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Cryptic and non-cryptic diversity in New Guinea ground snakes of the genus *Stegonotus* Duméril, Bibron and Duméril, 1854: a description of four new species (Squamata: Colubridae)

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ABSTRACT

The island of New Guinea has been identified as biologically megadiverse but many taxa are still poorly known. This is especially the case for many of the island's snakes, which by their very nature can be difficult to collect and study. Here we examine the phylogenetic and phylogeographic structure of a poorly studied snake genus, *Stegonotus*, focusing on the species of New Guinea; until now, *Stegonotus* has never been examined using modern phylogenetic methods. Using molecular data from 49 individuals representing eight of the ten described species, and including all New Guinea taxa, we estimate a multilocus phylogeny and examine population structure to help identify undescribed taxa. We use morphological data from the corresponding museum vouchered specimens (where available) and also examine additional specimens for taxa not included in the molecular data set to determine morphological differences among putative taxa. We find molecular evidence for four new species of *Stegonotus*, both morphologically obvious and cryptic, and describe them herein. The recognition of these four species indicates that *Stegonotus* diversity has been previously underestimated and also suggests that there are likely additional undescribed taxa within the genus. These four taxa increase the number of described species by 40% and further confirm New Guinea as the centre of diversity for the genus.

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The island of New Guinea has been identified as biologically megadiverse; however, it remains one of the least studied regions of the world (Mittermeier and Mittermeier 1997). Epitomizing this lack of research most groups of snakes in New Guinea have been poorly studied and are in dire need of taxonomic revision. Among the most

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taxonomically neglected snakes of New Guinea are ground snakes of the genus *Stegonotus* (Colubridae: Colubrinae). Currently comprising 10 species (*Stegonotus batjanensis* (Günther 1865), *Stegonotus borneensis* Inger 1967, *Stegonotus cucullatus* (Duméril et al. 1854), *Stegonotus diehli* Lindholm 1905, *Stegonotus florensis* (De Rooij 1917), *Stegonotus guentheri* Boulenger 1895, *Stegonotus heterurus* Boulenger 1893, *Stegonotus modestus* (Schlegel 1837), *Stegonotus muelleri* (Duméril et al. 1854) and *Stegonotus parvus* (Meyer 1874)) found in the Philippines, Indonesia, Malaysia, Papua New Guinea and Australia, *Stegonotus* reaches its greatest diversity on the island of New Guinea with six described species (*S. cucullatus*, *S. diehli*, *S. guentheri*, *S. heterurus*, *S. modestus*, *S. parvus*; Figure 1). Although snakes are generally not afforded as much attention as



Figure 1. Photographs of six New Guinea *Stegonotus* species in life including voucher numbers: (a) *Stegonotus cucullatus* LSUMZ 94371, (b) *Stegonotus diehli* LSUMZ 92345, (c) *Stegonotus modestus* LSUMZ 92327, (d) *Stegonotus heterurus* BPBM 22556, (e) *Stegonotus parvus* LSUMZ 92335, (f) *Stegonotus guentheri* LSUMZ 94386. Photos from CCA (a, b, c, e, f) and F. Kraus (d).

other vertebrate groups, even among herpetologists the ground snakes have not garnered great research interest or efforts. This is probably because most *Stegonotus* are relatively inconspicuous, typically coloured in shades of brown and grey, can be difficult to study because they are active at dusk or night, and verge on semi-fossorial (O'Shea 1996), combined with the general remoteness of their distribution.

The genus *Stegonotus* has had no recent revisionary taxonomic work, with just a single species from Borneo described within the last 50 years (Inger 1967). All New Guinea species were described over a hundred years ago, between 1854 and 1905 (Duméril et al. 1854; Meyer 1874; Boulenger 1893; Lindholm 1905). Despite New Guinea being the centre of ground snake diversity, only the Australian population of *S. cucullatus* has been studied in any detail, and this with respect to its ecology (Shine 1991; Dubey et al. 2008), with no work using modern molecular methods or integrative approaches to address taxonomy.

Furthermore, no modern higher level molecular systematic study of snakes has included a representative of *Stegonotus* (Pyron et al. 2013; Figueroa et al. 2016) so its relationships to other snakes are essentially unknown, although tooth morphology suggests an affinity to the speciose Asian genus *Lycodon*. *Stegonotus* are known to eat a variety of prey types including frogs, lizards, and mammals but some species are squamate egg specialists (McDowell 1972; Shine 1991; O'Shea 1996). Like their suggested closest relatives, the Asian *Lycodon*, specifically those formerly in the genus *Dinodon* (McDowell 1972; synonymized in Guo et al. 2013), *Stegonotus* have enlarged rear maxillary teeth that likely aid in consuming a durophagous diet (McDowell 1972; see Jackson and Fritts 2004). Squamate eggs are the main dietary item found in New Guinea specimens (McDowell 1972; O'Shea 1996) as well as Australian *S. cucullatus* (Shine 1991). Although not considered dangerous, these snakes are also known for chewing behaviours when handled that may produce localized envenomation effects (O'Shea 1996). Whether all species produce toxins or have any medical significance is unknown. Overall, information on most aspects of *Stegonotus* biology or systematics is depauperate.

Here, using an integrative approach composed of a multilocus molecular data set and morphological characters from vouchered specimens, we describe four new species of *Stegonotus* from New Guinea and generate the first molecular phylogenetic hypothesis for the genus. Three of the new species we describe are part of complexes containing other wide-ranging *Stegonotus* species and the fourth represents a distinct lineage that is endemic to the islands of Manus Province, north of New Guinea.

Materials and methods

Molecular data and phylogenetic analyses

We sequenced one mitochondrial locus (NADH dehydrogenase subunit 4 = *ND4*) and four nuclear loci (Recombination activating gene 1 = *RAG1*, Brain-derived neurotrophic factor = *BDNF*, Melanocortin 1 receptor = *MC1R*, and *R35*) for 49 individuals from eight of the ten recognized species of *Stegonotus* and included a colubrine outgroup (*Sonora semiannulata* from GenBank: EU402659, EU402861, JX305527, JN703058, KU859745) and a non-colubrine outgroup (*Thamnophis* spp. from GenBank: AY136240, EU402862, KX694767, AY586156,

KT884231). Museum codes and abbreviations used throughout the manuscript are as follows: ABTC = Australian Biological Tissue Collection, AMS = Australian Museum, BJE = Benjamin J. Evans field series, BPBM = Bernice Pauahi Bishop Museum, CCA = Christopher C. Austin field series, FMNH = Field Museum of Natural History, LSUMZ = Louisiana State University Museum of Natural Science, MZB = Museum Zoologicum Bogoriense, RMB = Rafe M. Brown field series, SAMA = South Australian Museum, SJR = Stephen J. Richards field series, USNM = National Museum of Natural History, WAM = Western Australian Museum; for additional sample details see Supplementary Appendix 1. Laboratory methods (polymerase chain reaction and sequencing conditions) are included as a Supplementary Appendix 2. We used the program PHASE v.2.1 (Stephens et al. 2001; Stephens and Scheet 2005) on resulting sequences to estimate the most probable pair of alleles for individuals with multiple heterozygosities for use in some subsequent analyses, noted below. We used the web interface SeqPHASE (Flot 2010) to format fasta files for each gene, and PHASE was run for 1000 iterations, with a thinning interval of 1, and a burnin of 100 for each locus; PHASE runs were repeated three times for each locus to ensure consistency, with a different random starting seed for each run.

We initially explored the genetic diversity of *Stegonotus* using gene trees from the unphased molecular data set for all taxa. We inferred a mitochondrial gene tree, a gene tree with all five loci, and a nuclear gene tree using maximum likelihood in the program RAxML v.8.0 (Stamatakis 2014) with the GTRGAMMA model and searching for the best tree while simultaneously conducting a 100 replicate rapid bootstrap analysis. The loci were partitioned by site, and by locus for multilocus analyses.

We next examined population structure for *Stegonotus* using the program Structure v.2.3.4 (Pritchard et al. 2000). Structure is a Bayesian clustering method that uses multilocus genotype data to find genetic clusters of individuals that are in Hardy–Weinberg equilibrium and can be used to examine admixture and population structure within or among related species, as well as a tool to discover unrecognized diversity (Griffiths et al. 2010; Fournier et al. 2012; Warner et al. 2015). As our primary interest was determining population structure that may indicate species-level diversity, especially within the wide-ranging species of *Stegonotus*, we included individuals from the species groups that had higher numbers of samples across populations, evidence of genetic structure as determined by the initial gene tree analysis (see results), and/or support as distinct but undescribed in the morphological data set for the Structure analyses (this included an *S. diehli* complex, an *S. modestus* complex, and unidentified individuals from Manus Island that were formerly attributed to *S. modestus*; see results below). The Structure model was run assuming possible admixture among populations, and locality information for the samples (at the level of province) was included in the Structure parameter file as a prior; this information can allow for more robust population membership estimations when the signal from the data is not very strong (or some data are missing) and at the same time does not tend to cause oversplitting of populations (Hubisz et al. 2009). We ran 20 replicates for each value of k , with k ranging from three to eight populations. Burnin was set at 500,000 MCMC generations, with 1,000,000 generations collected post-burnin. Results from Structure were assessed using the probabilities for each k value and from the delta k scores (Evanno et al. 2005), all on the web interface Clumpak (Kopelman et al. 2015) to determine the best estimation of k .

As the populations recovered from Structure may indicate unrecognized species diversity, we ran the Bayesian species delimitation analysis software BPP v.3.0 (Yang and Rannala 2010) based on the resulting *Stegonotus* populations. *Stegonotus* individuals were assigned to taxon sets (putative species) for the BPP analyses based on their population memberships under the best supported value of k populations from Structure. This version of BPP has the advantage of including a non-fixed guide tree model, which requires that the samples are assigned to their putative species but does not require an informative fixed guide tree (Yang and Rannala 2014). Results indicate the probability that a putative species is a separate species. Similar to previous studies (e.g. Ruane et al. 2016), we ran BPP using multiple population size and divergence priors by parameterizing Θ and τ_0 using a gamma (γ) distribution (α , β) as BPP is known to be sensitive to population size and divergence priors in determining the probability of species (Leaché and Fujita 2010; Yang and Rannala 2010). For the putative *Stegonotus* species, we tested delimitations using large ancestral population sizes and deep divergences, γ (1, 10); small ancestral population sizes and shallow divergences, γ (2, 2000); large ancestral population sizes γ (1, 10) and shallow divergences γ (2, 2000); and intermediate population sizes γ (2, 100) with deep divergences γ (1, 10). Fine-tuning parameters were adjusted between 0.30 and 0.70 for each parameter to allow mixing of the rjMCMC among the species-delimitation models. For each of the specified parameterizations, we ran three replicates using different starting seeds to ensure consistency; each was run for 1 million generations with a burnin of 100,000 generations and a sample frequency of every five generations.

Morphological data

We examined the following morphological characters, with measurements (where applicable) taken in mm: snout–vent length, tail length, midbody dorsal scale rows, total ventral scales, total subcaudal scales; subcaudal scales divided or undivided, anal plate divided or undivided, presence/absence of a loreal scale, number of pre-ocular scales, number of postocular scales, number of supralabials in contact with eye, number of supralabial scales, number of infralabial scales, genial scales in contact or interrupted by gular scales, and presence/absence of apical pits on dorsal scales. For species descriptions additional measurements were taken as described below. Where obvious (i.e. everted hemipenes or notes from collectors) sex was recorded (Appendix 1) but as this information was not consistently available and not possible due to destructive sampling being problematic for the specimens, sex-specific differences were not considered here. Although genetic data were not available for all specimens, we included a total of 67 representatives from all currently described *Stegonotus* species for morphological comparative purposes for species descriptions (Appendix 1; Figure 2).

For each species newly described here, additional morphological information was recorded including detailed assessments of scalation, colour and pattern (see below). Measurements of scales from holotypes were taken using digital callipers on the right side of the snake's head where applicable; any differences in head scalation on the left side is noted in the text and Appendix 1.



Figure 2. Photographs of *Stegonotus* species with dorsal, ventral and lateral head views from left to right: (a) *Stegonotus batjanensis* USNM 237129, (b) *Stegonotus borneensis* FMNH 251054, (c) *Stegonotus muelleri* LSUMZ 41802, (d) *Stegonotus florensis* WAM 104606, (e) *Stegonotus guentheri* AM 129712, (f) *Stegonotus heterurus* BPBM 22556, (g) *Stegonotus cucullatus* LSUMZ 94371. Photos from SR. (h) *Stegonotus modestus* LSUMZ 92339, (i) *Stegonotus iridis* sp. nov. SJR 7514, (j) *Stegonotus diehli* LSUMZ 92344 (k) *Stegonotus melanolabiatus* sp. nov. AMS R115361 (l) *Stegonotus derooijae* sp. nov. SAMA R70467 (m) *Stegonotus admiraltiensis* sp. nov. LSUMZ 93597, (n) *Stegonotus parvus* LSUMZ 92333. Photos from SR and SJR.

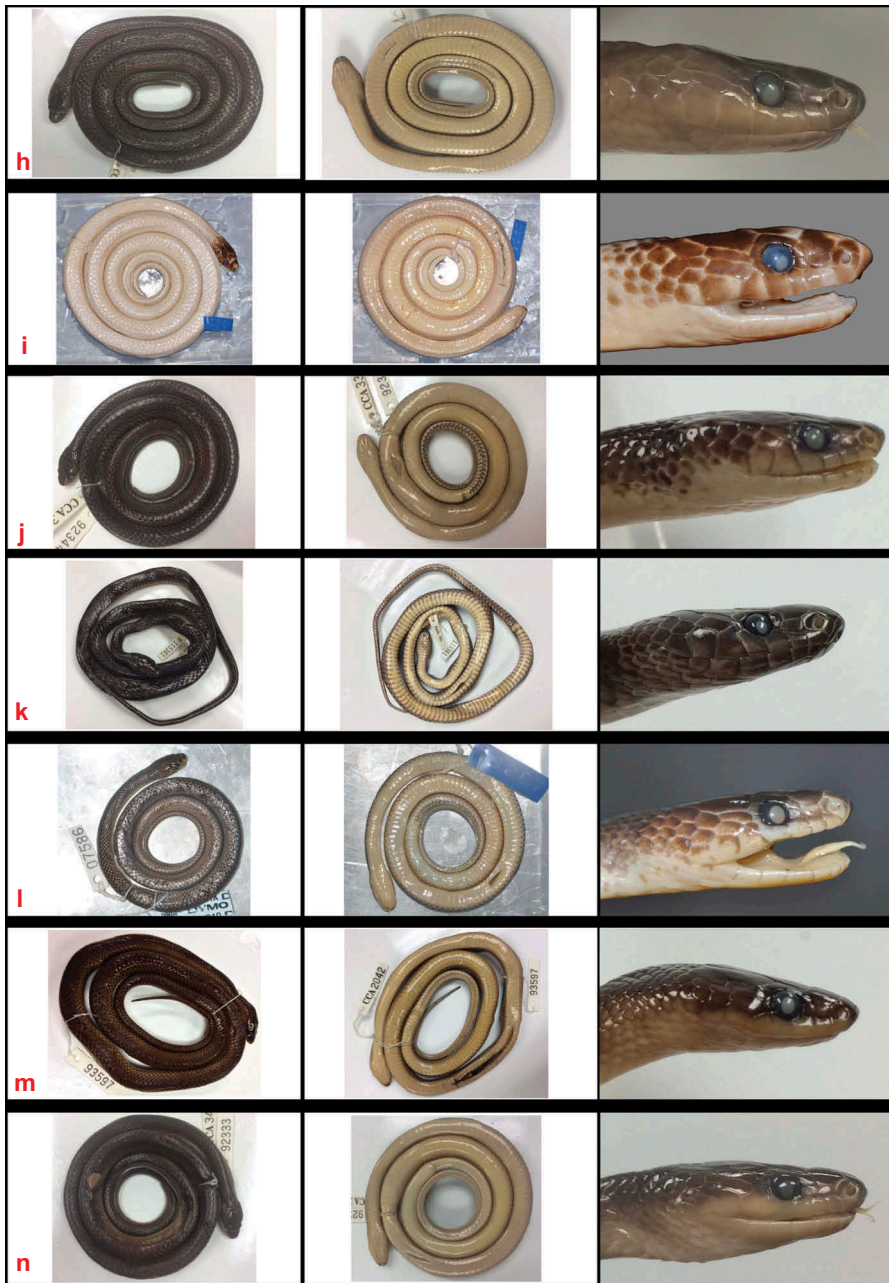


Figure 2. (Continued)

Data availability

All molecular and morphological data sets from this manuscript are available as online supplementary material and new sequences are accessioned on GenBank (MG099988–MG100201).

Results

We sequenced five loci for 49 *Stegonotus* individuals; the genes *ND4* (645 bp) and *BDNF* (573 bp) had sequence data for all 49 individuals; *MC1R* (410 bp) included 45 individuals, *R35* (554 bp) 37 individuals, and *RAG1* (449 bp) 34 individuals. The maximum-likelihood gene trees showed similar genetic structure between and within species for the mtDNA and the mtDNA + nucDNA trees, specifically geographic substructure within *S. diehli* and *S. modestus*, plus support for Manus Island specimens as a distinct clade (Figure 3; mtDNA tree included as Supplementary file). The nucDNA tree was poorly supported and lacked structure for many of the species, probably due to fewer informative sites and some missing data (tree available as Supplementary file). We used Structure to further examine the species and populations, excluding *S. batjanensis*, *S. cucullatus*, *S. guentheri*, *S. heterurus*, *S. muelleri* and *S. parvus*, due to their status as described taxa that were distinct from other species across gene trees, combined with low sample sizes or with little/no genetic structure (see Figure 3, Supplementary trees, and Appendix 1). The best value of *k* from Structure was six populations using the Evanno method and six populations when examining the *k*-value probabilities (Structure results in Supplementary materials). These populations corresponded to the genetic structure seen in the mtDNA and mtDNA + nucDNA gene trees (Figure 3), with three distinct populations within *S. diehli*, two within *S. modestus*, and a Manus Island population.

Testing the *Stegonotus* populations from Structure in BPP as separate species resulted in high support (posterior probabilities > 0.99) under all parameterizations for four undescribed species as well as a distinct *S. diehli* and *S. modestus*. The morphological data set for the putative new taxa also had consistent differences, notably differences in number of dorsal scale rows, ventral scale number, preocular scale number, and ventral colour and patterns (Table 1; Appendix 1) and corresponded to the species recovered by BPP. We recognize and describe four new species of *Stegonotus* based on genetics and morphology and, where relevant, we also used additional information from the literature in comparing the newly described taxa with previously described species (McDowell 1972).

Stegonotus iridis sp. nov.

(Figures 2–5, Table 1, Appendix 1)

Holotype

MZB.Ophi.3306 (field number SJR 7623, tissue ABTC 90141), adult male. Collected by S. Richards, B. Tjaturadi and K. Krey on 9 June 2005 from Warinkabom, Batanta Island, Raja Ampat Regency, West Papua Province, Indonesia, elevation 50 m above sea level (asl) (0.836942°S, 130.72162°E) (Figure 5).

Paratypes

SAMA R70466 (field number SJR 7514, tissue ABTC 90088) collected by S. Richards, B. Tjaturadi and K. Krey on 5 June 2005 from Waire Camp, Batanta Island, Raja Ampat Regency, West Papua Province, Indonesia, elevation 25 m asl (0.839738°S, 130.525546°E); MZB.Ophi.3305 (field number SJR 7624, tissue ABTC 90142) collected by S. Richards, B. Tjaturadi and K. Krey on 11 June 2005 from Urbinasopen, Waigeo Island, Raja Ampat

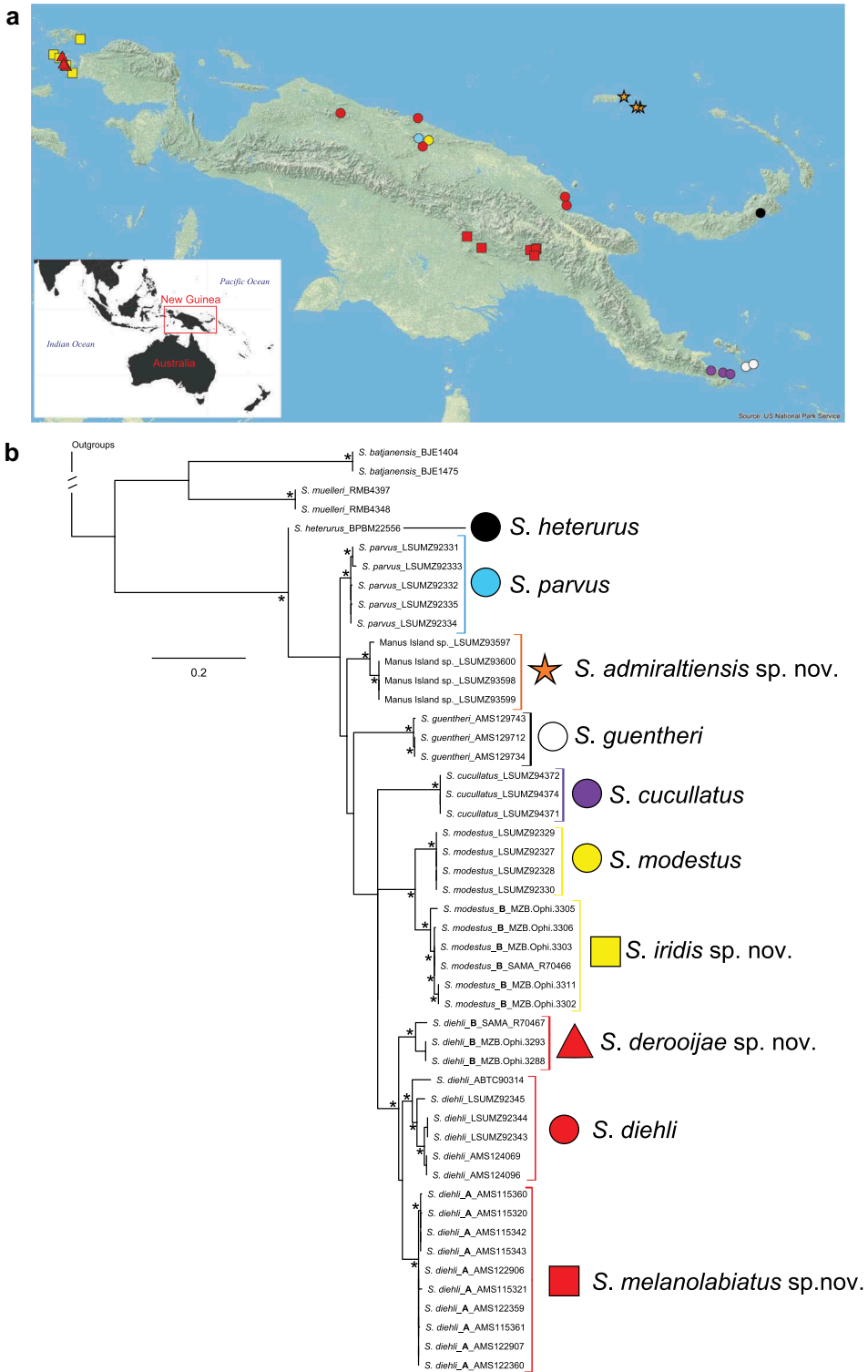


Figure 3. Map of New Guinea sampling localities for *Stegonotus* (a) and mtDNA + nucDNA maximum likelihood gene tree (b). Symbols for species/clades match those on the map; * indicates bootstrap values ≥ 70 . For some localities, symbols were adjusted for better visibility and so localities are approximate; see Appendix 1. for exact locality information.

Table 1. Morphological characters of *Stegonotus* examined.

Species	<i>n</i>	Rows	Ventral	Sub	Supr	Infr	Pre	Post	Aps	Ventral/sub pattern	Labial pattern
<i>S. diehli</i> **	5	15	162–170	73–85	7	8	1	1, 2	yes	mostly unmarked cream/with grey	some labials with grey
<i>S. melanolabiatus</i>	10	15, 17	179–197	89–98	7, 8	8, 9	1, 2	2	yes	marked with grey/dark grey	labials dark grey or mottled
sp. nov.**	4	17	178–197	90–94	7, 9	8, 9	2	2	no [†]	marked with grey/with grey	labials grey or yellow mottled
<i>S. derooijae</i>	8	17	183–214	60–88	7, 8	8, 9, 10	1, 2	2	no	unmarked cream/with some grey	with grey wash over labials
sp. nov.*	7	17, 19	198–211	78–88	8	9, 10	2	2	no	unmarked white/unmarked white	some grey/brown labials
<i>S. modestus</i> **	4	17, 19	202–214	93–98	8, 9	10	2	2	yes	unmarked cream/unmarked	unmarked labials
<i>S. iridis</i>	3	15	190–194	80–86	8, 9	9, 10	2	2	no	unmarked cream/unmarked	with grey wash over labials
sp. nov.*	3	17	182–186	75–76	8	9	1, 2	2	no	unmarked cream/unmarked	some labials with grey
<i>S. cucullatus</i> **	1	17	197	89	7	9	2	2	no	unmarked dark grey/very dark	supr. dark grey, infr with grey
<i>S. guentheri</i> *	5	17	173–180	89–102	8, 9	10	2	2	no	unmarked cream/unmarked	labials darker, some with mottle
<i>S. heterurus</i> *	12	17	207–229	82–90	7, 8	9, 10	1, 2	2	yes	unmarked yellow/edged with grey	labials with dark edges
<i>S. parvus</i> **	3	17	192–217	61–80	9	10	2	2	no	edged in grey/edged in grey	with grey wash over labials
<i>S. batjanensis</i>	1	21	229	83	9	10	2	2	no	edged in grey/grey wash	labials with dark marks
<i>S. borneensis</i>	1	17	235	85+	8	10	2	2	no	mottled grey/dark grey	supr. dark dorsally, infr. with grey
<i>S. florensis</i>											
<i>S. muelleri</i>											

Includes number of individuals examined for morphology (*n*), number of midbody dorsal rows (rows), range of ventral scale number (ventral), range of subcaudal scale number (sub), number of supralabial scales (supr), number of infralabial scales (infr), number of preocular scales (pre), number of postocular scales (post), presence of apical pits (aps), generalized ventral/subcaudal patterns (venter/sub pattern) and generalized labial patterns (labial pattern). New Guinean species indicated by *, mainland New Guinea by**. In cases of multiple numbers of scales the number in bold type represents the majority of specimens examined here. Specifics for individual specimens and additional morphological characters are in Appendix 1. A single *Stegonotus derooijae* sp. nov. was found with apical scales present, indicated by [†].

Regency, West Papua Province, Indonesia, elevation 45 m asl (0.337183°S, 131.258800°E); MZB.Ophi.3303 (field number SJR 7691, tissue ABTC 90173) collected by S. Richards, B. Tjaturadi and K. Krey on 18 June 2005 from Yakut Camp, Batanta Island, Raja Ampat Regency, West Papua Province, Indonesia, elevation 55 m asl (0.895817°S, 130.641633°E); MZB.Ophi.3311, MZB.Ophi.3302 (field numbers SJR 7794, tissue ABTC 90230; SJR 7793, tissue ABTC 90229), collected by S. Richards, B. Tjaturadi and K. Krey on 27 and 28 June 2005 from Waibya, Salawati Island, Raja Ampat Regency, West Papua, Indonesia, elevation 75 m asl (0.956383°S, 130.784333°E).

Referred specimens

MZB.Ophi.3301 (SJR7805, morphology only), collected by S. Richards, B. Tjaturadi and K. Krey on 27 and 28 June 2005 from Waibya, Salawati Island, Raja Ampat Regency, West Papua, Indonesia, elevation 75 m asl (0.956383°S, 130.784333°E).

Diagnosis

A new species of *Stegonotus* that can be diagnosed from its congeners by the following combination of characters: a completely white or white with a brownish washed, iridescent dorsum, with or without brown or black speckling which increases posteriorly, an immaculate white venter and white subcaudal scales or, in individuals that are more heavily pigmented dorsally, a white venter with a brownish wash increasing in intensity posteriorly, brown or black pigmentation on the dorsal scales of the head (including rostral, internasal, prefrontal, frontal, parietals, loreal, supralabial and ocular scales) usually extending down the neck two or three scale rows before fading away, 19 dorsal scale rows at midbody (infrequently 17), the absence of apical pits on dorsal scales, 198–211 ventral scales and 78–88 divided subcaudal scales, eight (infrequently nine) supralabial scales and 10 (infrequently nine) infralabial scales, with supralabial scales brownish or blackish and infralabial scales either white or, in highly pigmented individuals, brownish or blackish.

Description of holotype

Adult male in excellent state of preservation, with a short ventral slit midbody and hemipenes exposed, not fully expanded. Body shape is robust. Snout–vent length 713 mm with 201 ventral scales, tail length 238 mm with 88 divided subcaudal scales. Anal scale single. Head length 28.3 mm, as measured from the snout to the rear of the quadrate, width 14.9 mm as measured across the widest point of the head anterior to the quadrate. Eyes 3.6 mm horizontal diameter, pupil shape subcircular. Supralabials eight with the fourth and fifth in contact with the eye. Infralabials 10, with first pair in contact behind mental, infralabials one to five in contact with inframaxillaries. Rostral broader than high, 5.6 mm wide/4.5 mm high, visible from above. Nasal in contact with first supralabial. Single loreal, in contact with nasal, preoculars, prefrontal and supralabials one, two and three and slightly extending as to barely contact the eye. Circumoculars five: one supraocular, two preoculars, zero suboculars and two postoculars. Anterior temporals two. Dorsal surface of head includes pair of internasals (width 3.6 mm/length of suture 1.4 mm), pair of prefrontals (width 5 mm/length of suture 4.4 mm), pair of supraoculars (width 2.7 mm/length 4.1 mm), frontal longer than wide (length 6.5 mm/anterior width 6.4 mm), pair of parietals (length of suture 7.9 mm). Two pairs of inframaxillaries (anterior inframaxillary suture length 4.2 mm, posterior

inframaxillary suture length 2.9 mm), posterior inframaxillaries in contact with each other. Dorsal scale rows 17–19–15 (15th ventral from anterior, midbody, and 15th ventral anterior to cloaca).

Coloration in life

Dorsal coloration behind head white with no pattern or markings. Colour of iris black. Dorsum of head, including rostral, internasals, prefrontals, frontal, supraoculars and parietals, brown with white edges at the suture of most scales; several scales immediately posterior to the head with brown edges. Supralabials light brown/tan, infralabials white with light brown/tan pigment towards the ventral side of the scales. Ventral and subcaudal scales immaculate white and iridescent.

Coloration in preservative

Dorsal coloration in preservative of body posterior of head iridescent white with no pattern or markings down the entire dorsal side of the body and tail. Colour of iris opaque grey. Dorsum of head, including rostral, internasals, prefrontals, frontal, supraoculars and parietals, similar to coloration in life: brown with white edges at the suture of most scales; several scales immediately posterior to the head with brown edges. Supralabials light brown/tan, infralabials white with light brown/tan pigment towards the ventral side of the scales. Ventral and subcaudal scales immaculate white and iridescent.

Variation

Paratypes are similar to the holotype excepting the following: MZB.Ophi.3305 with 17 rather than 19 midbody dorsal scale rows, possibly nine rather than eight supralabials on the left (unclear), darker head pigmentation, dark speckling increasing posteriorly and a brownish-grey wash on the ventral and subcaudal scales; MZB.Ophi.3302, MZB.Ophi.3311, and MZB.Ophi.3301 with a brownish wash on the dorsal scales SAMA R70466 with 206 ventrals, 69 subcaudals (missing tail tip); MZB.Ophi.3305 with 198 ventrals, 78 subcaudals; MZB.Ophi.3303 with 203 ventrals, 83 subcaudals (missing tail tip); MZB.Ophi.3302 with 205 ventrals, 85 subcaudals; MZB.Ophi.3311 with 204 ventrals, 85 subcaudals; MZB.Ophi.3301 with 211 ventrals, 85 subcaudals.

Etymology

The species epithet is a noun in apposition and taken from the Latin word for rainbow. It refers to the high level of iridescence shown both dorsally and ventrally by this species.

Natural history and distribution

Currently known only from the Raja Ampat islands of Batanta, Salawati and Waigeo in eastern Indonesia where all of the animals encountered were active on the forest floor in moderately to heavily disturbed lowland (< 100 m asl) rainforest at night. The pale colour of this species made them extremely conspicuous against the dark forest floor.

Comparisons

The white or off-white dorsal and ventral colour of *Stegonotus iridis* sp. nov., with a dark coloured head that includes white edges on most head scales, is unique for the genus.

Although *S. cucullatus* has a pale phase that includes cream or yellowish-tan coloured dorsal scales with black edges resulting in a reticulated dorsal pattern (Figure 1(a)), the base coloration is not as white and appears more cream to tan when compared with *S. iridis* sp. nov. (Figures 2, 4, 5).

***Stegonotus derooijae* sp. nov.**
(Figures 2–4, 6, Table 1, Appendix 1)

Stegonotus diehli Lindholm 1905

Holotype

MZB.Ophi.3288 (field number SJR 7788, tissue ABTC 90225), adult male. Collected by S. Richards, B. Tjaturadi and K. Krey on 26 June 2005, from Waibya Camp, Salawati Island, Raja Ampat Regency, West Papua, Indonesia, elevation 75 m asl (0.956383°S, 130.784333°E) (Figure 4).

Paratypes

MZB.Ophi.3293 (field number SJR 7789, tissue ABTC 90226; Figure 6), same data as holotype; SAMA R70467 (field number SJR 7586, tissue ABTC 90123) collected by S. Richards, B. Tjaturadi and K. Krey on 9 June 2005 from Warinkabom, Batanta Island, Raja Ampat Regency, West Papua Province, Indonesia, elevation 50 m asl (0.836942°S, 130.72162°E).

Referred specimens

MZB.Ophi.3292 (field number SJR 7650, morphology only) collected by S. Richards, B. Tjaturadi and K. Krey on 13 June 2005 from Urbinasopen, Waigeo Island, Raja Ampat Regency, West Papua Province, Indonesia, elevation 45 m asl (0.337183°S, 131.258800°E).

Diagnosis

A new species of *Stegonotus* that can be diagnosed from its congeners by the following combination of characters: a dark grey or brown unpatterned dorsum with a white or cream venter with dorsal scale pigmentation continuing onto some or many of the ventral scales, dark grey pigmentation on the subcaudal scales extending from the dorsal scale pigmentation and with grey on the anterior edges of some subcaudal scales, 17 dorsal scale rows at midbody, 178–197 ventral scales and 90–94 divided subcaudal scales, two preocular scales, seven (rarely nine) supralabial scales, eight or nine infralabial scales, with the supralabial and infralabial scales cream and with grey pigmentation.

Description of holotype

Adult male in excellent state of preservation, with a short (< 5 cm) ventral slit midbody. Body shape relatively gracile with a narrow head. Snout–vent length 455 mm with 181 ventral scales, tail length 193 mm with 94 divided subcaudal scales. Anal scale single. Head length 17.0 mm, as measured from the snout to the rear of the quadrate, width 8.7 mm as measured across the widest point of the head anterior to the quadrate. Eyes



Figure 4. Photographs of three *Stegonotus* species described here in life; (a) *Stegonotus iridis* sp. nov. SAMA R70466 (b) *Stegonotus derooijae* sp. nov. MZB.Ophi.3288 (c) *Stegonotus admiraltiensis* sp. nov. from Manus Island, unregistered. Photos from SJR.



Figure 5. Photographs of holotype *Stegonotus iridis* sp. nov. MZB.Ophi.3306 showing (clockwise from top left) dorsal of body, ventral of body, dorsal of head, lateral of head. Photos from SJR.

2.6 mm horizontal diameter, pupil shape is subcircular. Supralabials seven with the third and fourth in contact with the eye. Infralabials eight, with first pair in contact behind mental, infralabials one to five in contact with inframaxillaries. Rostral broader than high, 3.2 mm wide/2.2 mm high, visible from above. Nasal in contact with first supralabial. Single loreal, in contact with nasal, preoculars, prefrontal, and supralabials one, two and three. Circumoculars five: one supraocular, two preoculars, zero suboculars and two postoculars. Anterior temporals two. Dorsal surface of head includes pair of internasals



Figure 6. Photographs of paratype *Stegonotus derooijae* sp. nov. MZB.Ophi.3293 showing (clockwise from top left) dorsal of body, ventral of body, dorsal of head, lateral of head. Photos from SJR.

(width 2.1 mm/length of suture 1.6 mm), pair of prefrontals (width 3.4 mm/length of suture 2.8 mm), pair of supraoculars (width 2.0 mm/length 2.7 mm), frontal longer than wide (length 4.6 mm/anterior width 4.0 mm), pair of parietals (length of suture 5.1 mm). Two pairs of inframaxillaries, (anterior inframaxillary suture length 2.6 mm, posterior inframaxillary suture length 1.5 mm), posterior inframaxillaries in contact with each other. Dorsal scale rows 17–17–15 (15th ventral from anterior, midbody and 15th ventral anterior to cloaca). A distinct pair of apical pits on most scales on the dorsum.

Coloration in life

Overall coloration in life similar to that described for preserved specimen except the white mottling on dorsal scales near the venter and lateral head scales has distinctly yellow pigment in life (Figure 4).

Coloration in preservative

Overall dorsal coloration dark grey-brown with no pattern down the dorsal side of the body and tail but some dorsal scales nearest the venter whitish-cream. Colour of iris opaque grey. Dorsum of head, including rostral, internasals, prefrontals, frontal, supraoculars and parietals brownish-grey and showing iridescence, with extensive white mottling on dorsal and lateral head scales including temporal scales. Supralabials with grey pigmentation that is darker on the dorsal edge and becoming almost entirely cream approaching the ventral edge of the scales. Infralabials cream with limited mottled grey pigment on the edges of each scale. Ventral scales cream with limited grey pigmentation from the dorsal scales extending on to some ventral scales in small patches but not crossing the ventral scales. Anal plate cream, subcaudals all with grey pigmentation concentrated on the anterior edge of each scale and becoming greyer moving posteriorly. Ventral scales show iridescence under lights.

Variation

The holotype is the only sexually mature individual in the type series. At just 290 mm snout-vent length, SAMA R70467 is clearly a juvenile, whereas MZB.Ophi.3293 is possibly a juvenile female because it lacks any sign of gonadal development under dissection despite being around the same size as the sexually mature male holotype. Apical pits are absent in the two paratypes (MZB.Ophi.3293, SAMA R70467) and referred specimen (MZB.Ophi.3292). In overall colour pattern, scalation and body shape paratypes are similar to the holotype excepting: MZB.Ophi.3293 and SAMA R70467 lack the extensive white mottling on the dorsal and lateral head scales; MZB.Ophi.3293 with 178 ventrals, 81 subcaudals (tail incomplete), nine rather than eight infralabials; SAMA R70467 with 178 ventrals, 90 subcaudals.

Etymology

The species epithet is a noun in the genitive case and is a patronym in honour of Dr Nelly De Rooij, who described many taxa from New Guinea and Indonesia, including *Stegonotus florensis*.

Natural history and distribution

Currently known only from the Raja Ampat islands of Batanta, Salawati and Waigeo in eastern Indonesia. This small, slender species was active on the forest floor in moderately to heavily disturbed lowland (< 100 m above sea level) rainforest at night. At each site it occurred in sympatry with *S. iridis* sp. nov., described above.

Comparisons

Stegonotus derooijae sp. nov. is part of the *S. diehli* complex (Figure 3) and this taxon would have been formerly considered *S. diehli*. It differs morphologically from *S. diehli* by having 17 dorsal scale rows at midbody versus 15 dorsal scale rows in *S. diehli*.

Stegonotus derooijae sp. nov. also differs from *S. diehli* in having higher numbers of ventral scales (178–197 in *S. derooijae* sp. nov. versus 162–174 in *S. diehli*) and subcaudal scales (90–94 in *S. derooijae* versus 73–85 in *S. diehli*) for the specimens we examined (excluding specimens with incomplete tails; Appendix 1). It differs from the new species (described below) from Southern Highlands and Chimbu Provinces by having two rather than (usually) one preocular scale. The overall dark coloration of *S. derooijae* sp. nov. distinguishes it from the sympatric *S. iridis* sp. nov. described above.

***Stegonotus melanolabiatu*s** sp. nov.
(Figures 2, 3, 7, Table 1, Appendix 1)

Stegonotus diehli Lindholm 1905

Holotype

AMS R115343 (field number R50; tissue ABTC 43740), adult male. Collected by S. Donnellan and K. Aplin, between 22 April and 4 May, 1984, from Doido, Chimbu Province, Papua New Guinea, elevation 1300 m asl (6.550000°S, 144.833333°E) (Figure 7).

Paratypes

AMS R122906 (field number B20; tissue ABTC 44739), collected by S. Donnellan and K. Aplin, November 1985, from Waro, Southern Highlands Province, elevation 550 m asl (6.533333°S, 143.183333°E); AMS R115361 (field number F46; tissue ABTC 43434), collected by S. Donnellan and K. Aplin, May 1984, from Noru, Chimbu Province, elevation 1150 m asl (6.583333°S, 144.650000°E) AMS R115320 (field number R22; tissue ABTC 43724), collected by S. Donnellan and K. Aplin, 1984, from Noru, Chimbu Province, Papua New Guinea, elevation 1150 m asl (6.533333°S, 144.850000°E).

Referred specimens

See Appendix 1.

Diagnosis

A new species of *Stegonotus* that can be diagnosed from its congeners by the following combination of characters: a dark grey or brownish unpatterned dorsum with a white or cream venter that includes dark grey markings, with dorsal scale pigmentation continuing onto some or many of the ventral scales, dark grey pigmentation on the subcaudal scales extended from the dorsal scale pigmentation, 17 dorsal scale rows at midbody (infrequently 15), the presence of two apical pits on most dorsal scales, 179–197 ventral scales and 89–98 divided subcaudal scales, one or (rarely) two preocular scales, seven or (rarely) eight supralabial scales, eight or (rarely) nine infralabial scales, with the supralabial and infralabial scales cream and marked with dark grey pigmentation or almost completely pigmented on the supralabials.

Description of holotype

Adult male in excellent state of preservation, tail complete, with two ventral slits, one in the heart-region (~5 cm) and the other midbody (~10 cm). Body shape is thin and gracile, with a

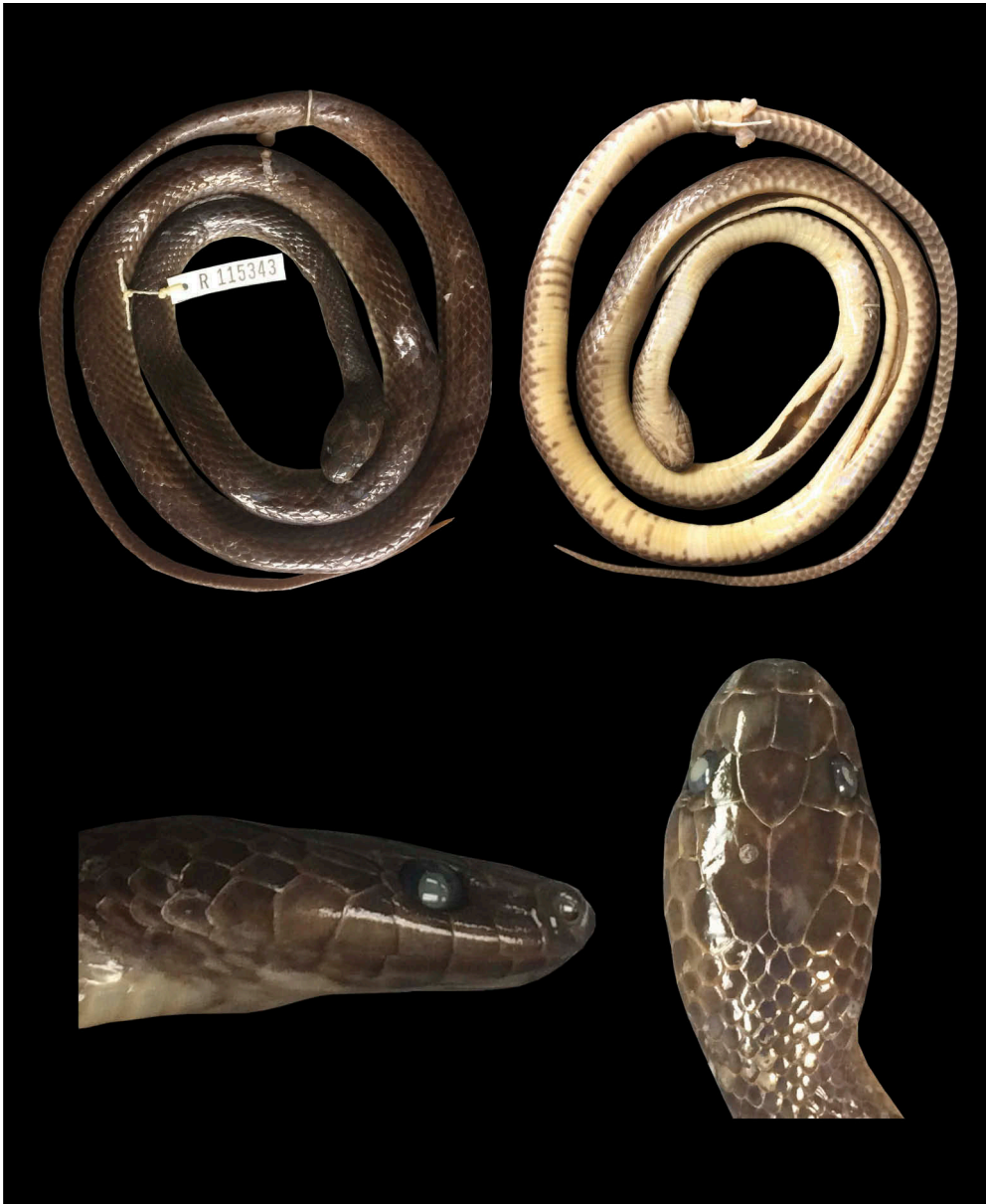


Figure 7. Photographs of holotype *Stegonotus melanolabiatu* sp. nov. AMS 115343 showing (clockwise from top left) dorsal of body, ventral of body, dorsal of head, lateral of head. Photos from SR.

relatively narrow head. Snout–vent length 615 mm with 197 ventral scales, tail length 192 mm with 92 divided subcaudal scales. Anal scale single. Head length 15.9 mm, as measured from the snout to the rear of the quadrate, width 11.5 mm, as measured across the widest point of the head anterior to the quadrate. Eyes 2.6 mm horizontal diameter, pupil shape is subcircular. Supralabials seven with the third and fourth in contact with the eye. Infralabials eight, with first pair in contact behind mental, infralabials one to five in contact with inframaxillaries. Rostral broader than high, 3.0 mm wide/1.7 mm high, visible from

above. Nasal in contact with first supralabial. Single loreal, in contact with nasal, preoculars, prefrontal and supralabials one, two and three and slightly extending as to barely contact the eye. Circumoculars four: one supraocular, one preocular, zero suboculars and two postoculars. Anterior temporals two. Dorsal surface of head includes pair of internasals (width 2.3 mm/length of suture 1.6 mm), pair of prefrontals (width 3.1 mm/length of suture 3.1 mm), pair of supraoculars (width 1.8 mm/length 2.8 mm), frontal longer than wide (length 3.9 mm/anterior width 3.6 mm), pair of parietals (length of suture 5.3 mm). Two pairs of inframaxillaries, (anterior inframaxillary suture length 2.4 mm, posterior inframaxillary suture length 2.1 mm), posterior inframaxillaries in contact with each other. Dorsal scale rows 17–17–15 (15th ventral from anterior, midbody and 15th ventral anterior to cloaca).

Variation

Paratypes similar to the holotype excepting the following: AMS R122906 with 15 rather than 17 dorsal scale rows; AMS R122906 with two rather than one preocular scale; AMS R115320 with 192 ventrals, 94 subcaudals; AMS R115361 with 186 ventrals, 89 subcaudals; AMS R122906 with 186 ventrals, 96 subcaudals.

Coloration in preservative

Overall dorsal coloration dark grey-brown in preservation with no pattern down the entire dorsal side of the body and tail. Colour of iris opaque grey in preservation. Dorsum of head, including rostral, internasals, prefrontals, frontal, supraoculars and parietals dark grey. Supralabials with grey pigmentation that is darker on the dorsal edge, becoming slightly lighter on the ventral edge. Infralabials cream with mottled grey pigment. Ventral scales cream with grey pigmentation from the dorsal scales extending on to many of the ventral scales, sometimes crossing the entire ventral scale and on the anal plate, subcaudals all with grey pigmentation and mostly grey moving posteriorly. Ventral scales show iridescence under lights.

Etymology

The species epithet comes from the Greek *melano* meaning black or dark and the Latin word *labia* for lips. The name refers to the dark coloration of the labial scales of this species.

Natural history and distribution

No information is known about the natural history of *S. melanolabiatus*. *Stegonotus melanolabiatus* sp. nov. is found south of the central mountain ranges (Figure 3) in Southern Highlands and Chimbu Provinces of Papua New Guinea. It may also occur in other provinces and regions south of the central cordillera across New Guinea.

Comparisons

Stegonotus melanolabiatus sp. nov. is part of the *S. diehli* complex (Figure 3) and this taxon would have been formerly identified as *S. diehli* Lindholm. It differs morphologically from *S. diehli* by typically having 17 dorsal scale rows at midbody (versus 15 in *S. diehli*). *Stegonotus melanolabiatus* sp. nov. also differs from *S. diehli* in having higher numbers of ventral scales (179 – 197 in *S. melanolabiatus* sp. nov. versus 162–174 in *S. diehli*) and subcaudal scales (89–98 in *S. melanolabiatus* sp. nov. versus 73–85 in

S. diehli) for the specimens we examined (Appendix 1). It differs from the morphologically similar *S. derooijae* sp. nov. in having (usually) one rather than two preocular scales, generally darker supralabial scales, and being found on the New Guinea mainland south of the central cordillera vs. known only from the Raja Ampat islands west of mainland New Guinea.

***Stegonotus admiraltiensis* sp. nov.**

(Figures 2–4, 8, Table 1)

Stegonotus modestus (Schlegel 1837)

Holotype

LSUMZ 93598 (field number CCA 2087), adult male. Collected by Christopher C. Austin on 1 September 2001 from Penchal Village on Rambutyo Island, Manus Province, Papua New Guinea, elevation 58 m asl, (2.3283333°S, 147.7666667°E).

Paratypes

LSUMZ 93599 (field number CCA 2092) and LSUMZ 93600 (field number CCA 2097), both collected by Christopher C. Austin on 3 September 2001 from northeast of Penchal Village on Rambutyo Island, Manus Province, Papua New Guinea, elevation 100 m asl (2.3405000°S, 147.7945000°E); LSUMZ 93597 (field number CCA 2042), collected by C. Austin on 29 August 2001 from near Peyon Village on Los Negros Island, Manus Province, Papua New Guinea, elevation 10 m asl (2.0326667°S, 147.4341667°E).

Diagnosis

Stegonotus admiraltiensis can be diagnosed from its congeners by the following combination of characters: a reddish-tan unpatterned dorsum with an immaculate white or cream venter that may be barely darker approaching and continuing posteriorly onto the subcaudal scales, 17 or 19 dorsal scale rows at midbody, the presence of two apical pits on most or all dorsal scales, 202–214 ventral scales and 93–98 divided subcaudal scales, two preocular scales, eight supralabial scales, nine or ten infralabial scales, with the supralabial and infralabial scales cream with little or no dark pigmentation.

Description of holotype

Adult male in excellent state of preservation, tail complete, short (~10 cm) ventral slit midbody for DNA tissue sample, hemipenes partially everted. Snout–vent length 658 mm with 208 ventral scales, tail length 185 mm with 98 divided subcaudal scales. Anal scale single. Head length 27 mm, as measured from the snout to the rear of the quadrate, width 15 mm, as measured across the widest point of the head anterior to the quadrate. Eyes 2.9 mm horizontal diameter, pupil shape subcircular. Supralabials eight with the fourth and fifth in contact with the eye. Infralabials 10 with first pair in contact behind mental, infralabials one to six in contact with inframaxillaries. Rostral broader than high, 5 mm wide/2.5 mm high, visible from above. Nasal in contact with first supralabial. Single loreal, in contact with nasal, preoculars, prefrontal and supralabials two and three. Circumoculars five: one



Figure 8. Photographs of holotype *Stegonotus admiraltiensis* sp. nov. LSUMZ 93598 showing (clockwise from top left) dorsal of body, ventral of body, dorsal of head, lateral of head. Photos from SR.

supraocular, two preoculars, zero suboculars and two postoculars. Anterior temporals two. Dorsal surface of head includes pair of internasals (width 2.9 mm/length of suture 1.5 mm), pair of prefrontals (width 4.0 mm/length of suture 4.0 mm), pair of supraoculars (width 2.5 mm/length 4.8 mm), frontal longer than wide (length 5.9 mm/anterior width 5.4 mm), pair of parietals (length of suture 6.5 mm). Two pairs of inframaxillaries, (anterior inframaxillary suture length 2.8 mm, posterior inframaxillary suture length 1.7 mm), posterior inframaxillaries in contact with each

other. Dorsal scale rows 17–19–15 at 15th ventral from anterior, midbody, and 15th ventral anterior to cloaca.

Variation

Paratypes similar to the holotype excepting the following: LSUMZ 93597 and LSUMZ 93599 with 17 rather than 19 dorsal scale rows midbody; LSUMZ 93599 with nine rather than ten infralabial scales; LSUMZ 93597 with slightly darker/grey wash on the subcaudal scales compared to the holotype; LSUMZ 93597 with 214 ventrals, 94 subcaudals; LSUMZ 93599 with 206 ventrals, 93 subcaudals, LSUMZ 93600 with 202 ventrals, 43 subcaudals (missing large portion of tail).

Coloration in life

Dorsal ground colour in life dark brown along the vertebral scale row and fading to yellowish lighter tan/light brown ventrally but with no distinct pattern down entire dorsal side of body and tail. Dorsum of head dark brown, ventrals and subcaudals cream with no patterns. Colour of iris in life dark brown-black.

Coloration in preservative

Overall coloration reddish brown in preservation and lighter in colour approaching the ventrals with no pattern down the dorsal side of body and tail. Colour of iris opaque grey in preservation. Dorsum of head, including rostral, internasals, prefrontals, frontal, supraoculars and parietals reddish brown. Supralabials one to five cream, with six to eight cream with a light wash of reddish brown infringing on the anterior of the scale where the supralabials come into contact with the temporals. Ventral scales cream with no pattern, subcaudals cream with no pattern. Ventral scales show iridescence under lights.

Etymology

The species epithet refers to the Admiralty Islands where this species is found, an archipelago of 18 islands to the north of New Guinea, comprising Manus Province, Papua New Guinea.

Natural history and distribution

As with all New Guinea *Stegonotus*, *S. admiraltiensis* sp. nov. is nocturnal. All four specimens were collected at night as they were moving on the forest floor on the leaf litter. Typical for *Stegonotus*, once picked up *S. admiraltiensis* sp. nov. rapidly attempted to bite the collector's hand and writhed violently in a side-to-side motion. Nothing more is known about the natural history or ecology of *S. admiraltiensis* sp. nov. *Stegonotus admiraltiensis* sp. nov. is found on the islands of Rambutyo and Los Negros in Manus Province of Papua New Guinea. Based on descriptions of similar specimens from Manus (McDowell 1972) and recent collections there by SJR that will be registered in the near future (Richards and Aplin 2015), we conclude that *S. admiraltiensis* sp. nov. is also found on Manus Island proper and that all specimens of *Stegonotus* from the Admiralty Islands are *S. admiraltiensis* sp. nov.

Comparisons

The Manus population of *Stegonotus* was thought to be conspecific with *S. modestus*; however, in our phylogeny it is not sister to *S. modestus* (Figure 3). Due to the poorly

supported node, it is unclear what the relationship of *S. admiraltiensis* is to other species in the genus. *Stegonotus admiraltiensis* sp. nov. differs morphologically from *S. modestus* by having no or little dark pigmentation on the subcaudal scales and in lacking extensive dark/grey pigmentation on the supralabial and infralabial scales, which is seen in some *S. modestus*. *Stegonotus admiraltiensis* also has two apical pits on all or most dorsal scales, but these are absent in *S. modestus*. Superficially, *S. admiraltiensis* most closely resembles *S. parvus*. Both species are more tan/brown than the grey/black typical of most New Guinea *Stegonotus* (Figure 2), and they both have an unpatterned cream venter and no grey mottling on the labial scales. Apart from genetic differences, *S. admiraltiensis* differs from *S. parvus* in having apical pits on all or most dorsal scales, (absent in *S. parvus*), as well as a higher number of ventral scales (202–214 in *S. admiraltiensis* versus 165–196 in *S. parvus*).

Discussion

New Guinea is on the border of one of the most distinct biogeographic demarcations in the world. Wallace's line, which coincides with the boundary between the ancient supercontinents of Laurasia and Gondwana, separates the dramatically different Oriental and Australian faunas (Wallace 1863; Michaux 1994); molecular work has shown a sharp taxonomic demarcation for reptiles (Schulte et al. 2003). The southern region of New Guinea has comprised the northern portion of the Australian Plate since the break up of Gondwana. In the early Cenozoic (55 million years ago) this plate separated from Antarctica and began moving northward, colliding in the late Oligocene with a complex subduction system consisting of island arcs, oceanic plateaus, sea mounts and plate fragments. Over the last 5 million years inter-plate impact and accretion of more than 30 terrains along the north coast has resulted in considerable uplift and volcanism. Additionally, these events were associated with dramatic fluctuations in sea level and changes in precipitation (Dow 1977; Axelrod and Raven 1982; Hill and Gleadow 1989; Haig and Medd 1996; Read and Hope 1996), during which New Guinea was at least twice joined with Australia across the Torres Strait and connected to many of the adjacent islands by land bridges. These various events have produced a biota with a high degree of regional endemism (Beehler 1993; Supriatna et al. 1999). *Stegonotus* crosses this major biogeographic barrier, with species being found across Wallace's line. However, the taxon sampling available here, particularly with respect to the genus *Lycodon*, does not allow us to determine the origination of the group. We note that the earlier diverging *Stegonotus* species, all found west of New Guinea, fall outside of a monophyletic New Guinea clade (Figure 3), which now includes 10 species. This might suggest that dispersal is from west to east, crossing Wallace's line and with speciation increasing upon arrival at New Guinea. Although support values for and within the subclades of *Stegonotus* are generally high, the backbone of this tree is poorly resolved and with short internodes (Figure 3); this may be due to rapid speciation. Additional genetic sampling that includes many species of *Lycodon*, as well as other colubrids, and framed within a species-tree context would help us better determine the origin, speciation and relationships of *Stegonotus* with respect to other snakes.

The most distinctive topological feature of New Guinea is the 2500 km long cordillera of steep mountains running the length of the island. The crests of the cordillera

commonly reach 3000 m and in some areas approach 5000 m. By 3–4 million years ago the central cordillera was sufficiently high to act as a potential barrier to gene flow for lowland-restricted taxa (Pigram and Davies 1987; Welzen 1997; Polhemus and Polhemus 1998). The specific role of this recent tectonic and palaeoclimatological activity, however, in shaping the biodiversity of the island is poorly understood, particularly with respect to the reptile fauna (e.g. Austin et al. 2010). The cordillera appears to be a biogeographic barrier for the *S. diehli* complex with *S. diehli* north, *S. melanolabiatum* sp. nov. south and *S. derooijae* sp. nov. west of the cordillera (Figure 3). We expect that further sampling across the island will show similar results, especially for the widespread species *S. cucullatus*, for which we have limited sampling in this study. Likewise, island endemics such as *S. guentheri* and *S. heterurus* that occur across numerous islands may be shown to be species complexes with cryptic diversity.

While cryptic diversity in these unassuming snakes is almost to be expected, the genus *Stegonotus* also contains more obvious yet undescribed taxa. For example, two of the species newly described here, *S. admiraltiensis* sp. nov. from Manus Province and *S. iridis* sp. nov. from Raja Ampat both have noticeable morphological characters differentiating them from others in the genus. In fact, *S. admiraltiensis* sp. nov. has been previously mentioned as having characters distinct from other *Stegonotus* (McDowell 1972), but had not been further examined or considered a separate taxon from *S. modestus*. In the case of *S. iridis* sp. nov., its coloration is unlike that found among other species of *Stegonotus*, being white bodied while all other species tend towards greys and browns, excepting the light phase of *S. cucullatus* (Figures 1, 4). A lack of interest in the genus combined with the difficulty of conducting field work in New Guinea is at least partly the reason these snakes have gone so long undescribed.

Our results also suggest niche division among *Stegonotus*. In at least two localities we find two or more sympatric species of *Stegonotus*, none of which are sister taxa, indicating that *Stegonotus* have invaded the same regions of New Guinea more than once (Figure 3). To partition resources, these snakes may be specializing on different prey items. Although it is beyond the scope of this study to determine how these somewhat superficially similar species co-exist, we note that these snakes do have differences in their body forms. For example, at Utai, Papua New Guinea, C. Austin has observed and collected three species of *Stegonotus* – *S. diehli*, *S. modestus* and *S. parvus* – in similar habitats and active around the same time of night. However, these three species have different body types, with *S. diehli* having a wiry, gracile body shape and a narrowish head, *S. modestus* being thicker and heavy-bodied (compared with *S. diehli* even at the same approximate snout–vent length) and with a blocky head, and *S. parvus* falling somewhat intermediate between the two (Figure 2). Additional studies on co-occurring *Stegonotus* species that include average adult body sizes, stomach contents and possibly computerized tomography scans of teeth, which were considered an important character by previous authors (McDowell 1972) would help to determine how each species functions independently in the same general habitat.

While the work presented here increases the number of *Stegonotus* species by 40%, it is likely that this genus includes additional undescribed species. We plan further sampling across New Guinea to examine more fully the pattern and tempo of diversification within *Stegonotus*. Furthermore, *Stegonotus* has not previously been included within any large molecular phylogeny of snakes, and despite its alleged close relationship to

Lycodon, this hypothesis is yet to be confirmed. Future work will focus on sampling additional localities, including high-throughput genetic data for all described *Stegonotus* species, and placement of the genus within a larger sampling of colubrid snakes.

Geolocation Information. – This work was conducted in New Guinea (Papua New Guinea and Indonesia, and surrounding islands); general locality 6.550000°S, 144.833333°E.

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Disclosure statement

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