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A new species of the genus *Pulchrana* Dubois, 1992 (Amphibia: Ranidae) from Sumatra, Indonesia

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Abstract. We describe a new species of *Pulchrana* from the island of Sumatra, in western Indonesia. *Pulchrana fantastica*, new species, is currently only known from Aceh and Sumatera Utara provinces. It is related to *P. siberu* and *P. centropeninsularis* as inferred from morphological similarity and phylogenetic relationships, estimated from DNA sequences. It can be diagnosed by the following unique combination of characters: (1) SVL adult males 40.32–45.19 mm; (2) males have large humeral glands on the anteroventral surface of brachium, nuptial pads absent; (3) dorsal skin finely granular to granulated, with or without asperities at the tip of granules; (4) webbing formula: I(1 — 1–11/2)II(1/2 — 2)III(1 — 2–21/3)IV(2–21/3 — 1)V; (5) straight dorsolateral stripes, thin, continuous, anteriorly confluent at snout, posteriorly interconnected by a series of spots; (6) middorsum in adults black with light medial line or combination of spots and line, black without marking in juveniles; (7) dense cream or yellow to orange spots on flanks, and dorsal side of limbs, spots non-uniform in shape; (8) venter greyish or brown, with small light dots on throat and chest, sometimes reaching abdomen; (9) iris background black, lower part with dense orange stippling, upper region with orange reticulation with gold in the middle, pupil encircled with solid orange-golden line; (10) upper and lower lip grey or brown with cream or yellow spots. We also report the presence of *P. centropeninsularis* from Sumatra; a species previously known only from a single locality in the Malay Peninsula; and discuss the biogeographic implications of this significant range extension.

Key words. molecular systematics, morphology, new species, *Pulchrana signata* Complex, Sumatra, taxonomy

INTRODUCTION

Despite being renowned for its high herpetofaunal diversity, the island of Sumatra remains severely understudied (e.g., Iskandar & Colijn, 2000; Stuart et al., 2006; Inger et al., 2009). Many new species of anuran amphibians have been described from Sumatra in the last decade, such as *Duttaphrynus totol* (Teynie et al., 2010), *Sigalegalephrynus mandailinguensis*, *S. minangkabauensis* (Smart et al., 2017), *Limnonectes sisikdagu* (McLeod et al., 2011), *Pulchrana rawa* (Matsui et al., 2012), *Sumaterana dabulescens*, *S. montana* (Arifin et al., 2018), *Chiromantis nauli*, *C. baladika* (Riyanto & Kurniati, 2014), *Rhacophorus indonesiensis* (Hamidy & Kurniati, 2015), *Philautus amabilis*, *P. polymorphus*, *P. thamyridion*, and *P. ventrimaculatus* (Wostl et al., 2017). Nevertheless, a substantial portion of Sumatra's anuran diversity likely remains hidden within common, morphologically cryptic, and widespread species (Stuart et al., 2006; Inger et al., 2009).

The *Pulchrana signata* group is one such complex of relatively abundant ranid frogs, distributed across Sundaland and the Philippines with at least nine nominal species (Brown & Guttman, 2002; Brown & Siler, 2013; Chan et al., 2014; Oliver et al., 2015). In total, the genus *Pulchrana* currently includes 16 species that were formerly subsumed under the genus *Hylarana* (Frost, 2018). The most recently described species are *P. centropeninsularis* from the Malay Peninsula (Chan et al., 2014) and *P. guttmani* from Mindanao Island of the southern Philippines (Brown, 2015). The first of these taxa initially had been assigned to the name *P. siberu* (Leong & Lim, 2004), based on phenotypic similarity to an endemic taxon from the Mentawai Islands (Dring et al., 1990). The addition of genetic data (Brown & Siler, 2013) revealed this to be a distinct species based on phylogenetic relationships. In a subsequent analysis, Chan et al. (2014) reported the presence of another hitherto undescribed lineage from the Batak Mountains of Sumatera Utara Province, which was closely related to, yet also markedly distinct from both *P. siberu* and *P. centropeninsularis*.

During fieldwork on the island of Sumatra between the years 2013–2014, several individuals belonging to the genus *Pulchrana* of uncertain taxonomic affinities, were collected from Aceh and Jambi provinces. Upon further investigations, based on molecular and morphological approaches, these specimens were identified as two taxa: *P. centropeninsularis* and the hitherto unnamed species mentioned in Chan et al. (2014). In this paper we provide a formal species description for the latter, and we justify the recognition of the new species

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Table 1. List of morphometric characters, acronyms, character definitions (and their citations) used in this study.

Primary Name	**Primary Acronym**	**Definition**	**Citation**
Anterior Eye to Eye Distance	EED	The distance from anterior of left eye to the anterior of right eye	Chan et al., 2014
Brachium Length	BL	The distance from axilla to flexed elbow	Chan et al., 2014
Disc Width of Finger I, Finger II, Finger III, Finger IV	Fin1DW, Fin2DW, Fin3DW, Fin4DW	The widest horizontal diameter of disc of Finger I, Finger II, Finger III, Finger IV	Watters et al., 2016
Disc Width of Toe I, Toe II, Toe III, Toe IV, Toe V	Toe1DW, Toe2DW, Toe3DW, Toe4DW, Toe5DW	The widest horizontal diameter of disc of Toe I, Toe II, Toe III, Toe IV, Toe V	Modified from Watters et al., 2016
Dorsolateral Stripe Width	DLSW	Maximum width of dorsolateral stripe, recorded above tympanum	Brown & Guttman, 2002
Eye Diameter	ED	The distance between anterior and posterior corner of upper and lower eyelids	Chan et al., 2014
Eye-Nostril Distance	END	The distance from anterior of eye to the posterior of nostril	Chan et al., 2014
Femur Length	FL	The distance from vent to outer margin of flexed knee	Chan et al., 2014
Finger I Length	Fin1L	The distance from proximal margin of the inner metacarpal to the tip of the Finger I	Duellman & Trueb, 2015
Finger II, Finger III, Finger IV Length	Fin2L, Fin3L, Fin4L	The distance from proximal margin of the palmar tubercle to the tip of the Finger II, Finger III, Finger IV	Watters et al., 2016
Forearm Length	FAL	The distance from flexed elbow to base of inner metacarpal tubercle	Chan et al., 2014
Head Length	HL	The distance from posterior margin of lower jaw to tip of snout	Chan et al., 2014
Head Width	HW	The distance taken immediately from posterior to eyes	Chan et al., 2014
Humeral Gland Length	HG	The horizontal length of humeral gland	Chan et al., 2014
Internarial Distance	IND	The shortest distance between the inner margins of the nostrils	Chan et al., 2014
Interorbital Distance	IOD	The distance across top of head between medial margins of orbits at their closest points	Chan et al., 2014
Inner Metatarsal Tubercle Length	IMTL	Greatest length of inner metatarsal tubercle	Modified from Watters et al., 2016
Inner Metatarsal Tubercle Width	IMTW	Greatest width of inner metatarsal tubercle	Modified from Watters et al., 2016
Inner Metacarpal Tubercle Length	IMCL	Greatest length of inner metacarpal tubercle	Modified from Watters et al., 2016
Inner Metacarpal Tubercle Width	IMCW	Greatest width of inner metacarpal tubercle	Modified from Watters et al., 2016
Length of Toe I, Toe II, Toe III	Toe1L, Toe2L, Toe3L	The distance from the base of inner metatarsal to the tip of the Toe I, Toe II, Toe III	Watters et al., 2016
Length of Toe IV, Toe V	Toe4L, Toe5L	The distance from the base of outer metatarsal to the tip of the Toe IV, Toe V	Watters et al., 2016
Nostril-Snout Distance	NSD	The distance from anterior of nostril to the tip of the snout	Chan et al., 2014

Primary Name	Primary Acronym	Definition	Citation
Outer Metatarsal Tubercle Length	OMTL	Greatest length of outer metatarsal tubercle	Modified from Watters et al., 2016
Outer Metatarsal Tubercle Width	OMTW	Greatest width of outer metatarsal tubercle	Modified from Watters et al., 2016
Outer Metacarpal Tubercle Length	OMCL	Greatest length of outer metacarpal tubercle	Modified from Watters et al., 2016
Outer Metacarpal Tubercle Width	OMCW	Greatest width of outer metacarpal tubercle	Modified from Watters et al., 2016
Palmar Tubercle Length	PTL	Greatest length of palmar tubercle	Modified from Watters et al., 2016
Palmar Tubercle Width	PTW	Greatest width of palmar tubercle	Modified from Watters et al., 2016
Snout Length	SL	The distance from anterior corner of the eye to tip of snout	Chan et al., 2014
Snout-Vent Length	SVL	The distance from the tip of snout to vent	Chan et al., 2014
Tarsal Length	TL	The distance from outer margin of flexed tarsus to base of inner metatarsal tubercle	Chan et al., 2014
Tympanum Diameter	TD	The horizontal width of tympanum as its widest points	Chan et al., 2014
Tympanum-Eye Distance	TED	The distance from anterior tympanum to posterior eye	Chan et al., 2014
Tibia Length	TBL	The distance from outer margin of flexed knee to outer margin of flexed tarsus	Chan et al., 2014
Width of Terminal Phalange Finger I, Finger II, Finger III, Finger IV	Fin1TPW, Fin2TPW, Fin3TPW, Fin4TPW	Measure at midpoint of terminal phalange of the Finger I, Finger II, Finger III, Finger IV	Modified from Watters et al., 2016
Width of Terminal Phalange Toe I, Toe II, Toe III, Toe IV, Toe V	Toe1TPW, Toe2TPW, Toe3TPW, Toe4TPW, Toe5TPW	Measure at midpoint of terminal phalange of the Toe I, Toe II, Toe III, Toe IV, Toe V	Modified from Watters et al., 2016

based on genetic and morphological evidence. Furthermore, our collected material of *P. centropeninsularis* is the first Sumatran record for this species and significantly extends its known range (formerly known only from the Malay Peninsula).

MATERIALS AND METHODS

Morphology. We examined a total of 21 frogs from three provinces in Sumatra (Aceh: n males = 10, n juveniles = 6; Sumatera Utara: n males = 2; and Jambi: n males =3). No female was collected during the trip. The specimens were fixed in 4% neutral-buffered formalin and later stored in 70% ethanol. All material examined in this study are deposited at the Museum Zoologicum Bogoriense (MZB), Indonesia. In the future, some of the paratypes and reference specimens shall be deposited at the Zoologisches Museum Hamburg (ZMH), Germany. Morphometric measurements were only taken from adult specimens (n = 15) in order to avoid bias due to ontogenetic variation. Sexual maturity was determined in males by the presence of humeral glands and vocal sacs. We followed Duellman & Trueb (1986), Brown & Guttman (2002), and Kok & Kalamandeen (2008) for qualitative morphology assessment (e.g., head shape, skin texture, and colouration). For the webbing formula of toes we adopted the approach from Savage & Heyer (1997) with the refinements suggested by Guayasamin et al. (2006). We applied the same characters and terminology used by Chan et al. (2014) to make measurements comparable. Additional measurements follow Duellman & Trueb (2015) and Watters et al. (2016), for more detailed morphological descriptions. All measurements, acronyms, definitions, and citation are presented in Table 1, and were taken with digital calipers (0.02 mm precision reading). We applied standard descriptive statistics (mean, standard deviation, range, in mm) to summarise morphological data.

Phylogenetic analyses of molecular data. Tissue samples of two specimens from Aceh (MZB.Amph.28891 and MZB.Amph.28946) and two specimens from Jambi (MZB.Amph.28765–66) were selected for molecular work. Additionally, we included five samples from the collection of the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, USA from the Mentawai

Islands (Siberut, Sipora, and Pagai Selatan: MVZ272082, MVZ272086, MVZ272089–91). DNA was extracted from liver samples (preserved in either 96% ethanol or RNAlater) using DNA Analytic Jena® Kit (Germany). We made 20 µL PCR reactions as follows: 10 µL Green Taq Promega, 8 µL H_2O, 0.5 µL forward primer, 0.5 µL reverse primer, and 1 µL DNA. The primers used for this study were 12S (12SZ-L: 5′-AAAGGTTTGGTCCTAGCCTT-3′ and 12SK-H: 5′ -TCCRGTAYRCTTACCDTGTTACGA-3′; Goebel et al., 1999) and 16S, which included $tRNA^{val}$ (12sm: 5′ -GGCAAGTCGTAACATGGTAAG-3′ and 16sd: 5′-CTCCGGTCTGAACTCAGATCACGTAG-3′; Pauly et al., 2004; Oliver et al., 2015). Annealing temperature for 12S and 16S was 52°C and 51°C, respectively. PCR products were purified with ExoSAP-IT®. Sequencing was performed by Macrogen (Netherland). Sequences were edited and assembled in Geneious v 8.0 (Kearse et al., 2012) prior to alignment.

We combined our 12S and 16S (including $tRNA^{val}$) sequence data (n = 9) with the *Pulchrana* dataset downloaded from GenBank (n = 24), 22 of which came originally from Brown & Siler (2013) and were later incorporated by Chan et al. (2014), along with two from Matsui et al. (2012). These downloaded sequences also comprise a species group of related marsh frogs (i.e., *P. banjarana*, *P. glandulosa*, and *P. baramica*) that we used as outgroup. Sequence information and GenBank accession numbers are provided in Table 2. We aligned sequences for each locus using MAFFT v7.7 (Katoh & Standley, 2013), as implemented in Geneious v 8.0 and concatenated the aligned sequences for a final alignment of 2,285 base pairs. Partition Finder V1.1.1 (Lanfear et al., 2012) was used to determine the best partitioning schemes and model of substitutions of the concatenated sequences under the Bayesian Information Criterion (BIC) using the "greedy" search algorithm. GTR+I+G was selected as the best model, however, phylogenetic estimation using maximum likelihood (ML) was performed with a GTR+G model because the 25 discrete categories are better at approximating invariant sites (Stamatakis, 2014). The aforementioned analysis was executed using RAxML v.8 (Stamatakis, 2006, 2014) at the CIPRES Science Gateway server (Cyberinfrastructure for Phylogenetic Research; www.phylo.org/sub.sections/portal; Miller et al., 2010). We used MrBayes v3.2.6 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) with the same server to perform Bayesian inference (BI) analysis using default priors. The MCMC sampling was performed for 50 million generations using two independent runs, each with four chains, and sampling every 1,000 generations with a 25% burn-in. Successful convergence of runs was assessed using trace plot and ESS values (>200) in Tracer v.1.6 (Rambaut & Drummond, 2009). The output from RAxML and MrBayes analyses was visualised in FigTree v1.4.3 (Rambaut, 2007). Corresponding figures were prepared using CorelDRAW X6. Bootstrap (BS) node values ≥ 70 (Hillis & Bull, 1993) and a posterior probability (PP) of ≥ 0.95 (Alfaro et al., 2003; Huelsenbeck & Rannala, 2004; Mulcahy et al., 2011) were considered high support.

RESULTS

Phylogenetic analyses. Our final concatenated (12S + 16S + $tRNA^{val}$) sequence matrix consisted of 2,285 bp and included 5.32% gaps and undetermined character states. The topology of the optimal ML tree (lnL = -12646.925261) was identical to that inferred in our BI analysis (Fig. 1). These topologies match the topology recovered by Brown & Siler (2013) and Chan et al. (2014), except for the arrangement of *Pulchrana signata*. Chan et al. (2014) suggested *P. signata* as sister taxon to a four taxon clade comprising ([*P. mangyanum* + *P. moellendorffi*] + [*P. grandocula* + *P. similis*]). In our trees, *P. signata* was instead recovered as a sister taxon to *P. mangyanum* + *P. moellendorffi*. The clade comprising these species was sister to *P. grandocula* + *P. similis*. Nodal support was generally high for both BS and PP, with exceptions including the node joining *P. signata* to *P. moellendorffi* + *P. mangyanum* (BS = 69; PP = 0.96), the sister taxon relationship between *P. grandocula* and *P. similis* (BS = 74; PP = 0.89), the node joining the two *P. similis* (BS = 59; PP = 0.62), and the node joining the two *P. siberu* from Pagai Selatan and Sipora (BS = 57; PP = 0.63).

The two individuals from Jambi formed a strongly supported clade (BS = 100; PP = 1) together with the *Pulchrana centropeninsularis* sample from Brown & Siler (2013), with negligible genetic divergence (uncorrected *p*-distance = 0.003; Table 3). There was strong support (BS = 98; PP =1; Fig. 1) for the two individuals from Aceh being nested within the samples from Sumatera Utara, previously reported as being "*Hylarana* cf. *siberu* [Sumatra]" and "sp Sumatra" by Brown & Siler and (2013) and Chan et al. (2014) , respectively. All *P. siberu* samples formed a strongly supported clade (BS = 100; PP = 1) with minimal genetic divergence (Table 3) among the three sampled islands (Siberut, Sipora and Pagai Selatan).

Comparison between individuals of *Pulchrana centropeninsularis* from the Malay Peninsula and Sumatra. The observed morphological character states in three adult males from Hutan Harapan, Jambi Province, MZB.Amph.28765 (S 02.18010°, E 103.50215°); MZB.Amph.28766–67 (S 02.18431°, E 103.36633°) corroborate our genetic results; the specimens can be assigned to *P. centropeninsularis* following the characteristics described in Chan et al. (2014). A comparison of morphometric characters between *P. centropeninsularis* from the Malay Peninsula and Jambi is shown in Table 4 (individual measurements) and Table 5 (means and standard deviations). We noticed minor differences between specimens from the Malay Peninsula (Chan et al., 2014) and Jambi (Sumatra) specimens, and provide the following enumeration of these observations (with opposing character states for Sumatra specimens in parentheses): dorsal skin texture smooth to finely granulated (finely granulated to granular; Fig. 2); tear drop-shaped choana (circular); NSD/END = 70.0% (NSD/END = 44.4–55.7%); HG/BL = 52.5–57.5% (HG/BL = 31.6–45.9%); webbing formula for holotype (ZRC1.10536) and paratype (DWNP 1189) (Chan et al., 2014): I(1/2 — 2) II(1 — 21/2)III(1 — 3)IV(3 — 1)V [webbing formula for

Table 2. List of specimens included in our molecular phylogenetic analyses, corresponding museum catalog numbers, collection localities, GenBank accession numbers, and original citations.

Species	Voucher*	Locality	GenBank no.	Citation
Pulchrana baramica	FMNH 248218	Brunei, Borneo Island, Belait District	KF477628	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana baramica	KUHE 53640	Malaysia, Borneo Island, Sarawak, Mulu	AB719217, AB719234	Matsui et al., 2012
Pulchrana banjarana	LSUHC 5128	Malaysia, Malay Peninsula, Pahang, Cameron Highlands	KF477644	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana banjarana	ZRC 8326	Malaysia, Malay Peninsula, Pahang, Cameron Highlands	KF477645	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana centropeninsularis	DWNP 0489	Malaysia, Malay Peninsula, Pahang, Kuala Gandah	KF477745	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana centropeninsularis	MZB. Amph.28765	Indonesia, Sumatra Island, Jambi Province, Harapan Rain Forest	MG783353, MG783362	This study
Pulchrana centropeninsularis	MZB. Amph.28766	Indonesia, Sumatra Island, Jambi Province, Harapan Rain Forest	MG783352, MG783361	This study
Pulchrana fantastica, new species	MZB. Amph.28946	Indonesia, Sumatra Island, Aceh Province, Gunung Leuseur National Park	MG783359, MG783367	This study
Pulchrana fantastica, new species	MZB. Amph.28891	Indonesia, Sumatra Island, Aceh Province, Taman Buru Linge Isaq	MG783360, MG783368	This study
Pulchrana fantastica, new species	MK 334	Indonesia, Sumatra Island, Sumatera Utara Province, Langkat, Bandar Baru, Batak Mountains	KF477646	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana fantastica, new species	MZB. Amph.13011 (MK 335)	Indonesia, Sumatra Island, Sumatera Utara Province, Langkat, Bandar Baru, Batak Mountains	KF477648	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana glandulosa	KUHE 53618	Malaysia, Borneo Island, Sarawak, Mulu	AB719206, AB719223	Matsui et al., 2012
Pulchrana grandocula	KU 306492	Philippines, Samar Island, Samar Province, Municipality of San Jose de Baun, Barangay Poblacion	KF477660	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana grandocula	PNM 8848	Philippines, Mindanao Island, Davao City Province, Municipality of Calinan, Barangay Malagos	KF477676	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana mangyanum	KU 303566	Philippines, Mindoro Island, Municipality of Paypayama, Barangay Carmundo	KF477687	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana mangyanum	KU 303578	Philippines, Mindoro Island, Municipality of Bongabong, Barangay Formon	KF477686	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana moellendorffi	KU 309009	Philippines, Palawan Island, Palawan Province, Municipality of Puerto Princesa City, Barangay Irawan	KF477696	Brown & Siler, 2013 and Chan et al., 2014

Species	Voucher*	Locality	GenBank no.	Citation
Pulchrana moellendorffi	KU 327050	Philippines, Palawan Island, Palawan Province, Municipality of Nara, Barangay Estrella Falls	KF477695	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana picturata	FMNH 235707	Malaysia, Borneo Island, Sabah, Kota Marudu	KF477729	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana picturata	FMNH 238866	Malaysia, Borneo Island, Sabah, Tenom District	KF477731	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana picturata	FMNH 266930	Indonesia, Sumatra Island, Sumatera Barat Province, Limau Manis	KF477717	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana picturata	FMNH 266944	Indonesia, Sumatra Island, Sumatera Barat Province, Payakumbuh	KF477701	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana siberu	BJE 203	Indonesia, Siberut Island, Sumatera Barat Province	KF477741	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana siberu	BJE 236	Indonesia, Siberut Island, Sumatera Barat Province	KF477743	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana siberu	MVZ 272090	Indonesia, Siberut Island, Sumatera Barat Province	MG783357, MG783365	This study
Pulchrana siberu	MVZ 272091	Indonesia, Siberut Island, Sumatera Barat Province	MG783358, MG783366	This study
Pulchrana siberu	MVZ 272082	Indonesia, Pagai Selatan Island, Sumatera Barat Province	MG783354, NA	This study
Pulchrana siberu	MVZ 272086	Indonesia, Pagai Selatan Island, Sumatera Barat Province	MG783355, MG783363	This study
Pulchrana siberu	MVZ 272089	Indonesia, Sipora Island, Sumatera Barat Province	MG783356, MG783364	This study
Pulchrana signata	FMNH 238842	Malaysia, Borneo Island, Sabah, Sipitang District, Mendolong	KF477746	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana signata	ZRC 1.12388	Malaysia, Borneo Island, Sarawak, Matang	KF477748	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana similis	TNHC 63007	Philippines, Luzon Island, Camarines Norte Province, Municipality of Naga City, Barangay Panicuason	KF477764	Brown & Siler, 2013 and Chan et al., 2014
Pulchrana similis	PNM 5536	Philippines, Luzon Island, Laguna Province, Municipality of Los Banos, University of the Philippines campus, Mt. Makiling	KF477776	Brown & Siler, 2013 and Chan et al., 2014

*FMNH = Field Museum of Natural History; LSUHC = La Sierra University Herpetological Collection; ZRC = Zoological Reference Collection, Lee Kong Chian Natural History Museum, Singapore; MK = Mistar Kamsi field number; DWNP = Department of Wildlife and National Parks, Malaysia; BJE = Ben J. Evans field number; KU = University of Kansas; PNM = Philippines National Museum; TNHC = Texas National History Museum, University of Texas, Austin; MVZ = Museum of Vertebrate Zoology, University of California, Berkeley; MZB = Museum Zoologicum Bogoriense, Indonesia.

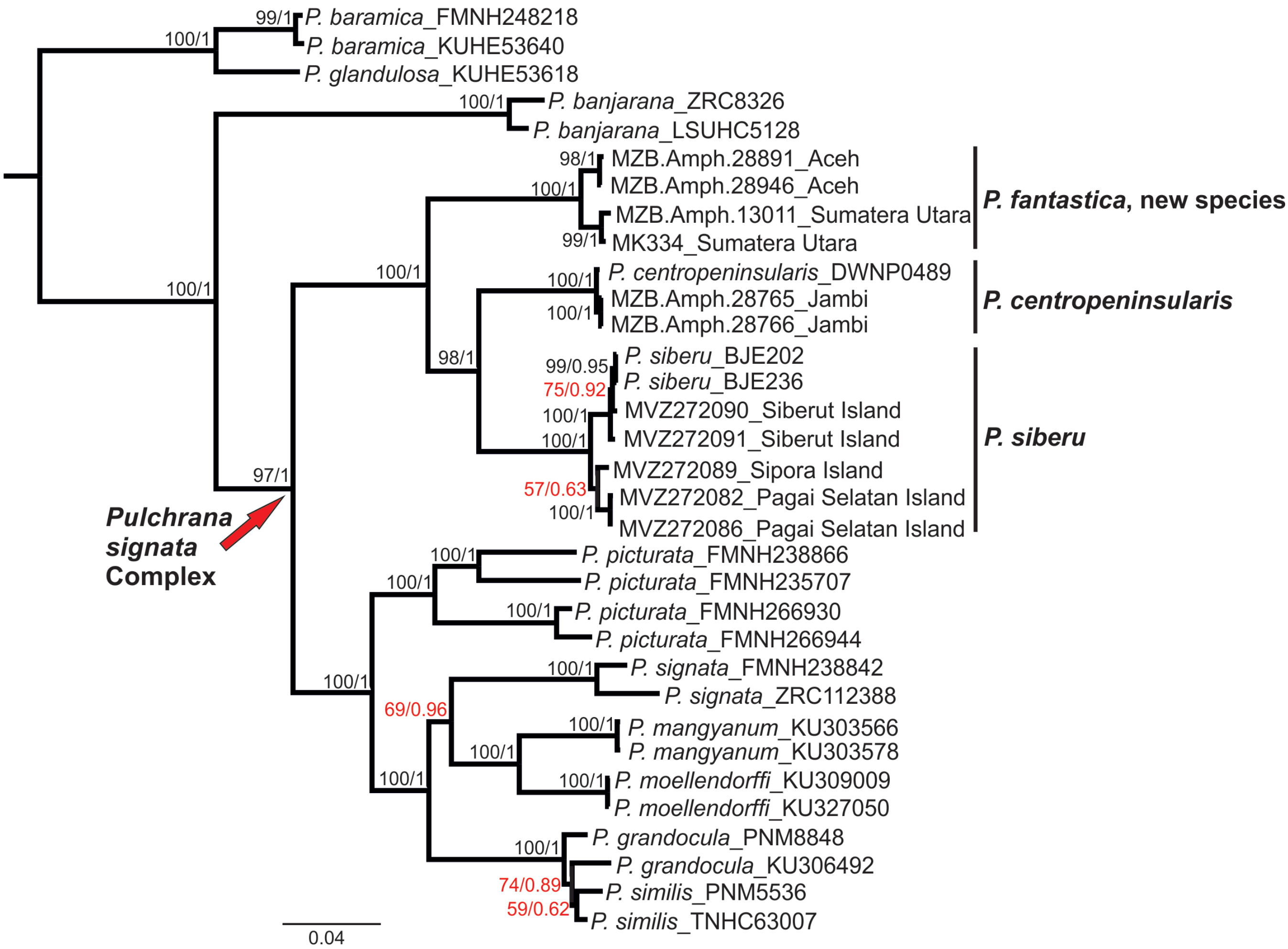

Fig. 1. Phylogenetic tree depicting the relationship between *Pulchrana fantastica*, new species and congeners based on BI. ML tree shows similar topology as BI. Node support representing bootstraps value and posterior probabilities (BS/PP).

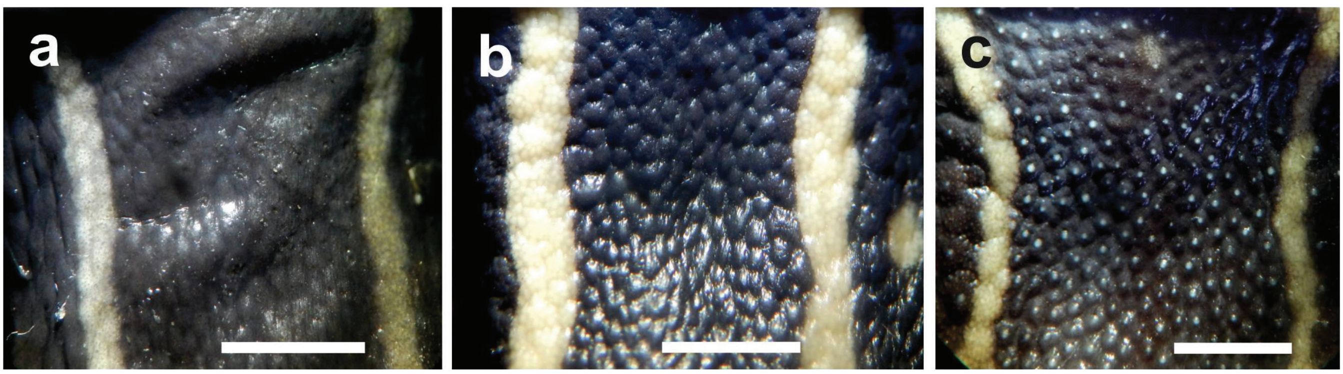

Fig. 2. Left to right; examples of dorsal skin textures in members of the *Pulchrana siberu*, *P. centropeninsularis*, and *P. fantastica*, new species: (a) finely granulated (MZB.Amph.28896); (b) granular (MZB.Amph.28765); (c) or with white tipped keratinised asperities (MZB. Amph.13011). Scale bar = 3 mm. Photo by G. Cahyadi.

MZB.Amph.28765: I(1^- — 1^+)II(1^0 — 2^-)III(1^- — 2^0)IV(2^- — 1/2)V; for MZB.Amph.28766: I(1/2—1^+)II(1/2—11/2)III(1^- — 2^0)IV(2^- — 1/2)V; for MZB.Amph.28767: I(1/2 — 1^+) II(1/2 — 11/2)III(1^- — 2^0)IV(11/2 — 1/2)V]. We consider these differences a representation of intraspecific variation.

In available literatures on *Pulchrana centropeninsularis* from the Malay Peninsula (Leong & Lim, 2004; Chan & Norhayati, 2009; Chan et al., 2014), this species was reported as a possible obligate swamp-adapted specialist. However, our Jambi specimens were collected from a stream in a lowland secondary forest (maximum elevation 50 m) that had been selectively logged approximately 40 years ago (Fig. 3a). The stream's width was approximately 0.5–5.7 m, and depth 0.01–1 m with a slow flow. The water was silty and had low visual clarity. In total, we encountered 14 specimens at the site, of which 12 were found along the stream. The resting sites of the specimens were recorded at 0.6–3.5 m distance from the water, always in forest habitat, away from the stream bank. The majority of these individuals perched on branches

Table 3. Uncorrected *p*-distances calculated from 16S sequences (in MEGA v.7) between *Pulchrana fantastica*, new species and congeners.

		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
1	*P. glandulosa* KUHE 53618											
2	*P. baramica* KUHE 53640	0.064										
3	*P. baramica* FMNH 248218	0.064	0.005									
4	*P. banjarana* ZRC 8326	0.163	0.172	0.170								
5	*P. banjarana* LSUHC 5128	0.160	0.168	0.167	0.012							
6	*P. picturata* FMNH 235707	0.169	0.155	0.154	0.161	0.163						
7	*P. picturata* FMNH 238866	0.169	0.166	0.166	0.170	0.172	0.066					
8	*P. picturata* FMNH 266944	0.151	0.150	0.152	0.151	0.152	0.087	0.090				
9	*P. picturata* FMNH 266930	0.157	0.150	0.151	0.150	0.149	0.088	0.090	0.021			
10	*P. signata* ZRC 112388	0.155	0.152	0.152	0.167	0.169	0.115	0.104	0.109	0.108		
11	*P. signata* FMNH 238842	0.154	0.152	0.152	0.166	0.166	0.110	0.103	0.108	0.109	0.022	
12	*P. siberu* MVZ 272086	0.156	0.156	0.153	0.147	0.145	0.125	0.131	0.128	0.124	0.141	0.133
13	*P. siberu* MVZ 272089	0.160	0.157	0.154	0.150	0.149	0.128	0.134	0.128	0.124	0.145	0.138
14	*P. siberu* MVZ 272090	0.155	0.154	0.151	0.150	0.148	0.129	0.135	0.129	0.121	0.141	0.138
15	*P. siberu* MVZ 272091	0.154	0.153	0.150	0.150	0.147	0.128	0.134	0.128	0.120	0.140	0.137
16	*P. siberu* BJE 202	0.154	0.153	0.150	0.151	0.147	0.129	0.135	0.130	0.122	0.141	0.138
17	*P. siberu* BJE 236	0.154	0.153	0.150	0.151	0.147	0.129	0.135	0.130	0.122	0.141	0.138
18	*P. centropeninsularis* MZB. Amph.28765	0.160	0.154	0.153	0.145	0.146	0.123	0.136	0.122	0.123	0.131	0.126
19	*P. centropeninsularis* MZB. Amph.28766	0.160	0.154	0.153	0.145	0.146	0.123	0.136	0.122	0.123	0.131	0.126
20	*P. centropeninsularis* DWNP 0489	0.160	0.154	0.153	0.143	0.144	0.123	0.136	0.122	0.123	0.130	0.124
21	*P. fantastica*, new species MK334	0.155	0.155	0.152	0.150	0.145	0.127	0.130	0.140	0.136	0.130	0.131
22	*P. fantastica*, new species MZB.Amph.13011	0.157	0.157	0.154	0.151	0.147	0.130	0.132	0.142	0.138	0.132	0.133
23	*P. fantatisca*, new species MZB.Amph.28946	0.158	0.156	0.153	0.151	0.147	0.128	0.131	0.140	0.136	0.134	0.133
24	*P. fantastica*, new species MZB.Amph.28891	0.158	0.156	0.153	0.150	0.145	0.128	0.131	0.138	0.134	0.134	0.133
25	*P. moellendorffi* KU 327050	0.163	0.155	0.154	0.170	0.164	0.113	0.109	0.117	0.113	0.106	0.103
26	*P. moellendorffi* KU 309009	0.163	0.155	0.154	0.170	0.164	0.113	0.109	0.117	0.113	0.106	0.103
27	*P. mangyanum* KU 303566	0.161	0.156	0.154	0.164	0.161	0.109	0.107	0.106	0.104	0.094	0.090
28	*P. mangyanum* KU 303578	0.162	0.157	0.155	0.165	0.162	0.109	0.107	0.106	0.104	0.093	0.091
29	*P. grandocula* KU 306492	0.173	0.172	0.174	0.171	0.171	0.112	0.114	0.114	0.118	0.110	0.109
30	*P. grandocula* PNM 8848	0.170	0.170	0.171	0.169	0.167	0.114	0.110	0.110	0.114	0.108	0.103
31	*P. similis* TNHC 63007	0.170	0.170	0.172	0.174	0.173	0.111	0.109	0.106	0.111	0.104	0.101
32	*P. similis* PNM 5536	0.171	0.171	0.173	0.172	0.171	0.110	0.110	0.109	0.113	0.107	0.102

		12	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
1	*P. glandulosa* KUHE 53618										
2	*P. baramica* KUHE 53640										
3	*P. baramica* FMNH 248218										
4	*P. banjarana* ZRC 8326										
5	*P. banjarana* LSUHC 5128										
6	*P. picturata* FMNH 235707										
7	*P. picturata* FMNH 238866										
8	*P. picturata* FMNH 266944										
9	*P. picturata* FMNH 266930										
10	*P. signata* ZRC 112388										
11	*P. signata* FMNH 238842										
12	*P.* s*iberu* MVZ 272086										
13	*P. siberu* MVZ 272089	0.010									
14	*P. siberu* MVZ 272090	0.016	0.014								
15	*P. siberu* MVZ 272091	0.015	0.015	0.003							
16	*P. siberu* BJE 202	0.017	0.015	0.001	0.004						
17	*P. siberu* BJE 236	0.017	0.015	0.001	0.004	0.000					
18	*P. centropeninsularis* MZB. Amph.28765	0.083	0.084	0.083	0.082	0.083	0.083				
19	*P. centropeninsularis* MZB. Amph.28766	0.083	0.084	0.083	0.082	0.083	0.083	0.000			
20	*P. centropeninsularis* DWNP 0489	0.082	0.083	0.083	0.082	0.083	0.083	0.003	0.003		
21	*P*. *fantastica*, new species MK334	0.100	0.103	0.101	0.100	0.101	0.101	0.103	0.103	0.103	
22	*P*. *fantastica*, new species MZB. Amph.13011	0.102	0.105	0.103	0.102	0.103	0.103	0.103	0.103	0.103	0.004
23	*P*. *fantastica*, new species MZB. Amph.28946	0.102	0.105	0.105	0.104	0.105	0.105	0.102	0.102	0.102	0.011
24	*P*. *fantastica*, new species MZB. Amph.28891	0.100	0.103	0.103	0.102	0.103	0.103	0.102	0.102	0.102	0.013
25	*P. moellendorffi* KU 327050	0.131	0.132	0.135	0.134	0.135	0.135	0.145	0.145	0.143	0.137
26	*P. moellendorffi* KU 309009	0.131	0.132	0.135	0.134	0.135	0.135	0.145	0.145	0.143	0.137
27	*P. mangyanum* KU 303566	0.125	0.128	0.131	0.130	0.131	0.131	0.130	0.130	0.129	0.133
28	*P. mangyanum* KU 303578	0.125	0.128	0.131	0.130	0.131	0.131	0.131	0.131	0.130	0.133
29	*P. grandocula* KU 306492	0.132	0.134	0.133	0.132	0.133	0.133	0.140	0.140	0.138	0.141
30	*P. grandocula* PNM 8848	0.130	0.132	0.134	0.133	0.134	0.134	0.135	0.135	0.133	0.142
31	*P. similis* TNHC 63007	0.132	0.134	0.136	0.135	0.136	0.136	0.138	0.138	0.136	0.137
32	*P. similis* PNM 5536	0.130	0.132	0.134	0.133	0.134	0.134	0.136	0.136	0.134	0.140

		22	23	24	25	26	27	28	29	30	31
1	*P. glandulosa* KUHE 53618										
2	*P. baramica* KUHE 53640										
3	*P. baramica* FMNH 248218										
4	*P. banjarana* ZRC 8326										
5	*P. banjarana* LSUHC 5128										
6	*P. picturata* FMNH 235707										
7	*P. picturata* FMNH 238866										
8	*P. picturata* FMNH 266944										
9	*P. picturata* FMNH 266930										
10	*P. signata* ZRC 112388										
11	*P. signata* FMNH 238842										
12	*P. siberu* MVZ 272086										
13	*P. siberu* MVZ 272089										
14	*P. siberu* MVZ 272090										
15	*P. siberu* MVZ 272091										
16	*P. siberu* BJE 202										
17	*P. siberu* BJE 236										
18	*P. centropeninsularis* MZB.Amph.28765										
19	*P. centropeninsularis* MZB.Amph.28766										
20	*P. centropeninsularis* DWNP0489										
21	*P. fantastica,* new species MK334										
22	*P. fantastica,* new species MZB. Amph.13011										
23	*P. fantastica,* new species MZB. Amph.28946	0.013									
24	*P. fantastica,* new species MZB. Amph.28891	0.015	0.002								
25	*P. moellendorffi* KU 327050	0.140	0.134	0.132							
26	*P. moellendorffi* KU 309009	0.140	0.134	0.132	0.000						
27	*P. mangyanum* KU 303566	0.133	0.133	0.133	0.058	0.058					
28	*P. mangyanum* KU 303578	0.132	0.133	0.133	0.058	0.058	0.002				
29	*P. grandocula* KU 306492	0.142	0.143	0.142	0.103	0.103	0.096	0.096			
30	*P. grandocula* PNM 8848	0.143	0.144	0.143	0.098	0.098	0.090	0.090	0.030		
31	*P. similis* TNHC 63007	0.138	0.139	0.140	0.099	0.099	0.098	0.098	0.024	0.025	
32	*P. similis* PNM 5536	0.141	0.142	0.143	0.099	0.099	0.091	0.091	0.024	0.017	0.011

Fig. 3. Habitat of *Pulchrana centropeninsularis*, Hutan Harapan, Jambi (a) and *P. fantastica*, new species, Taman Buru Linge Isaq, Aceh (b, c). Photo by A. Jankowski (a); G. Cahyadi (b, c).

Table 4. Morphometric variation (in mm) between specimens of *Pulchrana centropeninsularis* from the Malay Peninsula and Jambi.

	***P. centropeninsularis* (Malay Peninsula; Chan et al., 2014)**		***P. centropeninsularis* (Jambi; this study)**		
	ZRC1.10536 (holotype)	**DWNP1189 (paratype)**	**MZB.Amph.28765**	**MZB.Amph.28766**	**MZB.Amph.28767**
SVL	37.4	37.6	40.2	35.5	40.4
HL	14	15.2	15.2	14.5	15.2
HW	12	12.5	10.3	10.4	11.3
SL	5.9	6.4	6.2	5.8	6.2
IOD	3.2	3.5	3.7	3.9	3.8
IND	3.7	3.6	3.1	3.3	3.5
ED	6.0	5.1	5.3	5.4	5.3
TD	4.8	2.2	3.1	3.2	3.4
BL	7.3	8.0	8.9	9.1	8.8
FAL	8.1	8.2	9.6	9.2	10.5
FL	17.6	17.7	17.9	17.5	19.9
TBL	19.9	19.2	20.4	20.3	21.3
TL	12.9	10.6	11.0	11.1	11.6
HG	4.2	4.2	3.3	2.9	4.1

Table 5. Summary statistics of morphometric data for *Pulchrana centropeninsularis*, *P. siberu*, and *P. fantastica*, new species. Table entries are Mean (± SD), followed by range, in mm.

	P. centropeninsularis	***P. centropeninsularis***	***P. siberu***	***P. fantastica*, new species**
	Malay Peninsula, n=2; Chan et al., 2014	**Jambi, n = 3; this study**	**Siberut Island, n = 3; Brown & Guttman 2002; Chan et al., 2014**	**Aceh and Sumatera Utara, n = 12; this study**
SVL	37.5 ± 0.1 (37.4–37.6)	38.7 ± 2.7 (35.5–40.4)	37.0 ± 2.2 (35.4–39.5)	42.4 ± 1.3 (40.3–45.2)
HL	14.6 ± 0.8 (14.0–15.2)	14.8 ± 0.4 (14.5–15.2)	15.7 ± 0.1 (15.6–15.9)	15.0 ± 0.7 (14.1–16.0)
HW	12.3 ± 0.4 (12.0–12.5)	10.6 ± 0.6 (10.3–11.3)	13.0 ± 0.3 (12.6–13.2)	11.5 ± 0.9 (9.5–12.4)
SL	6.2 ± 0.4 (5.9–6.4)	6.0 ± 0.2 (5.8–6.2)	7.0 ± 0.5 (6.5–7.4)	6.7 ± 0.2 (6.4–7.0)
IOD	3.4 ± 0.2 (3.2–3.5)	3.8 ± 0.1 (3.7–3.9)	4.2 ± 0.3 (3.8–4.5)	4.0 ± 0.3 (3.4–4.4)
IND	3.7 ± 0.1 (3.6–3.7)	3.3 ± 0.2 (3.1–3.5)	4.1 ± 0.2 (4.0–4.3)	4.0 ± 0.2 (3.5–4.3)
ED	5.6 ± 0.6 (5.1–6.0)	5.4 ± 0.1 (5.3–5.4)	5.3 ± 0.3 (5.1–5.3)	6.0 ± 0.3 (5.5–6.5)
TD	3.5 ± 1.8 (2.2–4.8)	3.2 ± 0.2 (3.1–3.4)	3.6 ± 0.3 (3.3–3.9)	3.5 ± 0.2 (3.2–3.8)
BL	7.7 ± 0.5 (7.3–8.0)	8.9 ± 0.1 (8.8–9.1)	8.0 ± 0.6 (7.3–8.4)	10.1 ± 0.5 (9.1–10.6)
FAL	8.2 ± 0.1 (8.1–8.2)	9.8 ± 0.6 (9.2–10.5)	9.7 ± 0.5 (9.2–10.1)	9.5 ± 0.6 (8.5–10.5)
FL	17.7 ± 0.1 (17.6–17.7)	18.4 ± 1.3 (17.5–19.9)	18.7 ± 1.6 (17.0–20.2)	21.5 ± 0.9 (20.0–23.5)
TBL	19.6 ± 0.5 (19.2–19.9)	20.6 ± 0.5 (20.3–21.3)	20.9 ± 0.8 (20.0–21.6)	23.2 ± 0.9 (22.1–25.0)
TL	11.8 ± 1.6 (10.6–12.9)	11.2 ± 0.3 (11.0–11.6)	12.1 ± 0.4 (11.7–12.5)	12.3 ± 0.8 (11.2–13.9)
HG	4.2 ± 0.0 (4.2–4.2)	3.4 ± 0.6 (2.9–4.1)	4.5 ± 0.3 (4.3–4.8)	3.9 ± 0.3 (3.2–4.3)

or leaves of small bushes or saplings at 0.2–0.5 m above ground. Male advertisements calls were heard at these resting sites, suggesting the stream may have been the reproduction site of *P. centropeninsularis*. *Pulchrana picturata* was recorded in sympatry with *P. centropeninsularis* at that site. We also recorded *P. centropeninsularis* at other localities in Jambi with similar habitat types (Fig. 4).

TAXONOMY

Based on the phylogenetic placement and morphological distinctness of the Sumatran lineage, we consider these specimens to represent a new species, exhibiting characteristics of a separately evolving lineage, in accordance with the General Unified Lineage-based concept (sensu de Queiroz, 2005). As a result, we describe this unnamed North Sumatran species as a member of the *Pulchrana signata* Complex, within which it is unequivocally nested (Brown & Siler, 2013; Chan et al., 2014), and of which it exhibits diagnostic characters as formalised by Brown & Guttman (2002).

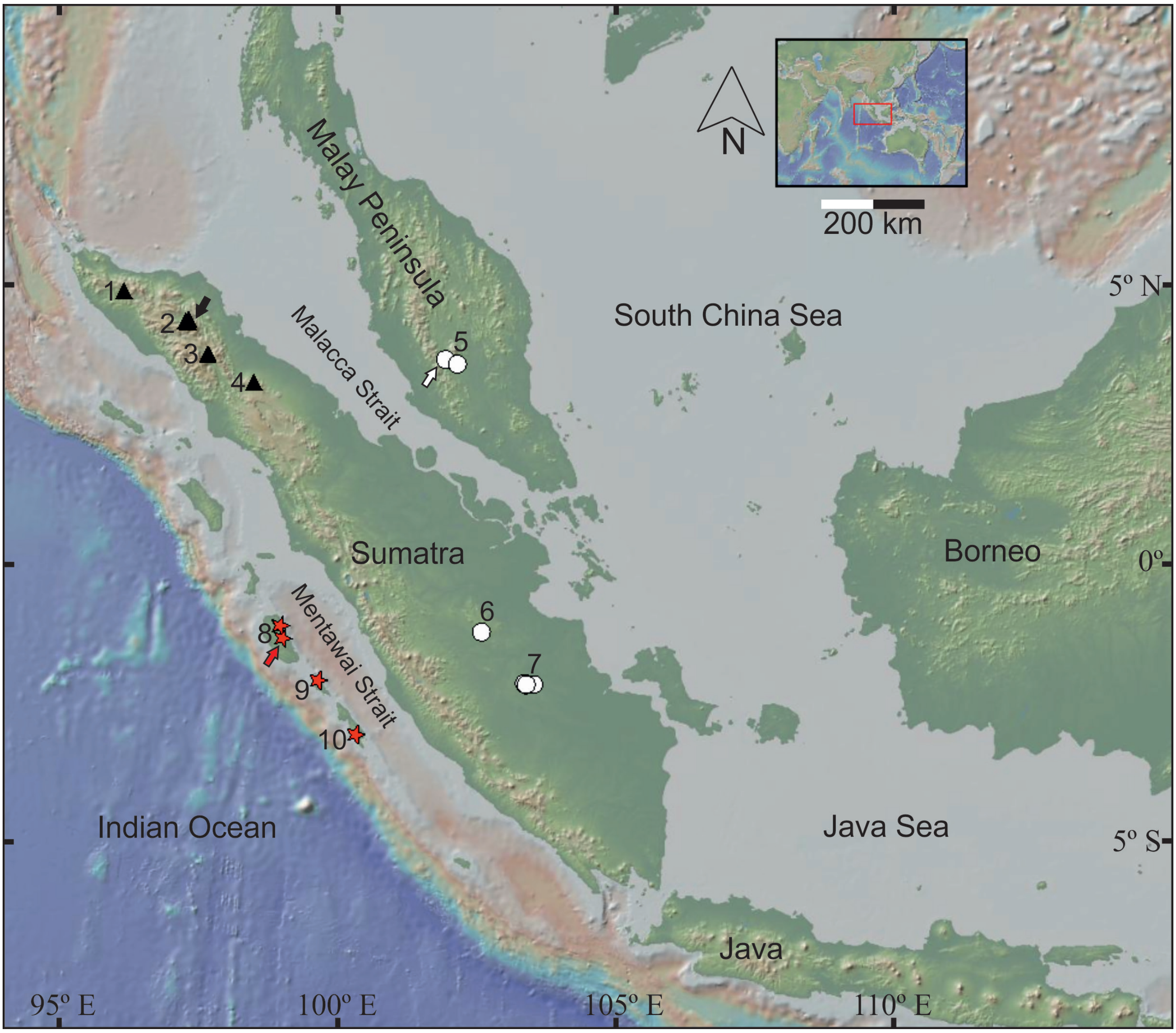

Fig. 4. Geographical distribution of *Pulchrana centropeninsularis* (white circles), *P. fantastica*, new species (black triangles), and *P. siberu* (red stars). Locality information: Mane (1); Taman Buru Linge Isaq (2); Taman Nasional Gunung Leuser (3); Bandar Baru (4), Lakum Forest Reserve & Kuala Gandah, Pahang (5); Bukit Tigapuluh (6); Hutan Harapan (7); Siberut (8); Sipora (9); and Pagai Selatan (10). Type locality for each species indicated by arrow. Map was prepared using GeoMapApp (Ryan et al., 2009).

Ranidae Batsch, 1796

***Pulchrana* Dubois, 1992**

***Pulchrana fantastica*, new species**
Splendid Stream Frogs (recommended common English name); Katak Elok (Bahasa Indonesia)
(Fig. 5a, b)

Hylarana cf. *siberu* (Montane NW Sumatra [Brown & Siler, 2013])
Hylarana sp. Sumatra (Chan et al., 2014)

Holotype. MZB.Amph.28891 (adult male, Fig. 6a–d) from Taman Buru Linge Isaq, Aceh Province, Sumatra, Indonesia (N 04.35868° E 097.24404°, 450 m elevation), coll. U. Arifin and G. Cahyadi, 7 March 2014 at 2054 hours.

Paratypes (6). MZB.Amph.28898 (adult male) and MZB. Amph.28890 (adult male), same information as the holotype, collected between 2036–2145 hours; MZB.Amph.28892–93, MZB.Amph.28894 (Fig. 5a) and MZB.Amph.28896 (adult males), at N 04.37958° E 097.29158° 1,000 m elevation, 9 March 2014, coll. U. Arifin and G. Cahyadi.

Referenced specimens (11). Seven specimens were collected from Taman Buru Linge Isaq, Aceh Province by U. Arifin and G. Cahyadi: MZB.Amph.28889 (male), MZB.Amph.28943 (juvenile; Fig. 5b), MZB.Amph.28948 (juvenile), at N 04.35868° E 097.24404°, 450 m elevation, 7 March 2014; MZB.Amph.28945 (juvenile) and MZB. Amph.28947 (juvenile), at N 04.36018° E 097.24580°, 450 m elevation, 7 March 2014; MZB.Amph.28897 (male), at N 04.338036° E 097.28096°, 600 m elevation, 8 March 2014; and MZB.Amph.28944 (juvenile), at N 04.37958° E 097.29158°, 1,000 m elevation, 9 March 2014. MZB.

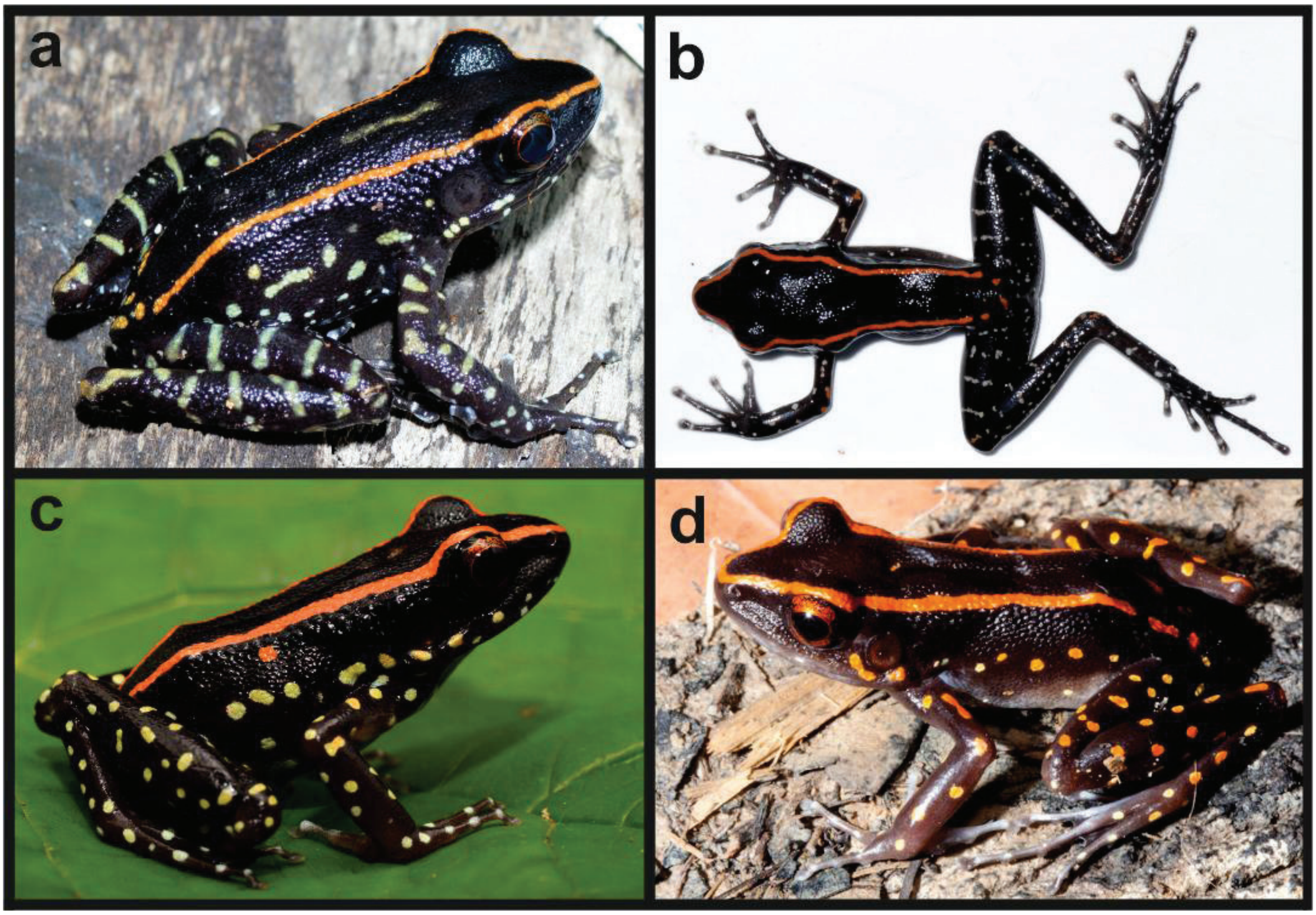

Fig. 5. Plates comparing the three closely allied Sumatran *Pulchrana* species (a) *P. fantastica*, new species, MZB.Amph.28894, adult male, paratype, Aceh; (b) *P. fantastica*, new species, MZB.Amph.28943, juvenile, Aceh; (c) *P. centropeninsularis*, adult male, Jambi; (d) *P. siberu*, female, Pagai Selatan. Photo by U. Arifin (a, b, d); A. Jankowski (c).

Amph.28895 (male), at a locally protected forest in Mane, Kecamatan Ulu Masen (N 04.89949° E 096.13168°, 700 m elevation), 21 March 2014, coll. U. Arifin and G. Cahyadi. MZB.Amph.28946 (juvenile), at Marpunge, Taman Nasional Gunung Leuser, Aceh Province (N 03.77146° E 097.63773°, 1,065 m elevation), 23 February 2014, coll. U. Arifin and G. Cahyadi. MZB.Amph.13015 and MZB.Amph.13011, both males, at Bandar Baru, Sumatera Utara Province (N 03.26287°, E 098.46793°), 5 December 2006 and 10 January 2007, coll. M. Kamsi.

Diagnosis. The following unique combinations of characters distinguish *Pulchrana fantastica*, new species, from its congeners: (1) a medium size frog, SVL adult males (n = 12) 40.3–45.2 mm; (2) males with large humeral glands (3.2–4.3 mm) on anteroventral surface of brachium, paired internal subgular vocal sacs, nuptial pads absent; (3) dorsal skin finely granular to granulated, with or without keratinised white asperities at tip of each granule (Fig. 2); (4) webbing formula: I(1 — 1–11/2)II(1/2 — 2)III(1 — 2–21/3)IV(2–21/3 — 1)V; (5) dorsolateral stripe, thin (0.7–0.9 mm), orange, continuous, anteriorly confluent and posteriorly interconnected by spots; (6) middorsum black with orange line or combination of spots and line in the center, variable in number and length of the line and spots, black without marking in juveniles; (7) dense spots on flanks and dorsal surface limbs, cream or yellow to orange, shape of spots elongated or circular, variable in size; (8) skin of venter smooth, greyish or brown with small light dots on throat and chest, occasionally extending posteriorly to abdomen; (9) iris background black, dense orange stippling ventrally, orange reticulation dorsally, golden centrally, with orange-golden line encircling pupil; (10) upper and lower lip grey or brown with cream or yellow spots (upper lip: 3–7; lower lip: 2–5).

Description of holotype. Adult male with large humeral gland (HG/BL = 40.6%) on anteroventral surface of brachium, paired internal subgular vocal sacs, nuptial pad absent; body slender; head longer than wide (HL/HW = 129.8%); snout obtusely pointed in dorsal view, slightly protruding in lateral view; nares closer to snout than to eye (NSD/END = 56.8%); canthus rostralis sharp, constricted behind nares; loreal region sloping, deeply concave; vomerine teeth distinct, between choana, left (n=3) and right (n=2), teeth barely separated (distance 1.0 mm); choana circular (diameter = 1.0 mm), interchoanal distance 5.3 mm; tongue lanceolate, widening posteriorly, deeply notched in the center, 17.3% free of its total length; eye diameter > interorbital distance (ED/IOD = 151.2%); internarial distance subequal interorbital distance (IND/IOD = 95.3%); tympanum diameter 58.5% eye diameter; supratympanic fold conspicuous.

Dorsum granulated (Fig. 2); flanks finely granular; venter smooth; forelimb relatively slender. Forearm length subequal to brachial length (BL/FAL = 103.9%); fingers long and slender, without webbing; Fin1L/Fin2L = 103.8%, Fin1L/Fin4L = 86.5%, Finger III longest; fingertips slightly expanded into rounded disc, circummarginal groove present; disc width of finger wider than width of terminal phalanx of finger: Fin1DW/Fin1TPW = 142.9%, Fin2DW/Fin2TPW = Fin3DW/Fin3TPW = Fin4DW/Fin4TPW = 128.6%; subarticular tubercles present, round, raised prominently; one subarticular tubercle on Finger I and II, two on Finger III and IV; supernumerary tubercles between the base of each finger and subarticular tubercle present, smaller and less prominent than subarticular tubercles, translucent; outer metacarpal tubercle and palmar tubercle distinct, elongate (OMCL/OMCW = 254.5%, PTL/PTW = 227.3%), in contact, not prominent, subequal in length and width (OMCL/PTL = 112.0%, OMCW/PTW = 100.0%); inner metacarpal tubercle oval, prominent, slightly longer than outer metacarpal tubercle and palmar tubercle (IMCL/OMCL = 107.1%; IMCL/PTL = 120.0%).

Hindlimbs long, tibia longer than femur (TBL/FL = 109.3%); relative length of femur, tibia, and tarsus, to SVL is 50.2%, 54.9%, and 30.4%, respectively; skin texture of dorsal side of tibia and posterior region of the thigh finely granulated; tip of toes expanded, circummarginal groove present, widths of the toe disc larger than widths of terminal phalanx of the respective toes: Toe1DW/Toe1TPW = 118.2%, Toe2DW/Toe2TPW = 137.5%, Toe3DW/Toe3TPW = Toe4DW/Toe4TPW = 128.6%, Toe5DW/Toe5TPW = 133.3%; subarticular tubercles distinct, round, highly elevated, translucent; number of subarticular tubercle for each toe: I(1), II(1), III(2), IV(3), V(2); relative toe length: I < II < V ≤ III < IV, Toe3L/Toe5L = 104.4%; outer metatarsal tubercle raised, oval (OMTL/OMTW = 112.5%), translucent; inner metatarsal tubercle distinct and long (IMTL/IMTW = 200.0%), elevated, translucent, larger than outer metatarsal tubercles (IMTL/OMTL = 200.0%); webbing formula: I(1^- — 1^0)II(1/2 — 2^-) III(1^- — 2^+)IV(2^- — 1^-)V.

Colouration. In life, dorsal skin black; middorsum with orange spot behind the eyes continued by orange line (divided into two, equal length) up to approximately level of sacral vertebra, two yellow spots, and one orange spot in the pelvic region (in the middle of two ilium, in line with joint between ilium and femur); continuous straight, orange stripes (width = 0.7 mm), from tip of snout, along canthus rostralis, following lateral margin of palpebra, continuing dorsolaterally to sacrum, breaking up into five orange-round spots at the posterior pelvic region that connect the dorsolateral stripes from both sides into a loop; flanks brown, lighter ventrally; yellow spots from behind tympanum to groin; round cream spot present between tympanum and eye; two cream spots at end of rictus; venter greyish-brown; whitish dots on throat, chest, and abdomen; iris background black, dense orange reticulation ventrally, orange reticulation dorsally, with golden centrally, solid orange line encircling pupil; upper lip brownish-grey with white spots (n = 6 on left, 5 on right); lower labial region grey, with three small white spots on each side of lower lip; dorsal surface of limbs brown, with dense round spots and elongate, yellow to orange markings, variable in size; small whitish spots on rear of thigh; interdigital webbing brown. In preservative, dorsal skin dark brown; flanks and dorsal surface of limbs brown, lighter than dorsum; ventral skin creamy brown, with whitish spots; dorsolateral stripe and spots on dorsum, flanks, and dorsal surface of limbs faded to cream or whitish; iris grey.

Variation. We observed variation within 18 specimens of *Pulchrana fantastica*, new species; comparison of morphological traits among the seven type specimens of *P. fantastica*, new species, is provided in Table 6. Dorsum texture of adults finely granulated (flat surface with distinct granules; Fig. 2a) or granular (granule distinct, more raised, with white tipped asperities present or absent; Fig. 2b, c). Juvenile specimens lack middorsal marking, adults middorsum with markings (yellow line and or spots from central postocular region, extending posteriorly to vent, variable in length), except for MZB.Amph.28896 without marking; in life, juvenile colouration of spots on dorsal surfaces of limbs whitish or pale yellow (except for MZB.Amph.28943 and MZB.Amph.28946 possess few orange spots); venter grey to brown, with light dots, variably from throat to abdomen; orange dorsolateral stripe in juveniles and adults, straight, in most cases continuous from rostrum to beyond sacrum, occasionally with one or two interruptions of the stripe (Table 6); pattern of spots on dorsal surfaces of limbs in adults vary in colour and shape: usually yellow to orange, round or elongated, from two or more connected spots; posterior surfaces of thighs brown (similar to dorsum), with yellowish spots, smaller than those on the dorsum; number of vomerine teeth 2–3 on each side; number of spots on upper lip (left, right): 3–6, 3–7; number of spots on lower lip 2–5 on each side; webbing formula I(1 — 1–11/2) II(1/2–1 — 2)III(1 — 2–21/3)IV(2–21/3 — 1)V.

Range. *Pulchrana fantastica*, new species, is currently known from Aceh Province (Marpunge, Taman Nasional Gunung Leuser; Taman Buru Linge Isaq; Mane) and Sumatera Utara Province (Bandar Baru, Langkat) at an elevation between 450–1,065 m (Fig. 4).

Natural history. The new species is currently known only from primary forest. All Aceh specimens were collected from within protected areas (Taman Nasional Gunung Leuser, Taman Buru Linge Isaq, and local protected forest in Mane). The holotype was first observed calling from among leaf litter, under low vegetation, about 2.5 m from a small stream (2–3 m width). Two of the paratypes (MZB.Amph.28890 and MZB.Amph.28898) and three juveniles (referenced specimens: MZB.Amph.28889, MZB.Amph.28943, MZB.Amph.28948) were collected the same night at the type locality. MZB.Amph.28889 was perched on a fern growing over above dead log, approximately 1.0 m from a nearby stream at 2038 hours. MZB.Amph.28890 was perched on a dead branch in a stream, approximately 5 cm above the surface of the water at 2145 hours. MZB.Amph.28898 was encountered at 2048 hours on a dead log (d = 30 cm), approximately 1.2 m from the stream. MZB.Amph.28943

Table 6. Comparison of morphological traits between the type specimens of *Pulchrana fantastica*, new species.

Trait	MZB.Amph.28891 (holotype)	MZB.Amph.28890 (paratype)	MZB.Amph.28892 (paratype)	MZB.Amph.28893 (paratype)	MZB.Amph.28894 (paratype)	MZB.Amph.28896 (paratype)	MZB.Amph.28898 (paratype)
SVL (mm)	42.8	41.8	41.1	40.3	42.9	43.2	42.3
HL (mm)	15.7	14.4	14.9	14.1	15.3	15.7	15.9
HW (mm)	12.1	11.3	11.6	11.1	12.1	12.3	12.2
SL (mm)	6.9	6.8	6.7	7.0	6.5	6.8	6.8
IOD (mm)	4.3	4.0	4.0	4.0	4.0	4.2	3.9
IND (mm)	4.1	4.0	3.9	4.3	4.3	4.1	4.1
ED (mm)	6.5	5.8	5.6	6.3	5.8	6.1	5.9
TD (mm)	3.8	3.2	3.6	3.5	3.5	3.4	3.2
BL (mm)	10.6	10.6	9.4	10.2	9.8	10.1	10.1
FAL (mm)	10.2	9.2	8.5	8.9	9.0	9.1	9.9
FL (mm)	21.5	21.2	20.9	21.6	22.2	21.7	21.7
TBL (mm)	23.5	22.9	22.2	22.8	22.3	22.9	23.7
TL (mm)	13.0	12.1	11.2	11.7	11.3	12.2	13.3
HG (mm)	4.3	4.1	3.6	3.2	3.5	4.1	3.7
TED (mm)	1.6	1.8	1.7	1.0	1.2	1.6	1.4
NSD (mm)	2.5	2.5	2.6	2.7	2.2	2.6	2.5
END (mm)	4.4	4.3	4.1	4.3	4.3	4.2	4.4
EED (mm)	7.9	7.5	7.2	7.5	7.2	7.5	8.0
DLSW (mm)	0.7	0.8	0.8	0.7	0.7	0.8	0.7
Toe1L (mm)	8.0	7.2	7.6	7.5	7.4	7.3	7.8
Toe2L (mm)	11.5	10.8	10.8	10.4	10.6	10.3	11.5
Toe3L (mm)	16.5	14.9	15.0	15.0	15.9	14.5	15.9
Toe4L (mm)	22.0	20.8	20.3	20.0	20.3	20.2	20.2
Toe5L (mm)	15.8	15.0	14.6	14.3	14.7	14.6	15.2
Toe1DW (mm)	1.3	1.1	1.0	1.2	1.1	1.1	0.9
Toe2DW (mm)	1.1	1.0	0.9	1.1	1.2	1.0	1.2
Toe3DW (mm)	0.9	1.1	1.1	1.1	1.3	1.0	1.2
Toe4DW (mm)	0.9	0.9	1.0	1.0	1.1	1.0	1.1
Toe5DW (mm)	0.8	0.8	0.9	0.9	1.2	0.7	1.0
Toe1TPW (mm)	1.1	0.8	0.6	0.7	0.6	0.7	0.5

Trait	MZB.Amph.28891 (holotype)	MZB.Amph.28890 (paratype)	MZB.Amph.28892 (paratype)	MZB.Amph.28893 (paratype)	MZB.Amph.28894 (paratype)	MZB.Amph.28896 (paratype)	MZB.Amph.28898 (paratype)
Toe2TPW (mm)	0.8	0.7	0.7	0.8	0.7	0.6	0.7
Toe3TPW (mm)	0.7	0.8	0.5	0.6	0.6	0.7	0.6
Toe4TPW (mm)	0.7	0.6	0.6	0.8	0.8	0.6	0.6
Toe5TPW (mm)	0.6	0.6	0.6	0.6	0.6	0.5	0.7
Fin1L (mm)	10.9	9.4	9.2	9.3	9.5	9.9	10.0
Fin2L (mm)	10.5	9.3	9.0	9.2	9.0	9.1	9.6
Fin3L (mm)	13.1	12.4	11.3	11.5	12.0	11.9	12.5
Fin4L (mm)	12.6	10.8	9.9	10.4	10.1	10.1	11.6
Fin1DW (mm)	1.0	1.0	1.0	1.1	1.2	1.0	1.0
Fin2DW (mm)	0.9	1.0	0.8	1.0	1.1	0.8	1.0
Fin3DW (mm)	0.9	1.2	0.8	1.0	1.2	1.0	1.1
Fin4DW (mm)	0.9	1.3	1.2	1.1	1.2	1.2	1.2
Fin1TPW (mm)	0.7	0.7	0.7	0.7	0.7	0.7	0.6
Fin2TPW (mm)	0.7	0.7	0.6	0.5	0.6	0.7	0.7
Fin3TPW (mm)	0.7	0.7	0.6	0.6	0.7	0.7	0.6
Fin4TPW (mm)	0.7	0.7	0.6	0.6	0.7	0.6	0.7
IMTL (mm)	1.8	1.7	1.8	1.7	2.0	1.9	1.8
OMTL (mm)	0.9	0.9	0.8	0.9	1.0	0.9	0.9
IMTW (mm)	0.9	0.8	0.9	0.9	1.0	1.1	1.0
OMTW (mm)	0.8	1.0	0.8	0.8	0.9	1.0	0.8
IMCL (mm)	3.0	2.3	2.1	2.3	2.3	2.1	2.7
OMCL (mm)	2.8	2.4	1.6	2.0	2.3	2.0	2.6
IMCW (mm)	1.6	1.2	1.3	1.6	1.3	1.7	1.5
OMCW (mm)	1.1	1.1	0.9	1.1	1.2	1.1	1.1
PTL (mm)	2.5	1.8	1.5	2.0	1.7	2.1	2.1
PTW (mm)	1.1	1.1	0.9	1.0	1.2	1.2	1.2

Trait	MZB.Amph.28891 (holotype)	MZB.Amph.28890 (paratype)	MZB.Amph.28892 (paratype)	MZB.Amph.28893 (paratype)	MZB.Amph.28894 (paratype)	MZB.Amph.28896 (paratype)	MZB.Amph.28898 (paratype)
Number of spots on upper labial (left, right)	6, 5	4, 4	5, 5	4, 5	4, 4	4, 4	4, 7
Number of spots on lower labial (left, right)	3, 3	2, 2	3, 4	5, 3	4, 4	4, 4	5, 3
Number of vomerine teeth (left, right)	3, 2	3, 3	3, 2	3, 3	3, 2	3, 3	3, 3
Dorsum texture	granular without white asperities	granular with white asperities	granular without white asperities	granular without white asperities	granular without white asperities	finely granulated	granular with white asperities
Middorsum color pattern (in life)	black with yellow lines and spots	black with yellow line and spots	black with yellow line	black with yellow spots	black with yellow line	black, unmarked	black with yellow line and spots
Dorsolateral stripes shape	continuous, with one left side interruption; five posterior interconnecting spots	continuous; four posterior interconnecting spots	continuous; three posterior interconnecting spots	continuous, with interruptions (right: 2, left: 1); three interconnecting spots	continuous; three posterior interconnecting spots	continuous, with one left side interruption; each followed by one spot posteriorly	continuous; one interconnecting spot
Throat coloration	grey with light spots	brown with light spots	brown with light spots	brown with light spots	brown with light spots	greyish brown with light spots	grey with light spots
Venter coloration	grey with light spots reaching abdomen	brown with light spots reaching abdomen	brownish with light spots reaching abdomen	greyish brown with light spots reaching abdomen	brown with light spots reaching abdomen	greyish brown with light spots reaching abdomen	grey with light spots reaching abdomen
Webbing formula	I(1^- — 1^0)II(1/2 — 2^-)III(1^- — 2^+)IV(2^- — 1^-)V	I(1^0 — 11/2)II(1/2 — 2^-)III(1^- — 2^+)IV(2^+ — 1^-)V	I(1^- — 1^0)II(1/2 — 2^-)III(1^- — 2^+)IV(2^- — 1^-)V	I(1^0 — 11/2)II(1/2 — 2^-)III(1^- — 2^+)IV(2^+ — 1^-)V	I(1^- — 1^0)II(1/2 — 2^-)III(1^- — 2^+)IV(2^+ — 1^-)V	I(1^0 — 11/2)II(1/2 — 2^-)III(1^- — 21/3)IV(2^+ — 1^-)V	I(1^- — 1^0)II(1/2 — 2^-)III(1^- — 21/3)IV(2^- — 1^-)V

was caught seated on an orchid leaf, on the forest floor at 2036 hours. MZB.Amph.28948 was collected at 2036 hours from an orchid leaf, approximately 10 cm above the ground. At the time, the nearby stream was narrower than its usual width, due to low seasonal precipitation. Other species recorded in the same vicinity included one species of ranid frog (*Huia sumatrana*), two species of colubrid snakes (*Boiga nigriceps* and *B. jaspidea*), one species of scincid lizard (*Eutropis* sp.), and orangutans (*Pongo abelii*). The forest type was a typical lowland dipterocap forest. The four remaining paratypes (MZB.Amph.28892, MZB. Amph.28894, MZB.Amph.28896, and MZB.Amph.28944) were collected in the same region, but at higher elevation (1,000 m). The stream at this elevation was surrounded by primary forest, and was approximately 5–6 m wide. Large rocks were prevalent and the stream water was silty and red in colour. The resting perches of collected animals included rocks, dead logs, and roots. Pictures of habitat for this species are provided (Fig. 3b, c).

Etymology. The specific epithet is nominative feminine derivative of the Greek *phantastikós*. We apply this adjective with a contemporary spelling and an implied meaning of "being beyond imagination" with reference to the extraordinary beauty of this species.

Comparisons. *Pulchrana banjarana*, *P. centropeninsularis*, *P. fantastica*, new species, *P. guttmani*, *P. grandocula***,** *P. mangyanum*, *P. moellendorffi*, *P. picturata*, *P. siberu*, *P. signata*, and *P. similis* can be distinguished from *P. baramica*, *P. glandulosa*, *P. laterimaculata*, *P. melanomenta*, *P. rawa*, and *P. debussyi* by having light spots (yellowish white, grey, orange or red in life) on dark (often black) dorsum; dorsolateral stripes present or absent, when present then in the form of a continuous or broken stripe from snout to sacral region or beyond.

Pulchrana centropeninsularis, *P. fantastica*, new species, and *P. siberu* differ from *P. banjarana*, *P. guttmani*, *P. grandocula*, *P. mangyanum*, *P. moellendorffi*, *P. picturata*, *P. signata*, and *P. similis* by the absence (vs. presence) of nuptial pads in males; the presence of distinct pale spots on the limbs (vs. broad bars or indistinct blotches in all other species); the presence of orange to red dorsolateral stripes (vs. white, yellow, pale orange or tan in other species), by reduction in webbing of toes: one phalanx free for Toe III and Toe V, and two to two and half phalanges free for Toe IV (vs. web nearly complete) (Brown & Guttman, 2002).

Pulchrana fantastica, new species, (n = 12) can be distinguished from *P. centropeninsularis* (Jambi specimens, n males = 3) by larger body size (mean SVL 42.4 mm vs. 38.7 mm); larger humeral gland (mean HG length 3.9 mm vs. 3.4 mm); number of spots on upper lip 3–7 (vs. 2–4) on each side; number of spots on lower lip 2–5 (vs. 1–3) on each side; mean ratio of tongue length of notched region and total tongue length 18.5% (vs. 22.2%); dorsal skin texture finely granulated to granular (vs. granular); with or without (vs. without) white tipped asperity at center of each granule; dorsolateral stripe thin, mean of width 0.8 mm (vs. 1.2 mm); middorsum black, marked with short or longer line with breaks in adults and unmarked dorsum in juveniles (vs. black, unmarked); ventral skin grey to brown, with white spots on throat, chest, and sometimes to abdomen (vs. grey to brown, with light spots on throat and light reticulation on venter); mean of tibia length 23.2 mm (vs. 20.6 mm); yellow to orange (vs. yellow spots), round or elongate (vs. usually round), dense spots on dorsal side of limbs; webbing formula: I(1 — 1–11/2)II(1/2 — 2)III(1 — 2–21/3)IV(2–21/3 — 1) V [vs. I(1/2–1 — 1–2)II(1/2–1 — 11/2–21/2)III(1 — 2–3) IV(11/2–3 — 1/2–1)V]. Morphological comparison showing dorsal, ventral, palmar and plantar views of these two species are provided in Fig. 6.

Pulchrana fantastica, new species, differs in morphology from *P. siberu* (Dring et al., 1990; Brown & Guttman, 2002) by larger body size (mean SVL 42.4 mm vs. 37.0 mm); shorter humeral gland (mean HG length 3.9 mm vs. 4.5 mm); dorsal skin texture finely granulated to granular (vs. granular); with or without white tipped asperity at center of each granule; dorsolateral stripe thin, mean of width 0.8 mm (vs. 1.1 mm in *P. siberu*); middorsal colour pattern black, marked with short or longer line with break in adults and unmarked in juveniles (vs. black, unmarked); yellow to orange (vs. usually orange), round or long (vs. round), dense (vs. sparse) spots on dorsal side of limbs; throat grey to brown with light spots in life (vs. light grey); abdomen grey to brown with light reticulation in life (vs. light grey); ventral skin of throat, chest, abdomen, limbs grey to brown, with white spots on throat, chest, and sometimes to abdomen (vs. light grey, usually without spots or reticulation); mean of tibia length 23.2 mm (vs. 20.9 mm). Morphological comparison showing dorsal, ventral, palmar and plantar view of these two species is provided in Fig. 6.

DISCUSSION

In an attempt to infer the phylogeny and revisit the systematics and biogeography of ranid frogs, Oliver et al. (2015) elevated numerous phylogenetically distinct sub genera (including *Pulchrana*) to genera. The constituents of *Pulchrana* previously had been referred to as *Hylarana*. The genus *Pulchrana*, as currently known, is distributed across Sundaland, and comprises 16 species (Frost, 2018), including 11 species recognised within the *P. signata* Complex, namely, *P. banjarana*, *P. centropeninsularis*, *P. debussyi* (by implication; see Oliver et al., 2015)*, P. grandocula*, *P. mangyanum*, *P. moellendorffi*, *P. picturata*, *P. siberu*, *P. signata*, and *P. similis* (Brown & Guttman, 2002; Chan et al., 2014), and the recently described *P. guttmani* (Brown, 2015).

Both Brown & Siler (2013) and Chan et al. (2014) reported that *Pulchrana siberu* and *P. centropeninsularis* formed a distinct clade, separate from the remaining species of the *P. signata* Complex. Although *P. fantastica*, new species, comes from the type locality of an enigmatic congener, *P. debussyi* (Van Kampen, 1910), a species with no available genetic data (Chan et al., 2014), we support Chan et al.'s (2014) conclusion that *P. debussyi* is not allied to the *P. signata* Complex. Chan et al. (2014) considered morphological

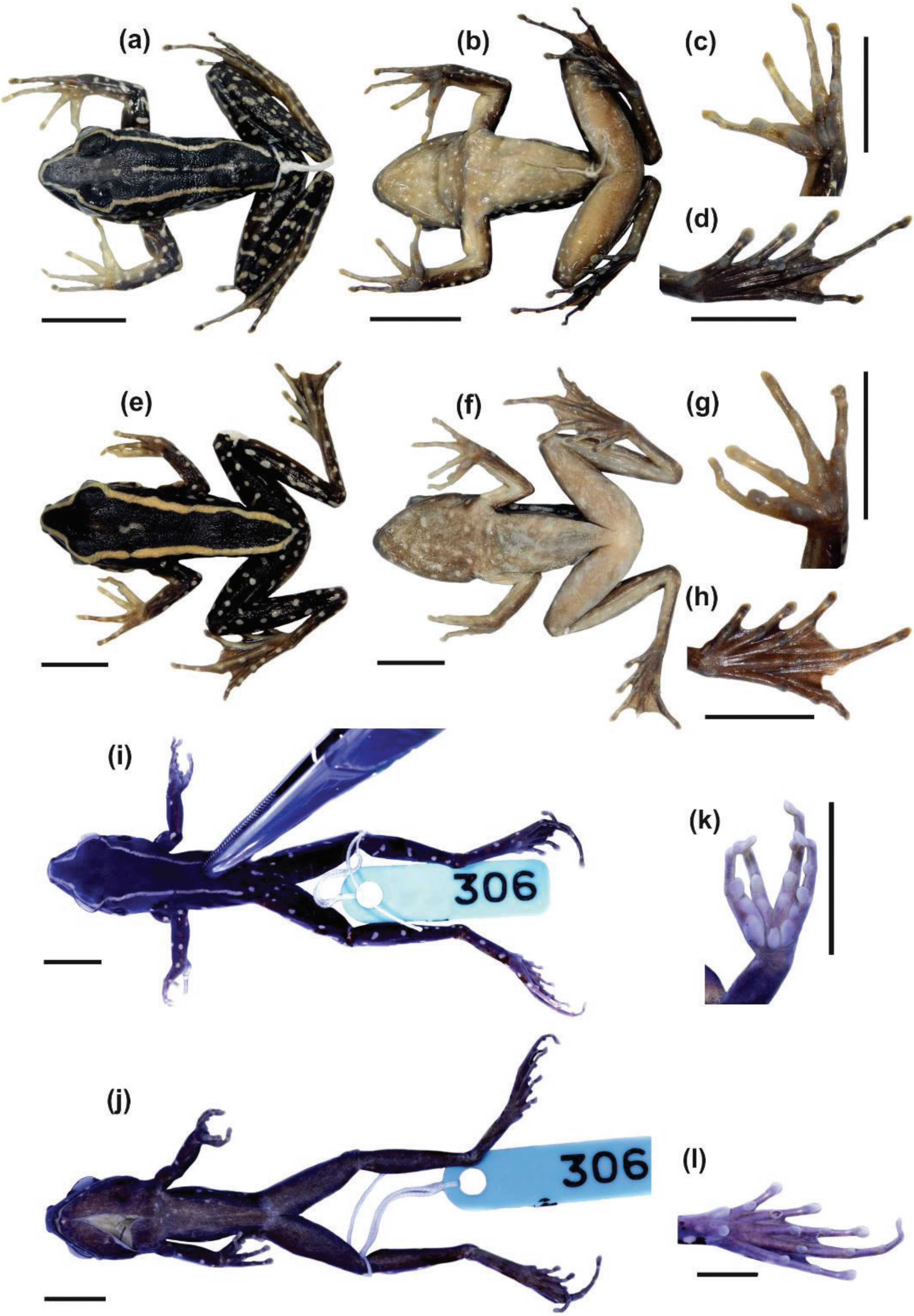

Fig. 6. Dorsal (a), ventral (b), palmar (c), and plantar (d) views of *Pulchrana fantastica*, new species (MZB.Amph.28891, male, holotype, Aceh); (e–h) *P. centropeninsularis* (MZB.Amph.28767, male, Jambi); (i–l) *P. siberu* (BMNH 1979.306, male, holotype, Siberut). Scale bar = 10 mm. Photo by G. Cahyadi (a–h); U. Arifin (i–l).

characters used in the original description *P. debussyi* and suggested this species was a probable synonym of *Amnirana nicobariensis*.

Our results corroborate Chan et al. (2014) in that, (1) *Pulchrana fantastica*, new species, was recovered as the sister taxon to *P. siberu* + *P. centropeninsularis*, and (2) the clade comprising these species was distinct from the remainder of the *P. signata* Complex (Fig. 1). However, our discovery of *P. centropeninsularis* on the island of Sumatra runs contrary to the suggestion by Chan et al. (2014) that *P. centropeninsularis* was endemic to the Malay Peninsula. The record of *P. centropeninsularis* on Sumatra furthermore supports the possibility that the shared most recent common ancestor of *P. siberu, P. centropeninsularis,* and *P. fantastica*, new species, probably originated on Sumatra. Under such a scenario, *P. centropeninsularis* may have dispersed to the Malay Peninsula across the Strait of Malacca. Similarly, *P. siberu* may have dispersed to Siberut, Sipora, and Pagai Selatan across the Strait of Mentawai possibly during the Pleistocene. At this time period, sea levels were ~120 m lower and the distance between these landmasses was considerably narrower (Geyh et al., 1979; Voris, 2000; Chan et al., 2014).

Considering that the genus *Pulchrana* comprises lineages that stem from an ancient process of diversification dating back to the late Eocene (Chan & Brown, 2017), we predict that several other deeply divergent species probably remain to be discovered, particularly in the clade containing *P. picturata* (Brown & Siler, 2013). This prediction can likely be applied to more taxa on the large, topographically heterogeneous island of Sumatra, which remains inadequately sampled. We suspect that even though the cumulative total of Sumatra's amphibians continues to increases every year (Stuart et al., 2006; Inger et al., 2009; Teynie et al., 2010), its anuran amphibian diversity will likely remain underestimated for some time.

Given that the understanding of global amphibian decline is at a critical stage (Stuart et al., 2004; Whittaker et al., 2013), comprehensive amphibian surveys are essential to assess the true diversity of anurans on the island. The documentation of frog distribution is also of paramount importance for the design of informed conservation priorities (Rowley et al., 2010). The IUCN (2017) estimated that 2,067 species of the globally known 6,533 taxa were threatened, and it is indeed troubling that almost 2% of these threatened species occur in Indonesia. Because thorough information concerning the status of most Indonesian amphibians is lacking, the actual number of threatened species likely is much higher. The loss of primary forest (resulting from deforestation and habitat degradation) is currently the foremost threat for Southeast Asian amphibians (Rowley et al., 2010). Indonesia has experienced an unprecedented loss of primary forest, and between 2000 and 2012, forest loss was at an estimated rate of 47,600 ha/yr. Within this same period, a staggering 2,857 kha of primary forest loss was recorded in Sumatra, of which 1,205 kha was lowland forest (Margono et al., 2014). This is a matter of severe concern for the species considered here, given that *Pulchrana siberu*, *P. centropeninsularis*, and *P. fantastica*, new species, all exclusively depend on lowland forests for survival.

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APPENDIX

Material examined. *Pulchrana centropeninsularis* (3). Indonesia—Jambi Province: Hutan Harapan, MZB.Amph.28765–67. *Pulchrana fantastica*, new species (18). Indonesia —Aceh Province: Mane, MZB.Amph.28895; Taman Buru Linge Isaq, MZB.Amph.28889–94, MZB.Amph.28896–98, MZB.Amph.28943–45, MZB.Amph.28947–48; Taman Nasional Gunung Leuser, MZB.Amph.28946. Sumatera Utara Province: Bandar Baru, MZB.Amph.13011, MZB.Amph.13015.