West Kalimantan, we found six different morphologies of the frontal scale: three had a small notch anteriorly, seven had a notch anteriorly reaching the center, two had notches anteriorly and posteriorly, two were fragmented into three scales, eight were totally divided, and 11 showed a single frontal.

Biogeography

The Indonesian archipelago comprises a complex mixture of oceanic and continental islands, of which the bio-

geography of many islands is still not well comprehended, especially for the Lesser Sundas and Malukku region. This poor understanding is due to a complex zone of tectonic and biotic activity, a poor fossil record, destruction of natural habitats, and an incomplete exploration of the region (Monk et al. 1997).

Based on our phylogenetic results, we have resolved three distinct lineages: populations of Tanahjampea, Selayar and SW Sulawesi, and populations of Sangihe Island (Figs. 1 and 2). The resultant distribution pattern of the former two geographically isolated taxa is hypothesized to be linked to paleogeographic and oceanographic parameters.

P. reticulatus is a SE Asian species with extant populations in eastern Indonesia (Seram, Tanimbar archipelagos) (Edgar and Lilley 1993; How and Kitchener 1997; Auliya and Abel 2000a). This snake is reputed to be an excellent colonizer, able to disperse across open oceans, as evident from sightings of the species on Rakata and Sertung of the Krakatau archipelago, 12 years after the violent eruption (Thornton 1996).

However, despite its extraordinary dispersal abilities, we detected at least two genetically isolated populations. The phylogenetic results show that the genetic structure of populations of mainland SE Asia (Vietnam, Malaysia), from the Greater Sundas (Borneo, Java) and Lesser Sundas (Bali) are concordant, whereas populations of Tanahjampea form a distinct clade, genetically closely related to Sunda shelf populations (Fig. 2). We consider that *P. reticulatus* colonized Tanahjampea via the Lesser Sundas, possibly when sea-levels lowered during the late Cretaceous and Tertiary or throughout the Pleistocene. During these periods and epochs, the continental shelf and the islands of the Sunda and Banda arcs were exposed, and connected, or were only separated by shallow shelves (How and Kitchener 1997; Monk et al. 1997; Brown and Lomolino 1998; Moss and Wilson 1998). The former oceanic barriers were broken up and the island chains functioned as “stepping stones”, creating a dispersal route for oriental and Australian faunas.

Geological studies on this regional scale that explain the evolution of the Flores Sea islands Tanahjampea and Selayar are scarce. However, according to Soeria-Atmadja et al. (1998), the formation of the Makassar Strait initiated the separation of Sumba and Selayar, both continental fragments, from mainland Sulawesi during the early Tertiary. Between the Late Cretaceous and the Early Miocene, the translation of Selayar and Sumba took place along the “N–S trending proto-Paternoster-Walanae-Salayar fault” (Soeria-Atmadja et al. 1998; Moss and Wilson 1998). In the same epoch, the early Miocene, the eastern Sunda-Arc (Sumbawa to Central Flores) evolved (van der Werff 1995). The island Tanahjampea probably belongs to arc material and, together with Selayar, both derive from Sundaland, and are not of Australian origin (B. Michaux, personal communication). These geological findings may support the existence of land bridges between the Lesser Sundas and Tanahjampea, and between SW Sulawesi and Selayar.

A land bridge – the “Saleyer bridge” – connecting Sulawesi with the Lesser Sundas was first proposed by Sarasin and Sarasin (1901) and likely facilitated colonization between both these terrains and vice versa (Mertens 1930). Auffenberg (1980) expanded upon these ideas and stated that after the Sunda and Sahul shelves collided, arc material of the Lesser Sunda chain was compressed, forming the “Saleyer bridge”, where faunal exchanges were likely. A Pleistocene land-bridge concept between Sulawesi and Flores along the Kaloatoa-Matjan ridge and the Tanahjampea and Selayar ridge was refined and supported by Audley-Charles and Hooijer (1973), White and Bruce (1986) and Whitten et al. (1987). Most likely Flores was connected to Sulawesi in the early Miocene, and separated since 12–10 Ma, definitely since 6 Ma (R. Hall, personal communication).

The close phylogenetic relationship of the nominotypic form to *P. r. jampeanus* indeed corroborate the existence of a former land bridge from Flores to Tanahjampea. Isolation during the Pleistocene of Tanahjampea from the Lesser Sundas is supported by the fact that populations of the latter are not present on Tanahjampea, and vice versa. In addition, colonization by sea dispersal has likely been inhibited by oceanic parameters such as strong abundant surface currents in the Flores Sea. In some areas of the Flores Sea, ocean currents, together with wind currents, can be strongly directional and persistent (Whittaker 1998). Surface currents in this region are created and maintained by the NW monsoon (November to March/April) and by the SE monsoon (April/May to November) (Ilahude 1980; Whitten et al. 1987) (Fig. 1).

Michida and Yoritaka (1996) used surface drifters to study the movement of surface currents in the area of the Indo-Pacific throughflow. One drifter, released in November, drifted along the South Java current via the Lombok Strait and arrived in the Flores Sea by mid-December. Drifting further east, it reached the Banda Sea in February. These experiments demonstrate the abundance of directional surface currents in the Flores Sea, which may represent effective barriers to sea dispersal, augmenting the isolation of the Tanahjampea population. Ocean currents also present barriers to the dispersal of reef fish, evolving biogeographically and genetically isolated taxa (Muss et al. 2001).

Wallace (1863) constructed an imaginary zoogeographical boundary separating oriental and Australian faunas, which was later termed the Wallace line. Wallace revised this first line in 1910 (Wallace 1910) and shifted the boundary to the east of Sulawesi, with regard to the predominance of Asian forms on Sulawesi. Interestingly, this line runs through the Flores Sea, separating Selayar from Tanahjampea (Fig. 1). Wallace indicated that the avifauna of Tanahjampea had more affinities with that of the Lesser Sundas, than with Selayar or Sulawesi. These findings were supported by White and Bruce (1986) who studied the birds of Wallacea. Dutson (1995) reports that the avifauna of Tanahjampea contains only three of the Sulawesi species found on Selayar, but 13 species in Ta-

nahjampea are found in the Lesser Sundas. The above evidence supports our hypothesis that a land bridge existed between the Lesser Sundas and Tanahjampea Island.

P. r. saputrai from Selayar and SW Sulawesi also yield a monophyletic clade distinct from populations of the Sunda Shelf. The consistency of the phylogenetic data of both these populations is supported by two parameters: firstly, Selayar Island is located only 20 km south of Sulawesi, thus colonization via sea dispersal is more likely and surface currents are less directional; secondly, the opening of the Makassar Strait, separating SE Borneo from SW Sulawesi, can be dated back to the late Cretaceous or early Tertiary, indicating a long period of isolation (*P. r. saputrai*) and restricted gene flow from the Sunda shelf (Cornée et al. 1995; Michaux 1996; Moss and Wilson 1998; Soeria-Atmadja et al. 1998). Borneo was connected by a land bridge to mainland SE Asia for much of the Tertiary (Michaux 1994; Hall 1998; Moss and Wilson 1998).

Biogeographically, we conclude that *P. r. jampeanus* evolved from colonists arriving via the Lesser Sundas and *P. r. saputrai* evolved from colonists arriving via Sundaland. According to Tougaard (2001), there is no geological, biogeographical or paleobiogeographical evidence of a migration route via Taiwan and the Philippines. If the "Selayar bridge" existed, connecting Sulawesi with the Central Lesser Sundas, this bridge was probably first broken up between Selayar and Tanahjampea. The subsequent isolation of these populations was further augmented by monsoon-directed surface currents (Fig. 1), which, according to paleoclimatological data, already prevailed in eastern Indonesia during the last two glacial periods (van der Kaars et al. 2000). In a later event, an oceanic gap disconnected Tanahjampea from the Lesser Sundas.

In summary, our new taxa originate from a "unique biogeographic subregion", and support the findings of How and Kitchener (1997) who reported a high level of endemism for Indonesian snakes, specifically 20% in the Lesser Sundas and 28.3% in Sulawesi.

Ecology

The Flores Sea islands fall into the rainshadow of the Australian continent and receive little rain during the SE monsoon, resulting in a long dry season lasting nearly 6 months, similar to that of the Lesser Sundas and SW Sulawesi. As a result, the natural vegetation is characterized as deciduous monsoon forest (Whitten et al. 1987). Selayar and Tanahjampea both are corraline islands (White and Bruce 1986), and largely support growth of dry-adapted vegetation, e.g. the invasive *Lantana camara* (Verbenaceae), the fire-resistant lontar palms (*Borassus flabellifer*) or *Pandanus* spp. Coastal areas of Selayar and Tanahjampea are today predominantly covered in vast coconut plantations. Evergreen forest and mangroves are shrinking, and the majority of the islands areas are cleared and cultivated (MacKinnon 1997).

In Bira, SW Sulawesi, juvenile and adult *P. reticulatus* are commonly found in deep, completely dark cave systems with stagnant air providing high humidity. Caves are also common on Selayar, in which locals frequently report sightings of *P. reticulatus*. On Tanahjampea, *P. reticulatus* is found in deforested areas and swamp forests.

Prey of cave-dwelling pythons primarily comprises bats (Auliya and Abel 2000b). Potential mammalian prey on Tanahjampea includes flying foxes (*Pteropus gris-eus*), squirrels, viverrids, porcupines (*Hystrix javanica*), deer (*Cervus moluccensis*), cuscus (*Phalanger* sp.), and domestic animals (Meise 1929).

Conservation status

Selayar pythons are exploited within the skin trade, and are favored by traders because of their more attractive and valuable color-patterned skins. Currently, three skin suppliers are established on Selayar Island. The small-sized *P. reticulatus jampeanus* is available through the international trade in live reptiles.

Unfortunately, no regional trade data is available to determine present harvest levels. Priority tasks for future studies are to examine harvest impact, population densities and natural history parameters. Conservation status must be reevaluated if trade effects on wild populations prove to be detrimental. In particular, additional fieldwork is required before balanced decisions on quotas can be made.

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