

THE MOLUCCAN SHORT-TAILED SNAKES OF THE GENUS *BRACHYORRHOS* KUHL
(SQUAMATA: SERPENTES: HOMALOPSIDAE), AND
THE STATUS OF *CALAMOPHIS* MEYER

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ABSTRACT. — *Brachyorrhos* Kuhl represents a terrestrial, fangless, vermivorous clade of the Homalopsidae. Most recent discussions of the genus consider it to contain two species, *Coluber albus* Linnaeus and *Calamophis jobiensis* Meyer. These poorly known snakes have had a deeply intertwined and confused nomenclatural history. Here we review *Brachyorrhos*, and find that *B. albus* is restricted to Seram and Ambon, but may be present on other nearby islands in the Seram group; *Rabdion gastrotaenia* Bleeker (from Buru) is assigned to the genus *Brachyorrhos*, and *Atractocephalus raffrayi* Sauvage (from Ternate) is also assigned to the same genus. The species on Halmahera is described and named *B. wallacei*. Meyer's genus *Calamophis* is resurrected for *jobiensis* and its undescribed relatives, which are endemic to the Bird's Head region of Western Papua and Yapen Island. *Brachyorrhos* species are endemic to the Moluccas and possibly the surrounding area in eastern Indonesia; *Calamophis* also appears to belong to the Homalopsidae.

KEY WORDS. — Moluccas, Bird's Head New Guinea, systematics, evolution, aquatic snakes, terrestrial snakes

INTRODUCTION

The Homalopsidae is a clade of snakes composed of morphologically and ecologically diverse species sharing grooved rear-fangs, crescent-shaped, valvular nares, small eyes, a tracheal lung, and hypapophyses throughout the vertebral column with the crown species estimated to have evolved about 18–20 MYA (Gyi, 1970; Alfaro et al., 2008). McDowell (1987) suggested that *Brachyorrhos* Kuhl in Schlegel be added to the family despite the absence of rear-fangs and a terrestrial lifestyle. Murphy (2007) was initially skeptical of the placement of *Brachyorrhos* within the Homalopsidae, but the first molecular evidence of the

relationships among *Brachyorrhos* species suggests that the placement is indeed accurate (Murphy et al., 2011). Thus, despite its terrestrial lifestyle, fangless maxillary bone, and vermivorous diet, *Brachyorrhos* is an early divergent lineage within the Homalopsidae.

The Homalopsidae therefore contains the terrestrial/fossorial *Brachyorrhos*; the semi-terrestrial fish and frog-eating *Enhydris plumbea*; highly aquatic, active foraging freshwater, fish-eating-species *Enhydris enhydris* and *E. subtaeniata*; the completely aquatic, freshwater ambush specialist *Erpeton tentaculatus*; the terrestrial-brackish water, fish-eating *Enhydris bennettii*; as well as the brackish water and marine

Table 1. Locality information and GenBank accession numbers for specimens used in the phylogenetic analyses.

Taxon	Collection locality	Museum number	GenBank accession number (cytochrome b)
<i>Brachyorrhos albus</i>	Gunung Gamalama, Ternate	MZB 4008	JX139711
<i>Brachyorrhos albus</i>	Desa Maliaro, Ternate	MZB 4009	JX139713
<i>Brachyorrhos albus</i>	Danau Laguna, Ternate	MZB 4010	JX139712
<i>Brachyorrhos wallacei</i>	Jailolo, Halmahera	MZB 3464	JX139714
<i>Brachyorrhos wallacei</i>	Jailolo, Halmahera	MZB 3462	JX139715
<i>Brachyorrhos wallacei</i>	Jailolo, Halmahera	MZB 3463	X139716
" <i>Brachyorrhos albus</i> "	Ambon	FMNH 134323	—

species that occasionally enter freshwater, and feed on fish, crustaceans, and gastropods (*Cantoria*, *Cerberus*, *Fordonia*, *Gerarda*, *Myron*). Homalopsids have adapted to an extremely broad range of terrestrial and aquatic lifestyles and diets (Murphy, 2007).

Here we examine the systematics and nomenclature of the early divergent homalopsid genus, *Brachyorrhos*, and the status of an affiliated fossorial-aquatic genus, *Calamophis*.

Linnaeus (1758) described *Coluber albus* on the basis of a single specimen with the type locality of "Indiis," (Ambon, South Maluku). The holotype (NRM 19) has 170 ventrals, 27 subcaudals, an immaculate venter, a fused prefrontal and loreal, and a single preocular (examined by Andersson, 1899, and by us using photographs). Kuhl (in Schlegel, 1826) erected the genus *Brachyorrhos* for Linnaeus' *Coluber albus*. Later, Bleeker (1857a), Meyer (1874), and Sauvage (1878) described species with similar morphology all in different genera. Peters and Doria (1878) placed *Calamophis jobiensis* Meyer in *Brachyorrhos*. Boulenger (1893) considered *Calamophis jobiensis*, *Atractocephalus raffrayi* Sauvage, and *Rabdion gastrotaenia* Bleeker junior synonyms of *Coluber albus* Linnaeus. Checklist authors (Rooij 1917; Kopstein, 1926; Haas, 1950; Welch, 1988) followed Boulenger's arrangement, until Iskandar and Colijn (2001) listed *B. jobiensis* as a valid species based upon a personal communication from Van Wallach.

The holotype of *Calamophis jobiensis* Meyer was destroyed during the Allied bombing of Dresden during World War II (fide Iskandar & Colijn, 2001). McDowell (1987) examined BMNH 1910.4.26.60 and on a note associated with BMNH 1910.4.26.60 wrote, "...I suspect this specimen is a Ceram record for *Brachyorrhos jobiensis*."

Murphy (2007) examined BMNH 1910.4.26.60 and BMNH 1998.330 from Seram, both specimens catalogued as *Brachyorrhos jobiensis*. Relatively few differences between BMNH 1998.330 and *B. albus* from Ambon and Seram were found. However, BMNH 1910.4.26.60 was clearly a *Brachyorrhos* with a distinct loreal, a preocular, an exceptionally low ventral count, and a greatly reduced adult body size (it will be discussed with elsewhere).

Meyer's *Calamophis jobiensis* was based on a specimen from Yapen Island, West Papua, Indonesia and was reported to have

164 ventrals, 10 subcaudals, six upper labials, eight lower labials, a single internasal, and a single postocular. Peters and Doria (1878) synonymised *Calamophis jobiensis* into *Brachyorrhos* because they did not consider the characters separating the two genera sufficient to warrant generic status. This, combined with questionable localities reported in the literature, has resulted in *Brachyorrhos albus* being reported from no less than 17 islands from Sumatra to Yapen Island, Western Papua. Taken together, the straight line distance from southern Sumatra to Yapen Island is more than 3500 km. Thus, the locations listed for this species by Rooji (1917) and others suggest that *B. albus* is a widespread species.

MATERIAL AND METHODS

We examined museum material related to *Brachyorrhos*. External morphological data were collected from 58 museum specimens and nomenclature used follows Peters (1964) and Lillywhite (2009). Measurements of body and tail lengths were taken to the nearest 1 mm; ventral scales were counted following Dowling (1951); the terminal scute was not included in the number of subcaudals. Dorsal scale row counts were made about 10 ventrals behind the head, at midbody, and about 10 ventrals anterior to the vent. Values for paired head scales and subcaudals are given in left/right order. Univariate analyses of morphological data, ANCOVA, Student t-tests, principal component analysis, and cluster analysis were applied when necessary. Statistical analysis was done with Excel and DataLab®. Institutional abbreviations are in the Acknowledgements section. Other abbreviations are: *MY* – millions of years; *N* – number of specimens; \bar{x} – mean value; *SVL* – snout vent length; *SD* – standard deviation; *SE* – standard error.

Molecular methods. — We sampled seven *Brachyorrhos albus* tissues for molecular analyses: three individuals from Ternate, North Moluccas; three from Jailolo, West Halmahera, North Moluccas; and one from Ambon, Central Moluccas. These tissues have accompanying voucher specimens that were included in the morphological analyses and are accessioned in the Museum Zoologi Bogor (MZB), Cibinong, Indonesia, and the Field Museum of Natural History in Chicago (FMNH). Specimen localities and GeneBank accession numbers are given in Table 1.

Standard protocols (Genra Systems, Inc) were used to extract genomic DNA from ethanol preserved liver and muscle samples. ~1100 base pairs of the mitochondrial cytochrome *b* gene were amplified by PCR using HotMaster Taq reagents (Perkin Elmer/Applied Biosystems) and the following primers: Forward Elapid Cytb Lb (5'-GGA CAA ATA TCA TTC TGA GCA GCA ACA G-3') and Reverse Elapid Cytb H (5'-TTG TAG GAG TGA TAG GGA TGA AAT GG-3') (Lukoschek & Keogh, 2007). Double-stranded sequencing was outsourced to the Australian Genome Research Facility Ltd (AGRF) in Adelaide, Australia.

Sequences were checked for ambiguities, and alignments were assembled from consensus sequences of forward and reverse reads using Geneious Pro v5.1.7 software (Drummond et al., 2010). Polymorphism and divergence statistics were calculated using DnaSP v5 (Librado & Rozas, 2009) and the Species Delimitation plugin for Geneious Pro (Masters et al., 2000).

RESULTS

Molecular results. — PCR amplification was unsuccessful for the Ambon specimen loaned from the Field Museum (FMNH134323), leaving a final data matrix of 6 individuals and 1093 sites. Translation of the aligned sequences did not reveal frameshifts, unexpected stop codons, or indels.

The 3 Ternate specimens were represented by 2 haplotypes that differ at only 2 sites, whereas the 3 Halmahera specimens were represented by 2 haplotypes that differ at 1 site. In contrast to the low haplotype diversity within localities, the Ternate and Halmahera populations showed 56 fixed nucleotide differences and a mean pairwise (Jukes Cantor) distance of 7.2%.

Morphological results. — *Brachyorrhos* (sensu Boulenger, 1893) contains small (<74 cm) snakes with 19 scale rows at mid body and short tails (3–18% of SVL). Most species have the prefrontal, loreal, and preocular fused (*B. albus* is the exception with a preocular). While some specimens show a pattern of head markings and nape bands (these are most often present in neonate and juvenile specimens), and a mid ventral stripe, most specimens are uniform brown above and yellow or cream below. Some have a single internasal, others have a divided internasal, some show a posterior reduction in dorsal scales; and some have a single postocular.

However, the cluster analysis and PCA results (Figs. 1, 2) prompted a closer examination of the six specimens from Papua. They formed a group of specimens that are morphologically distinct and geographically disjunct from the other 52 specimens examined. Specimens of *Brachyorrhos* clustered together, as did those of *Calamophis*. Table 2 compares the two genera for 12 anatomical traits used in the analyses, suggesting these two clades are distinct, but likely to be closely related. Based on our translation of the description of *Calamophis jobiensis* by Meyer (1874), he describes a snake with 19 dorsal scale rows, six upper labials, a

pentagonal rostral, a preocular, a postocular, 164 ventrals, and 10 subcaudals. The type locality was the village of Ansum on Yapen Island in the Bird's Head Region of West Papua. Peters and Doria (1878) reported on five specimens of *Calamophis* collected in 1875 by A. A. Bruijn at two localities (Mt Arfak and Andai in Papua) and critiqued Meyer's new genus. In fact, there are only four extant specimens (Museo Civico di Storia Naturale, Genoa), two from each of these localities. Peters and Doria considered the differences between Meyer's *Calamophis* and *Brachyorrhos* insignificant. They cited the single internasal in *Calamophis* as what separates it from *Brachyorrhos* and considered this trait to be inconsistent in *Calamophis*. They noted *Calamophis* specimens have a shorter head and consequently smaller head shields; and placed *Calamophis jobiensis* in *Brachyorrhos*.

Peters and Doria were also looking at MSNG 56342, a specimen reported to be from the Aru Islands that was presumably collected by Mr. Hoedt (an Ambon resident). The juvenile specimen was given to Beccari who presented it to the Genoa Museum (Italy) in 1873. Superficially, this specimen has the same colouration and pattern as the two specimens from Andai, but it has a divided internasal, two postoculars, no posterior reduction in dorsal scale rows, as well as all of the other morphology associated with *Brachyorrhos*.

We examined the Arfak and Andai specimens (as well as the Aru specimen) discussed by Peters and Doria and compared them to *Brachyorrhos*. Contrary to their findings, none of the specimens from Arfak and Andai had two internasals. We also examined two specimens from other Papuan localities, the Kebar Valley and Ambuaki. All six specimens resemble Meyer's generalised description of *Calamophis*. However, we found additional significant morphological differences between *Brachyorrhos* and the Papua specimens. These differences have been summarised in Table 2. Thus, we are redefining *Brachyorrhos* Kuhl and revalidating *Calamophis* Meyer.

Brachyorrhos Kuhl in Schlegel, 1826

Coluber Linnaeus, 1758: 128

Brachyorrhos Kuhl in Schlegel, 1826: 236

Brachyorrhus Agassiz, 1847: Emendation of *Brachyorrhos*

Calamaria (in part) Schlegel, 1837: 25

Rabdion Bleeker, 1860b: 42

Brachyorrhos Doria, 1874: 329. Error for *Brachyorrhos*

Atractocephalus Sauvage, 1879: 62

Oxyorrhos Fischer, 1879: 89

Brachyura Edgar & Lilley, 1993: 136

Type species. — *Coluber albus* Linnaeus by original designation

Comment on some taxonomic confusion. — The names *Brachyorrhos kuhlii* Boie, 1827, *Coluber brachyurus* Shaw, 1802, and *Calamaria brachyorrhos* Schlegel, 1837 are in fact based on a specimen of *Atractus trilineatus* (see Hoogmoed, 1982), a Neotropical dipsadids, but have been considered synonyms of *Brachyorrhos albus* by various authors. Macleay (1877) described *Mainophis robusta* from Papua New Guinea and Boulenger (1893)

Table 2. A comparison between *Brachyorrhos* and *Calamophis*.

Morphological traits	<i>Brachyorrhos</i>	<i>Calamophis</i>
N =	52	6
Posterior reduction in dorsal scale rows	no	yes
Dorsal scales imbricate	no	yes
Dorsal scales mostly juxtaposed	yes	no
Nasal scale bilobed	yes	no
Internasal divided	yes	no
Two postoculars	yes	no
Rostral broader than tall	no	yes
Frontal shape hexagonal	yes	no
Tail slender and tapers to tip	yes	no
Slight constriction at base of tail	no	usually
Venter with a broad dark stripe	no	yes
Eye diameter equal to the seam of loreal with upper labials	no	yes

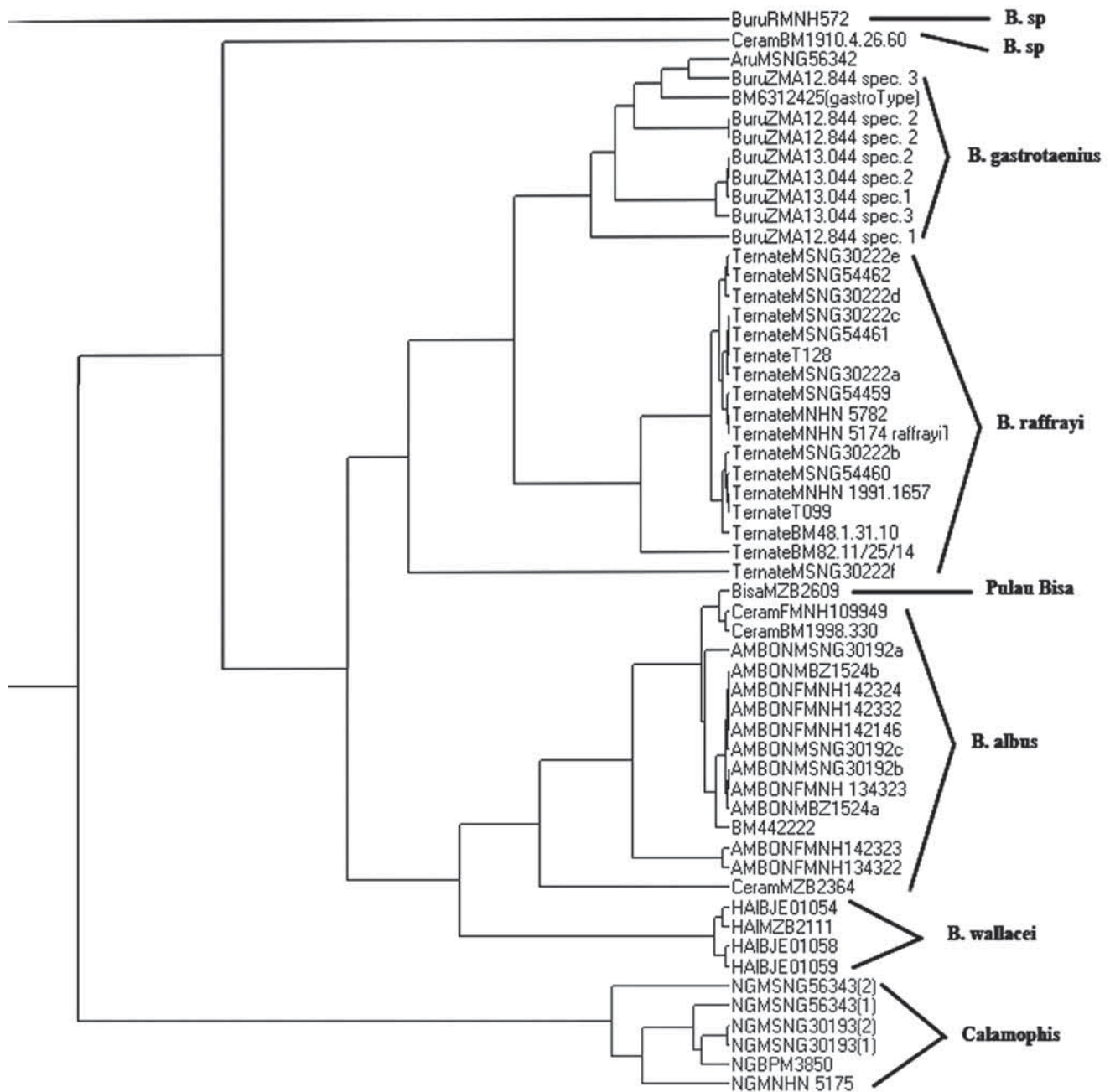


Fig. 1. A cluster analysis of *Brachyorrhos* based on a morphological analysis of 23 meristic characters.

placed this snake in the synonymy of *Brachyorrhos albus*. The type specimen is in fact the elapid *Furina tristis* (Shea & Sadlier, 1999), hence this name should be disregarded. All of these names have appeared in recent synonymies of *Brachyorrhos* (Iskandar & Colijn, 2001; Murphy, 2007; The Reptile Database (online), by Uetz, 2012) in part because of the complex nature of the confusion and the relatively obscure places the information has been published. Additionally, Heij et al. (1997) has confused *Brachyorrhos albus* with *Boiga irregularis*, suggesting that it eats bird eggs. Andersson (1899) reported that the type specimen is as described by Linnaeus, except that it has 27 subcaudals instead of 20, and that the fifth upper labial is divided (presumably horizontally divided) as opposed to what Boulenger (1893) reported for other specimens.

Diagnosis. — *Brachyorrhos* species are the only homalopsid snakes known to have bilobed nasal scales separated by the rostral—a rostral that is as broad as tall—and a divided internasal behind and dorsal to the nasals. Members of this genus can be distinguished from *Calamophis* (with which it has been long confused) by the lack of dorsal scale row reduction (*Brachyorrhos* has 19-19-19, *Calamophis* has 19-19-17); dorsal scales are ovate, slightly imbricate or juxtaposed compared to dorsal scales in *Calamophis*; a longer snout, a divided nasal scale, and a tail that lacks a constriction at its base and tapers gradually to the tip.

Description. — Small to medium snakes (adult size 30–74 cm) with a pointed head indistinct from the cylindrical, muscular body, and a relatively short but tapering tail. The

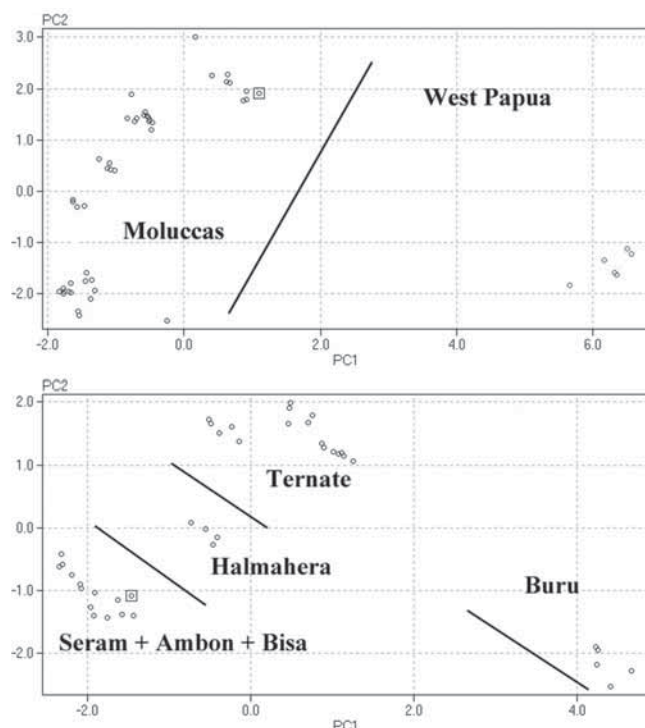


Fig. 2. A plot of 55 museum specimens catalogued as *Brachyorrhos* using a PCA. PC1 (ventrals) accounted for 43.93% of the variation; PC-2 (subcaudals) accounted for 19.23% of the variation, and PC-3 (mid-ventral stripe) accounted for 11.19% of the variation. Many of the other traits used in this analysis are listed in Table 1. The Moluccan *Brachyorrhos* are to the left, the West Papuan *Calamophis* are to the right. Bottom: PCA results for *Brachyorrhos* showing clumping by island. The square with internal circle is the specimen from Pulau [=Island] Bisa.

nasal scale is bi-lobed with the anterior lobe larger and containing the valvular nostril. Loreal usually fused with the prefrontal and preocular (a preocular is present in *B. albus*). One pair of chin shields makes contact with the first four lower labials. Five to seven upper labials, third, fourth, or 3 + 4 in orbit. Six to eight lower labials, first pair makes medial contact, fourth is the longest, four contact first pair of chin shields. Smooth dorsal scales in 19 rows on the neck, at mid-body, and just anterior to the vent, thus there is no posterior reduction in dorsal rows. Scales are ovate and juxtaposed or very slightly imbricate. Ventrals 159–195; divided subcaudals 18–42, anal scale divided. Males tend to have lower ventral counts, higher subcaudal counts, longer tails, and smaller SVLs than females (see Table 3 for morphometrics).

Distribution. — Literature reports of wide-ranging and often erroneous localities for *Brachyorrhos* have added confusion to the actual identity of these snakes. Despite the report of *Brachyorrhos* on Sumatra by Bleeker (1857a), Haas (1950) and David and Vogel (1996) found no evidence that it occurs there. Many of Bleeker's records, including the Sumatra locality, are considered unreliable (Barbour, 1912; Haas, 1950). In defense of Bleeker's Sumatran record, one of us (JCM) has recently found a Sumatran snake that looks remarkably like *Brachyorrhos* but most likely does not belong in the genus. Similarly, the species has been reported from Borneo, and examination of one museum specimen labelled as *Brachyorrhos albus* (SMNS 2749) collected in Borneo in 1897 by H. Rolle, was in fact a bleached specimen of *Calamaria cf. schlegelii*.

Brachyorrhos was reported twice from Timor in the 19th century. A Timor specimen supposedly in the Leiden museum was probably collected by Müller and described by Günther (1858) and possibly also by Boulenger (1893). Müller (1857) reported *Calamaria brachyorrhos* (= *B. albus*) on Ambon, but not Timor; this specimen was not found in the Leiden museum collection. We found this specimen in the British Museum (BMNH 442222) and doubt that it originated from Timor. However a second specimen (RMNH 576), also reported from Timor, was located in the Leiden museum. This specimen, collected by E. W. A. Ludeking in 1863, has



Fig. 3. The distribution of four species of *Brachyorrhos*, and the known distribution of *Calamophis* (based upon 6 specimens).

Table 3. A comparison of morphometrics for *Brachyorrhos albus* from three islands. nd = no data.

	Ambon	Seram	Pula Bisa
N =	13	3	1
	159–173	168–173	
Ventrals males	$\bar{x} = 168.7$ SD = 3.56 N = 9	$\bar{x} = 170.5$ N = 2	nd
	171–174		
Ventrals females	$\bar{x} = 173.5$ SD = 3.32 N = 4	175 N = 1	174
	30–36	26–27	
Subcaudals males	$\bar{x} = 32.89$ SD = 2.08 N = 9	$\bar{x} = 26.50$ N = 2	nd
	23–27		
Subcaudals females	$\bar{x} = 24.75$ SD = 1.71 N = 4	24 N = 1	28
	334–426	366–385	nd
Male SVL	$\bar{x} = 397$ SD = 42.17 N = 9	$\bar{x} = 375.5$ N = 2	
	47–61	32–35	nd
Male tails	$\bar{x} = 55.75$ SD = 4.55 N = 8	$\bar{x} = 33.50$ N = 2	
	0.126–0.17	0.83–0.96	nd
Male tail/body ratios	$\bar{x} = 14.36$ SD = 1.44 N = 8	$\bar{x} = 0.895$ N = 2	
	343–443		
Female SVL	$\bar{x} = 379.5$ SD = 44.61 N = 4	350 N = 1	378 N = 1
	9.3–11		
Female tails	$\bar{x} = 36.75$ SD = 3.50 N = 4	33 N = 1	30
	0.93–0.11		
Female tail/body ratios	$\bar{x} = 0.0978$ SD = 0.82 N = 4	0.094 N = 1	0.079
Ventral pattern	uniform cream	uniform cream	nd

several lines of evidence suggesting it originated in Seram. Data with Ludeking's specimen reported "Papoetikbaai" [= Paputik Bay], Timor. However, three specimens of *Draco lineatus bourouniensis* were collected by Ludeking in 1863 on Seram at "Papoetik bay" (Musters, 1983), as well as one specimen of *Varanus cerambonensis* (Philipp et al., 1999). The type location for the *V. cerambonensis* is Seram. Old maps of Seram leave only one option for the locality "Paputik Bay", it is now known as Elpaputih Bay in Southwest Seram. Additionally, Kaiser et al. (2011) failed to find *Brachyorrhos* in the Timor-Leste herpetofauna. In our cluster analysis and PCA, BMNH 442222 associates with the Ambon population; and RMNH 576 associates with the Seram population.

There is a single specimen from the Aru Islands (MSG 56342), received in 1873 by Beccari. In our cluster analysis and PCA this specimen associates closely with the Buru species, it is identical to the Buru species in almost every detail, although it has one primary temporal (most Buru specimens have two). Its presence in the Aru Islands seems improbable but cannot be completely ruled out.

Given the work of How and Kitchener (1997) and De Lang (2011) in the Lesser Sundas, Steubing and Inger (1999) in Borneo, and Hoesel (1959) in Java all of these localities are highly improbable for *Brachyorrhos*, and in the absence of voucher specimens its presence on these islands should not be assumed.

Reports of *Brachyorrhos* in Western Papua are based on members of the genus *Calamophis* Meyer. Therefore, *Brachyorrhos* is endemic to the Moluccas based on current information and our analysis suggests it is polytypic, containing at least four species. Note added in proof. Since this writing specimens have been collected at Kofiau Lake, Kopiau, Raja Ampat Islands, Papua (01°09'09.2"S, 129°51'42.5"E).

Results from a cluster analysis and PCA prompted a closer examination of the six specimens from Papua. They form a group morphologically distinct and geographically disjunct from the other 58 specimens examined. Fig. 3 illustrates the known distribution of *Brachyorrhos* and the related genus *Calamophis*.

Etymology. — *Brachyorrhos* is derived from the Greek words *brachy* = short, and *orrhos* = rump or tail; the gender is masculine.

Brachyorrhos albus (Linnaeus, 1758)

(Fig. 4a)

Coluber albus Linnaeus, 1758: 128

Holotype. — NRM19 (Sweden) not described here

Type Locality. — "Indiis" (Ambon, Indonesia)

Brachyorrhos albus Kuhl in Schlegel, 1826: 236

Calamaria brachyorrhos Müller, 1857: 39

Material Examined. — Ambon: Waai – FMNH 134322–24, 142332, 142145–46; MZB 1524A–B. No specific locality – MSG 30192a;

Seram: Honitoe – FMNH 109949, 119654; BMNH 442222, 6312425; Saunulu – MZB 2364; RMNH 576; ZMA 10494(2); ZMA 10104(2). Pulau Bisa – MZB 2609.

Diagnosis. — A distinct preocular scale present; seven upper labials, fourth (rarely 3+4) in the orbit, sixth is the tallest; dorsal scales more lanceolate (elongated and taper posteriorly) than congeners; usually a single temporal scale contacting the postoculars in the Ambon population; two primary temporals in some Seram individuals. The preocular scale will readily distinguish this species from most other members of the genus. About 35% of *B. raffrayi* have preoculars, but they have the third (rarely 3+4) upper labial in the orbit and the third is the tallest. Some *B. wallacei* also have a preocular, but they have higher ventral (more than 168) and subcaudal counts in both sexes, and a venter that has diffuse dark pigment.

Description. — Rostral visible from above and separates the nasals; nasals are divided or semi-divided with the nostril in the anterior portion of the scale; prefrontal and loreal fused into a large shield; preocular scale single, in 3/26 sides the preocular is fused with loreal-prefrontal forming a large shield that makes contact with the upper labials and the orbit. Large occipital scales make contact with the temporal scale(s). Seven upper labials, 2–3 or 2–4 make contact with the fused loreal-prefrontal shield; the fourth upper labial enters the orbit with the third sometimes making very narrow contact; the sixth upper labial is the tallest. Lower labials seven, rarely eight, the first pair makes contact on the midline of the chin posterior to the mental, first four contact the chin shields. Ambon specimens have a single primary temporal scale; Seram specimens have one or two primary temporals. Table 3 compares the island populations for meristic traits. Dorsal scales smooth, in 19 rows, the number of rows on the neck may be 20 by exception, and there is no posterior reduction in scale row numbers. Ventrals 159–173 in males, 171–178 in females. Subcaudal scales are 23–36, with male specimens having more subcaudal scales, and longer tails than females (N = 5, \bar{x} = 24.6, SD = 1.52) specimens. Two sample t-tests found the ventrals (p = 0.01) and subcaudals (p < 0.01) sexually dimorphic in this species.

Size. — *Brachyorrhos albus* males have SVLs that ranged from 337–472 mm (N = 12, \bar{x} = 393.09, SD = 39.24); tails were 32–61 mm (N = 10, \bar{x} = 55.75, SD = 4.55); females had SVLs of 343–443 mm (N = 5, \bar{x} = 373.6, SD = 36.52); tails were 33–41 mm (N = 5, \bar{x} = 36.00, SD = 3.1).

Biology. — Almost everything known about the biology of species in the genus comes from *Brachyorrhos albus*. *B. albus* hides by day beneath stones and logs and becomes active at dusk, in search of prey (Kopstein, 1926). On Seram it was found in lowland secondary forest, plantations and gardens, but also in human habitations at all altitudes. It is nocturnal, terrestrial and occasionally arboreal (Edgar & Lilley, 1993). One Seram specimen was found behind a village shed (De Lang & Verhaart, 2009). *Brachyorrhos albus* is viviparous, one female (SVL 350 mm) from Seram (FMNH 109949) contained four near term embryos (136–147 mm in total

length). The remains of annelid worms (including setae) were recovered from the digestive systems of several specimens, including FMNH142324 from Ambon (Murphy unpublished; Sanders unpublished).

Distribution. — Ambon and Seram. *B. albus* has been reported from Haruku, Nusa Laut, and Saparua (Kopstein, 1926), all satellites of Seram. We have not seen snakes from these populations but Kopstein's (1926) scale counts fit within our data. *B. albus* has also been reported from the Banda Islands (Boettger, 1892), without reporting scale counts; this locality needs verification. In addition, one specimen from Pulau Bisa (MZB 2609) is very similar to this species.

***Brachyorrhos gastrotaenius* (Bleeker, 1860)**

new combination

(Fig. 4b)

Rabdion gastrotaenia Bleeker, 1860a: 286

Oxyorrhos fusiformis Fischer, 1879: 89

Type locality. — Buru

Syntypes. — SMNS 1327(3) lost in WWII (fide Schluter & Hallermann, 1997)

Brachyorrhos albus Boulenger, 1893: 305

Material examined. — **Holotype.** BMNH 6312425. Note that RMNH 3977 (Leiden) from "O-I Archipel" (= East Indies Archipelago) is described as a "co-type" for this species. It has been skinned and scale count data is therefore not available. **Type Locality.** "Amboina" (= Ambon), in error. Buru – Fakal : ZMA 13.044(3); Rana – ZMA 12.844(3); no specific locality – RMNH 572.

Diagnosis. — Six upper labials, fourth (rarely 3+4) are in the orbit, the fifth is the tallest; a mid-ventral stripe is often present. This combination will separate this species from all other members of the genus.

Redescription of the Holotype. — BMNH 631242 is a juvenile, presumably female, 194 mm in total length (173 mm + 21 mm). Ventrals 180; subcaudals 27; dorsal scales in 19 rows throughout; two postoculars; six upper labials, fourth enters the orbit on the right side, 3+4 in the orbit on the left; upper labials 2-3 contact the PLP shield on the left, 2-3-4 contact the PLP shield on the right; the tallest upper labial is five; seven lower labials, the first four contact the anterior chin shields. There are two primary temporal scales on both sides.

Description. — Rostral is visible from above, separates nasals; nasals are divided or semi-divided with the nostril in the anterior portion of the scale, posterior lobe wedges

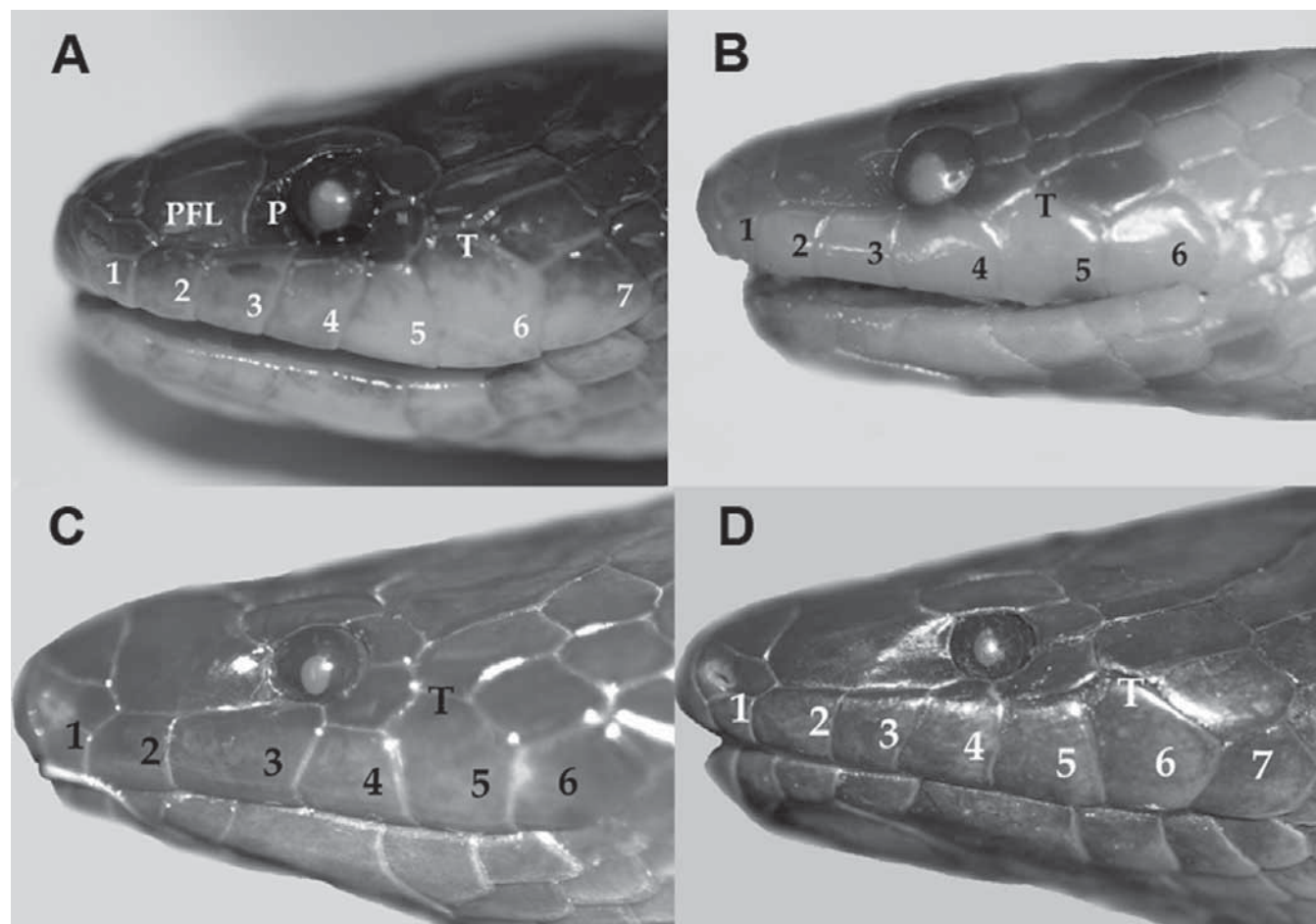


Fig. 4. A comparison of the labial architecture for four species of *Brachyorrhos*: (A) *B. albus* (FMNH 134323) Ambon; (B) *B. gastrotaenius* (BMNH 6312425) Buru holotype; (C) *B. raffrayi* (MNHN 5174) Ternate, holotype; (D) *B. wallacei* (MZB 3463) Halmahera holotype. Labials are numbered, T denotes tallest labial; P = preocular; PFL = prefrontal-loreal shield; PLP = preocular-loreal-prefrontal shield.

between second upper labial and prefrontal; prefrontal, preocular, and loreal fuse into a large shield; two postoculars; internasal divided; primary temporal scales may be one or two; large occipital scales contact the primary temporal(s). Upper labials six, 2-3 make contact with the fused loreal-prefrontal shield, usually the fourth (or 3 + 4) enter orbit (note that in the type specimen the third and fourth are in the orbit on the left, and the fourth enters the orbit on the right), the fifth is the tallest. Lower labials seven, rarely six; the first pair make contact on the midline of the chin posterior to the mental; first four contact the only pair of chin shields. Dorsal scales on the body are smooth and in 19 rows, and there is no posterior reduction in scale row numbers. In alcohol, a uniform brown-grey dorsum; the upper and lower labials are lighter in colour than the crown of the head. A mid ventral stripe is often present. In the type specimen (a juvenile) there is a light coloured occipital band followed by three indistinct bands. Four males have 177–193 ventrals, three males have 34–38 subcaudals, and tails are 12.3–17.6% of the SVL. Females have 187–195 ventrals, 18–29 subcaudals (N = 5, \bar{x} = 24.8, SD = 4.43) tails are 5.7–9.4% of SVL. Two sample t-tests found the ventrals ($p < 0.05$) were not sexually dimorphic but subcaudals ($p > 0.05$) were dimorphic in this species.

Size. — Two adult *Brachyorrhos gastrotaenius* males have SVLs of 342 and 415 mm and 42 and 73 mm tails, with tail/body ratios of 12.3 and 17.6%. Females had SVLs ranging from 338–595 mm (N = 5, \bar{x} = 470.8, SD = 118.3); tails ranged from 30–48 mm (N = 5, \bar{x} = 36.8, SD = 7.04); and tail/body ratios of 5.7–9.4% (N = 5, \bar{x} = 8.04, SD = 1.55).

Notes. — (1) While Bleeker's type specimen of *Rhabdion gastrotaenius* matches the other Buru specimens quite closely, there is one inconsistency, the subcaudal count and the tail/body ratio. The type specimen is a juvenile; it has 27 subcaudals and a tail/body ratio of 12.1. The subcaudal count would suggest it is a female, while the tail/body ratio suggests it is a male when compared with other Buru specimens. Bleeker's type associates with Buru specimens in both our PCA and cluster analysis, thus pending evidence to the contrary we are tentatively assigning Bleeker's name to the Buru population. (2) Kopstein (1926) described four specimens of *Brachyorrhos* from Buru that had 163–174 ventrals; 25–32 subcaudals; six upper labials, the 4th in the orbit; and three lower labials contacting the chin shields. His ventral counts extend ours downward, and we have not seen any specimens with only 3 lower labials contacting the chin shields, our sample has 4 lower labials contacting the chin shields. The specimens examined here, collected by Toxopeus in 1921, came from Fakal (southwest Buru) and from Lake Rana in the center of the island. Both locations are at relatively high elevations, at 1451 m and 773 m respectively. Kopstein's specimens may represent a different population or a different species than the one under discussion. However, the drawings by Fischer (1879) and scale count data for *Oxyorrhos fusiformis* are in close agreement with the specimens examined for this study.

Distribution. — Buru

Etymology. — The epithet *gastrotaenius* is derived from the Greek *gaster*, pertaining to the belly, and the Latin *taenia* referring to a ribbon, in reference to the mid-line stripe on the venter of this snake. We have changed the suffix of Bleeker's *gastrotaenia* so that the gender of the epithet is in agreement with the gender of the genus.

***Brachyorrhos raffrayi* (Sauvage, 1879)
new combination
(Fig. 4c)**

Atractocephalus raffrayi Sauvage, 1879: 62
Brachyorrhos albus var *conjunctus* Fischer, 1880: 879
Brachyorrhos albus Boulenger, 1893: 305

Material Examined. — **Holotype.** MNHN 5174 from Ternate, Indonesia. Ternate: BMNH 82.11.25.14, and 48.1.31.10; MNHN 5782 and 1991.1657; MSNG 30222a–f, 54459–62; MZB 4010, 4009.

Diagnosis. — A *Brachyorrhos* with six upper labials, the third, rarely 3 + 4, enter the orbit, the tallest upper labial is number three; this snake also has a very pointed snout. A preocular is present in about 35% of the specimens examined, making it possible to confuse this species with *B. albus*. However, it has seven upper labials with four or 3 + 4 in the orbit. The Halmahera species has seven upper labial, the fourth enters the orbit, and the tallest is the fifth.

Redescription of the Holotype. — MNHN 5174 is a female with a total length of 530 mm (480 + 50 mm) it has 176 ventrals and 28 subcaudals. Upper labials 6/6, the third is the tallest and enters the orbit, 2+3 contact the PLP shield. There is one primary temporal scale on each side (contrary to Sauvage's report of two primary temporals). The dorsum is a uniform dark brown that lightens laterally, the ventral surface is a light yellow-brown, and there is a mid-line stripe on the ventral surface of the tail.

This specimen was accompanied by a second specimen 5174A (now MNHN 1991.1657), while not designated as a syntype or paratype, it is very similar to MNHN 5174; it is a 380 mm (345 + 35) female with 180 ventrals and 27 subcaudals. It is otherwise the same as the type.

Description. — The snout is exceptionally pointed; the rostral is visible from above and separates the nasals. The nasals are divided or semi-divided with the nostril in the anterior portion of the scale. The prefrontal, preocular, and loreal are usually fused into a large shield. However, six (35%) of our 17 specimens have a preocular scale. The primary temporal scale is single and plate-like. There are large occipital scales that make contact with the primary temporal scale. Upper labials number six; upper labials 2-3 make contact with the fused loreal-prefrontal shield; the third upper labial (rarely 3 + 4), enters the orbit, third upper labial is the tallest. Lower labials seven, rarely six; the first pair of lower labials make contact on the midline of the chin posterior to the mental. The first four contact the only pair of chin shields. Dorsal scales on the body are smooth and in 19 rows, the number

of rows on the neck may be 19 or by exception 20, and there is no posterior reduction in scale row numbers. Ventrals in males 168–177 (N = 10, \bar{x} = 171.80, SD = 3.01); in females 176–182 (N = 7, \bar{x} = 178.71, SD = 2.21). Subcaudal scales in males 33–37 (N = 10, \bar{x} = 34.50, SD = 2.22); in females 27–28 (N = 7, \bar{x} = 27.29, SD = 0.49). Two sample t-tests found the ventrals ($p < 0.01$) and subcaudals ($p < 0.01$) sexually dimorphic in this species.

In alcohol one juvenile specimen has a light cream nape stripe, cream colored upper labials, and some indistinct bands on the anterior body immediately behind the head. Adults are a uniform brown-grey above and have a lighter, brown-grey ventral surface. In life, one specimen is red-brown above.

Size. — Males: SVL 317–395mm (N = 10, \bar{x} = 231, SD = 106.98); tails: males 17–54 mm (N = 10, \bar{x} = 34.90, SD = 14.83); tail/SVL ratios for males were 13.6–17.4% (N = 10, \bar{x} = 15.41, SD = 2.04). Females: SVL 345–575mm (N = 7, \bar{x} = 424.14, SD = 79.88); tails 35–65 mm (N = 7, \bar{x} = 44.71, SD = 10.37); tail/SVL ratios for females were 8.9–11.3% (N = 7, \bar{x} = 10.37, SD = 1.20).

Distribution. — Ternate, Indonesia

Etymology. — Named after French diplomat and zoologist Achille Raffray who donated the specimen to the Paris museum.

Brachyorrhos wallacei new species

(Fig. 4d)

Brachyorrhos albus Boulenger, 1893: 305

Brachyorrhos albus Setiadi & Hamidy, 2006 (two un-numbered photographs, no pagination)

Material Examined. — **Holotype.** MZB 3463 an adult female with a total length of 722 mm from Jailolo, Halmahera. This new species is based on 10 adults from the island of Halmahera (Jailolo – MZB 3464, MZB 3462; Jailolo, Kampung PasirPatih – USNM 237145–150; Sidangoli – MZB 2111; Weda Bay Mines – MZB 4487.)

Diagnosis. — A *Brachyorrhos* with no preocular, usually seven (rarely six) upper labials, the tallest of which is six (rarely five); ventrals 177–182, subcaudals 38–42. This snake is very similar to *B. raffrayi* which has upper labial three in the orbit and the third is the tallest. Specimens of *wallacei* usually have the fourth upper labial (rarely 3 + 4) in the orbit, and the sixth is the tallest. Our mitochondrial data show that *B. raffrayi* and *B. wallacei* are separated by a deep molecular divergence at this locus.

Description of Holotype. — An adult female 660 mm SVL, 82 mm tail. Rostral visible from above, internasals paired, prefrontal fused with loreal and preocular; nasal scales bilobed with posterior lobe dorsal to the first labial; frontal longer than seam of parietals; parietals extend laterally to make contact with upper postocular; two postoculars; one primary temporal scale contacts the lower postocular, a secondary temporal on each side contacts upper labial six;

seven upper labials, 2–4 make contact with prefrontal, the fourth enters the orbit, the fifth is the tallest; seven lower labials, the first four make contact with the chin shields; dorsal scales rows are 19 at mid-body; ventrals 180; subcaudals 42. Dorsum grey, anterior body has scale rows one and two with red-brown pigment, replaced by grey posteriorly, ventral surface a uniform red brown.

Paratypes. — The nasals are divided or semi-divided with the nostril in the anterior portion of the scale. Primary temporal scale(s) can be one or two and plate-like. Upper labials number six (or seven), 2-3 (or 2-4) make contact with the fused loreal-prefrontal shield; when the third upper labial enters the orbit the fifth upper labial is the tallest; when the fourth upper labial enters the orbit the sixth is the tallest. One specimen (MZB 3464) has the postoculars fused on the left side. Lower labials seven, the first pair of lower labials make contact on the midline of the chin posterior to the mental. The first four contact the only pair of chin shields. Dorsal scales on the body are smooth and in 19 rows, the number of rows at the 10th ventral may be 19 or 20. Males have 169–182 (N = 7, \bar{x} = 177.14, SD = 4.25) ventrals and 33–42 (N = 7, \bar{x} = 38.5, SD = 3.35) subcaudals. Females have 170–174 (N = 3, \bar{x} = 171.3, SD = 1.88) ventrals and 26–31 (N = 3, \bar{x} = 28.6, SD = 2.04) subcaudals.

In alcohol, grey-black above with some yellow under the chin; Setiadi and Hamidy (2006) contains two photographs of a live specimen of this species, showing a uniform dark brown-purple snake with a white venter. The specimen in their photo has 7 upper labials, with 3rd upper labial in the orbit.

Size. — Males have SVLs of 453–660mm (N = 7, \bar{x} = 561.8, SD = 67.7); tails that are 56–82 mm (n = 7, \bar{x} = 71, SD = 10.03), and t/svl ratios 12.0–13.4 (N = 7, \bar{x} = 12.67, SD = 0.47). Females have SVLs of 394–462 mm (N = 3, \bar{x} = 417.0, SD = 31.8) and tails that are 29–51 mm (\bar{x} = 38.0, SD = 9.41); tail/SVL ratios 7–11% (N = 7, \bar{x} = 9%, SD = 0.015).

Etymology. — Named in honour of Alfred Russell Wallace for his contributions to the natural history of Halmahera.

Unresolved Brachyorrhos. — (1) The Aru Islands specimen clearly belongs with this genus despite the speculation that it is *jobiensis* (Iskandar & Colijn, 2001). It clusters with the Buru island *gastrotaenius* in our PCA and cluster analysis. Its locality data may be in error. (2) The island of Buru appears to have a second species with distinct labial architecture and a long tail. However, this specimen is poorly preserved and more sampling is needed to inform its status. (3) Seram also supports a second species of *Brachyorrhos* that is exceptionally small (smaller than late term embryos of *B. albus*) and sexually mature with a distinct loreal scale, preocular, and low ventral count. These specimens will be discussed elsewhere pending further investigation. (4) Morotai also supports a population of *Brachyorrhos* (USNM 159973) that is superficially similar to *B. raffrayi*, with a slightly different labial architecture, and it may require molecular analysis to confirm its relationships. (5)

Table 4. A comparison of the species in the genus *Brachyorrhos*. n = number.

	<i>B. albus</i> (n = 20)	<i>B. gastrotaenius</i> (n = 9)	<i>B. raffrayi</i> (n = 17)	<i>B. wallacei</i> (n = 10)
Distribution	Ambon, Seram, Bisa	Buru	Ternate	Halmahera
Preocular	present (by exception absent)	absent	absent (65%), present (35%)	both
Number of upper labials	7	6	6	7 (rarely 6)
Upper labial number in orbit	4 (rarely 3 + 4)	4 (rarely 3 + 4)	3 (rarely 3 + 4)	4 (or 3 + 4)
Tallest upper labial	6	5	3	6 (rarely 5)
Ventrals males	159–173	177–193	168–177	169–182
Ventrals females	171–178	187–195	176–182	170–174
Subcaudals males	26–36	34–38	30–37	33–42
Subcaudals females	23–27	18–29	27–28	26–31
Snout	pointed	pointed	very pointed	pointed
Mid-ventral stripe	absent	usually present	absent	absent

Brachyorrhos has also been reported from: Banda, Batjan, Haruku, Nusaulaut, and Saparua; all of these islands seem likely to support *Brachyorrhos* populations, but we have not located specimens to confirm their presence or identities.

Calamophis Meyer, 1874

Calamophis jobiensis Meyer, 1874: 135

Brachyorrhos jobiensis Peters & Doria, 1878: 371

Brachyorrhos albus Boulenger, 1893: 305

Material examined. — Indonesia – West Papua: Andai, MSNG 56343-1-2; Ambuaki, MNHN 5175; Kebar Valley, BPBM 3850; Mount Arfak, West Papua, MSNG 30193-1-2.

Type species. — *Calamophis jobiensis* Meyer by monotypy

Diagnosis. — Rostral broader than tall, nasal scale undivided and quadrangular; nares tiny, crescent-shaped and valvular; internasal single; postocular single; dorsal scales in 19 rows that are reduced to 17 anterior to the vent; dorsal scales are lanceolate, and imbricate; base of tail constricted; tail is thick and tapers slowly to an almost blunt tip; males of at least some species have tubercles on scales in first four rows just anterior and posterior to vent. This genus is polytypic and the lost holotype presents some nomenclatural challenges. This will be discussed in a later paper.

Distribution. — West Papua: Ambuaki, Andai, Kebar Valley, Mount Arfak, and Yapen Island. Iskandar and Colijn (2001) also list Biak Island, but we have not located specimens from this locality. The Papua New Guinea locality for *B. jobiensis* in Iskandar and Colijn (2001) is incorrect, since it is based on *Mainophis robusta*, which is a synonym of the elapid *Furina tristis* (Shea & Sadlier, 1999).

Content. — One described species and several undescribed species (Murphy, 2012)

Etymology. — Probably derived from the Latin *calamus* meaning reed, and the Greek *ophis* meaning snake.

Identification Key for the Species of *Brachyorrhos* and *Calamophis*

- 1a. A single internasal scale; one postocular scale; dorsal scale rows reduced to 17 anterior to vent (West Papua, Yapen Island), a broad ventral stripe composed of large dark spots on each ventral scale; a thick tail that tapers little *Calamophis jobiensis*
- 1b. Internasal scale divided; two postoculars; dorsal scales rows not reduced, they number 19 anterior to vent; rostral as tall as wide; ventral stripe usually absent, if present it is relatively narrow. 2
- 2a. Preocular present; tallest upper labial 6; males 159–173 v, females 171–178 v; mostly uniform brown above, cream or yellowish below (Seram, Ambon, Pulau Bisa). *B. albus*
- 2b. No preocular; tallest upper labial 3 or 5. 3
- 3a. Upper labials 3 + 4 in orbit; tallest upper labial 5; mid ventral stripe present, usually less than 75% of the width of ventrals (fades in preserved material); a light coloured band crosses the back of the head in neonates and juveniles; (Buru) males 177–193 ventrals, females 187–195 ventrals. *B. gastrotaenius*
- 3b. Six or 7 upper labials, of which 3 or 6 (rarely 5) tallest. 4
- 4a. Tallest upper labial is three and it enters the orbit; uniform brown grey above, light cream below 168–177 ventrals in males; 176–182 ventrals in females; (Ternate) 4th (or 3 + 4) *B. raffrayi*
- 4b. Tallest upper labial is 6 (rarely 5); 4 upper labials enter the orbit (rarely 3); uniform dark grey, almost black above, light coloured venter; 177–182 ventrals in females (Halmahera) ... *B. wallacei*

Table 4 compares the four species of *Brachyorrhos* for external morphological characteristics.

DISCUSSION

Brachyorrhos and *Calamophis* are poorly studied snakes that represent a highly distinctive and ecologically divergent lineage within the Homalopsidae. Our morphological analyses highlight the close affinity of these genera and reveal higher

levels of species diversity in *Brachyorrhos* than currently recognised. We redescribe *B. albus* from Seram and Ambon and resurrect two species within *Brachyorrhos*: *B. raffrayi* from Ternate and *B. gastrotaenia* from Buru, and describe one new species from Halmahera, *B. wallacei*. These species are readily diagnosed by (mostly non-overlapping) scale characters, and our mitochondrial data for *B. raffrayi* and *B. wallacei* show a deep divergence consistent with species-level delineations in snakes.

Other Moluccan snakes that show differentiation within a genus between northern (Halmahera) and southern (Seram and Buru) islands include pythons of the *Morelia amethystina* complex (Harvey et al., 2000); *Tropidonotus elongatus* (south) and *T. halmahericus*, *T. punctiventris*, and *T. truncatus* (north) (Malnate & Underwood, 1988); and *Typhlops bipartitus* (north) and *T. kraalii* (south) (How & Kitchner, 1997).

The Moluccan islands (Maluku) are located in the biogeographical region known as Wallacea, usually considered a transition zone between the Australian and Asian faunas. North Maluku (Halmahera and its associates) are composed of oceanic and island arc volcanics while South Maluku (Buru and Seram) is composed of Australasian continental basement and geology associated with the Bird's Head microcontinent. Therefore the continental basement found on Buru and Seram are extensions from western New Guinea (Michaux, 2010).

Wallace (1876) recognised the Australasian influence on the Moluccan fauna as well as the high level of endemism. Rosmayati-Natus (2005) reported 41 reptiles in the North Moluccas, 19 of which were shared with Sulawesi, 15 (36%) shared with New Guinea, and 9 (22%) endemics; and she reported 35 species of reptiles in the Seram Group (Seram and its satellites), with 6 (17%) endemics; and only 6 species of terrestrial reptiles on Buru, with only one (16%) endemic. Our results and those of more recent research (Ziegler et al., 2007; Weijola, 2010) suggest that the number of recognised endemics is likely to increase substantially as the fauna undergoes more detailed analyses.

Brachyorrhos and *Calamophis* may have evolved on the Vogelkop microcontinent complex, which formed more than 50 MYA from the Australia craton (Hall, 1996). The Vogelkop complex included what is now, Seram and Buru (the southern Moluccas), and the Bird's Head region of western New Guinea with *Brachyorrhos* dispersing or being carried to Halmahera (the north Moluccas) when the terrains were in close proximity (10–5 MYA). However, a Halmahera or New Guinea origin cannot be ruled out.

While *B. raffrayi* and *B. wallacei* do not show a great deal of morphological differentiation, the 7.2% pairwise difference reported here suggests the two species have been separated for a significant amount of time, despite the fact that there is only 14 km of water, albeit deep water, separating the populations. The terrestrial-fossorial habits of *Brachyorrhos* suggest that they have limited over-water dispersal abilities;

given their wide distribution throughout the Moluccan islands, it is highly likely that these populations comprise many more species than are recognised in the present study. Future studies should investigate the extent to which island populations represent endemic species and aim to reconstruct their history of dispersal and vicariance in this geologically complex region. Taxonomic studies are especially urgent in light of the increasing pressure on Moluccan ecosystems from anthropogenic development.

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