

**Phylogenetic systematics, diversity, and biogeography of the frogs
with gastromyzophorous tadpoles (Amphibia: Ranidae)
on Sumatra, Indonesia**

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“To reach the same destination, some people might only need one step but some other people might need two, three, a hundred, or a thousand steps. Never give up! Some are successful because they work harder than other people, not because they are smart.” –dti-



Preface

It is such a relief to have finally finished writing this dissertation entitled “Phylogenetic systematics, diversity, and biogeography of the frogs with gastromyzophorous tadpoles (Amphibia: Ranidae) on Sumatra, Indonesia”. Thank to Allah, who has always embraced me in any situation, especially during my doctoral studies. The work I have done over the past five years is dedicated not only to myself, but also to all the people, who came into my life for various reasons. Also, this thesis is my small contribution to Indonesia (the “Ibu Pertiwi”) and its fascinating biodiversity. I hope to continue actively contributing to the field of herpetology in the future, simply because it is my greatest passion!

During my childhood, especially through my high school years, it never crossed my mind that I would end up becoming a scientist. Coming from an ordinary Indonesian family and living in a small town made my parents worry about the education their children would need, in order to have a better life in the future. They sent the four of us to school, right through to university. I planned to find a job right after completing my bachelor’s degree. Up to that point, I had never thought about getting a master’s let alone a doctoral degree, especially overseas. This changed when I met Prof. Dr. Djoko T. Iskandar through a friend in 2004. Later on, he became my bachelor’s thesis supervisor. I am forever indebted to him because he first, introduced me to herpetofauna and made it possible for me to dig deeper into this field through various research expeditions all over Indonesia with many scientists (local and international). 2004 was the point where my life took a different direction from what is so called “normal” in my country (get a degree and make money) into an “unusual girl” who dreams big for her future. I fell in love with frogs and Indonesian biodiversity after a three month herpetofaunal expedition in Sulawesi with American and Canadian researchers. It was then that I convinced myself to stay in research and have decided to ever since. It was not an easy journey for me to finally step out of Indonesia and come all the way to Germany to pursue my doctorate with Prof. Dr. Alexander Haas in October 2013. Pak Djoko’s wisdom has helped me to stay focused on my goal. He once said that *“to reach the same destination, some people might only need one step but some other people might need two, three, a hundred, or a thousand steps. Never give up! Some are successful because they work harder than other people, not because they are smart.”*

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Although I had done some molecular work during my master's program, I still needed to learn from scratch when I started my doctoral studies. Thanks to Annamarie Vogt who first refreshed my knowledge on molecular techniques as well as introducing me to the lab procedures at Universität Hamburg (UHH). Thank you to Stefan Hertwig for the opportunity to learn and improve my skills on molecular genetics; Manuel Schweizer, Lea Waser, and Lukas Ruber for their kind assistance and discussion during my work at the Naturhistorische Museum Bürgergemeinde Bern (NHMBE); Eric Smith and all lab members of the University Texas at Arlington-UTA (Elijah Wostl, Kyle O'Connel, Kyle Shaney, Panupong Arm Thammachoti, Utpal Smart, and Carl Franklin) for the good research collaboration and a great time during fieldwork in Sumatra and during my visit at UTA.

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Phylogenetic systematics, diversity, and biogeography of the frogs with gastromyzophorous tadpoles (Amphibia: Ranidae) on Sumatra, Indonesia

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Summary

Sumatra boast an extraordinary level of vertebrate diversity, including many endemic species, especially of amphibians. A total of 104 species of amphibians, including frogs/toads (Anura) and caecilians (Gymnophiona) have been recorded on the island. In the last decade alone, several new species of amphibians were described from this island, and yet, many experts suspect that the true amphibian diversity of Sumatra still remains unknown. Lack of sampling and lack of molecular data remain the main impediments in ameliorating this predicament. My doctoral thesis focuses on the diversity and distribution of the family Ranidae on Sumatra, particularly the subgroup of taxa that possess gastromyzophorous tadpoles as an adaptation for living in torrential habitats. Ranids with gastromyzophorous tadpoles (collectively known as Cascade Frogs) were previously known only for the genus *Amolops*, *Meristogenys*, and *Huia*. In Sumatra, until my study, only *Huia sumatrana* had been positively known to have this larval type. Despite the abundance of many suitable stream habitats no other forms with gastromyzophorous tadpoles has been reported. The aim of my doctoral research was twofold: 1) investigate the existence of additional species with this highly specialized tadpole type in Sumatra, and 2) given the high dependency of the larval stage on stream habitat, this group of frogs is a suitable taxon for testing the hypothesis whether distribution patterns of Sumatran species are congruent with patterns of the Pleistocene-river systems.

Species discovery. My study was the first comprehensive sampling of riparian ranid frogs along a full range longitudinal transect of Sumatra, with special emphasis on the Cascade Frogs. This study was also the first to employ a molecular genetic approach to confirm the identity (barcoding) of frogs and their gastromyzophorous tadpoles from Sumatra. My data reveal more diversity within the Sumatran Cascade Frog assemblage than previously known. I have successfully identified gastromyzophorous tadpoles from Sumatra as larval forms of the endemic frog previously thought to belong to *Chalcorana crassiovis*, using the 12S and 16S mitochondrial gene fragments. My larger phylogenetic analyses from both mitochondrial and nuclear gene fragments also suggest the recognition of two other previously unrecognized distinct lineages that are related to the aforementioned species. Thus, along with corroborating evidence (e.g., molecular, morphology, distribution, and larval forms), I delimited three distinct lineages (frogs previously known as *C. crassiovis* and the two new described species) by proposing a new genus *Sumaterana*. My phylogenetic work also shows unexpected levels of genetic diversity within *Huia* samples from Sumatra. My analyses suggest the recognition of at least three distinct lineages of the genus *Huia* on this island. In assessing character

evolution, my phylogenetic analysis suggests that gastromyzophory in Southeast Asian ranids might have evolved independently twice - once in the most recent common ancestor of the *Huia+Sumaterana+Meristogenys* clade, and again in the more distant genus *Amolops*.

The effect of paleo-drainage systems on lineage diversification. The Sundaland Pleistocene drainage systems that connect to Sumatra are the Malacca Strait river system, Siam river system, North Sunda river system, and East Sunda river system. My phylogenetic analyses show no conclusive evidence for the watersheds driving cladogenesis in these frogs. However, the results demonstrated that distribution of the Sumatran Cascade Frogs were genetically structured into the northern and southern lineages on the island. According to this study, I believe that for certain groups of animals, especially those that are not entirely restricted to river habitats in their life cycle (e.g., ranids with gastromyzophorous tadpoles), the paleo-drainage hypothesis probably is not relevant. Adult frogs seem to have more potent dispersal abilities in the terrestrial habitat compared to their larval stages in the rivers, which might maintain gene flow independent of river geography. Furthermore, based on my divergence time analysis, the Cascade Frogs have diversified in Sumatra much earlier than the occurrence of the paleo-river systems. The result of my study are anticipated to help with predicting geographic patterns of their diversity as well as guiding research on anurans in the Sunda region for bio-discovery and conservation.

In conclusion, my study is convincing evidence that Sumatran frog diversity is still significantly underestimated and new discoveries can be expected. Strategic sampling efforts need to be undertaken to reveal the unknown diversity and geographic patterns present on the island. For example in my thesis, I also delimited a new *Pulchrana* species from Sumatra as well as extend the geographical range of its sister species (*P. centropeninsularis*) from the Malay Peninsula region. On broader level, my work demonstrated that comprehensive geographic and thorough sampling of adult and larva forms in biological hotspots such as Sumatra, as well as integration of different sources of evidence are essential to disentangle the taxonomic and phylogenetic problems of the tropical regions, particularly for cryptic or near cryptic species commonly found in the tropics. Furthermore, my finding on the north-south geographical partitioning of Cascade Frogs on the island needs further corroboration with other taxa. This distribution patterns might shed light on the geographical history of the island that will be beneficial for designing conservation priorities in the region.

Phylogenetische Systematik, Diversität und Biogeografie der Frösche mit gastromyzophoren Kaulquappen (Amphibia: Ranidae) in Sumatra, Indonesien

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Zusammenfassung

Sumatra weist eine bemerkenswerte Wirbeltier Diversität auf, einschliesslich vielen endemischen Arten, insbesondere Amphibien. Insgesamt 104 Amphibienarten (Froschlurche [Anura] und Blindwühlen [Gymnophiona]) wurden auf der Insel nachgewiesen. Alleine im letzten Jahrzehnt wurden einige neue Amphibienarten auf dieser Insel beschrieben, dennoch vermuten Experten, dass die eigentliche Amphibiendiversität immer noch unbekannt ist. Das Fehlen von Proben und das Fehlen molekularer Daten stellen die grössten Hindernisse zur Beseitigung dieser Wissenslage dar. Meine Doktorarbeit konzentriert sich auf die Diversität und die Verteilung der Familie Ranidae auf Sumatra, insbesondere der Untergruppe der Taxa, die gastromyzophore Kaulquappen besitzen, als Anpassung an kaskadieren Bach- und Flusshabitats. Frösche mit gastromyzophoren Kaulquappen (insgesamt zusammengefasst als Kaskadenfrösche) waren bisher nur bei Arten der Gattungen *Amolops*, *Meristogenys* und *Huia* bekannt. Vor meiner Studie war auf Sumatra nur *Huia sumatrana* dafür bekannt, eine solche Larvenform zu besitzen. Trotz vieler geeigneter Bachhabitats waren bisher keine anderen gastromyzophoren Kaulquappen nachgewiesen worden. Die Ziele meiner Dissertation waren: 1) Die Untersuchung, ob weitere Arten dieses hochentwickelten Kaulquappentyps in Sumatra vorkommen und 2) ob durch die hohe Abhängigkeit der Larven von den Fluss- und Bachhabitats diese Taxa von Froschlurchen geeignet sind, die Hypothese zu testen, dass Verteilungsmuster der Taxa kongruent mit Fusssystemen des Pleistozäns sind.

Artentdeckung. Meine Studie war die erste umfassende Aufsammlung uferlebender Frösche der Ranidae entlang eines vollständigen Längstransekts in Sumatra, mit besonderem Schwerpunkt auf den Kaskadenfröschen. Diese Studie war auch die erste, die einen molekularbiologischen Ansatz (Barcoding) verwendete, um die Identität gastromyzophoren Kaulquappen in Sumatra nachzuweisen und sie den Fröschen eindeutig zuzuordnen. Meine Daten zeigen mehr Diversität innerhalb der Kaskadenfrösche Sumatras auf, als bisher angenommen. Ich konnte erfolgreich mittels mitochondrialer Genfragmente (12S/16S) gastromyzophore Kaulquappen als Larvenformen des endemischen Frosches identifiziert, der bislang als *Chalcorana crassiovis* bekannt war. Meine umfangreichen phylogenetischen Analysen, sowohl von mitochondrialen als auch nuklearen Genfragmenten, legen die Anerkennung zweier bisher nicht bekannte Abstammungslinien als eigene Arten nahe, die eng mit der genannten Arten verwandt sind.

Zusammen mit anderen Beweisen (z.B. Molekül-, Morphologie-, Verteilungs- und Larvenformen) habe ich also insgesamt drei verschiedene Abstammungslinien (die

vormals als *Chalcorana crassiovis* bekannte Art und zwei neu beschriebene Arten) abgegrenzt und eine neue Gattung *Sumaterana* für sie vorgeschlagen. Meine phylogenetische Arbeit zeigt auch eine unerwartete genetische Diversität innerhalb der *Huia*-Proben aus Sumatra. Meine Analysen legen die Anerkennung von mindestens drei verschiedenen Linien der Gattung *Huia* auf Sumatra nahe. Bei der Beurteilung der Merkmalsevolution deutet meine phylogenetische Analyse darauf hin, dass sich Gastromyzophorie innerhalb der südostasiatischen Raniden zweimal unabhängig voneinander entwickelt haben könnte - einmal im letzten gemeinsamen Vorfahren der *Huia+Sumaterana+Meristogenys* Klade und ein weiteres Mal in der weiter entfernten Gattung *Amolops*.

Die Wirkung des Paläo-Drainagesystems auf die Diversifizierung. Die alten Flusssysteme von Sundalands im Pleistozän, die Wasser von Sumatra ableiteten sind, sind das Flusssystem der Straße von Malakka, das Flusssystem Siams, das Flusssystem Nord-Sundas und das Flusssystem Ost-Sundas. Meine phylogenetischen Analysen zeigen keine klaren Beweise für einen Zusammenhang zwischen Flusssystemen und Kladogenese dieser Frösche. Die Ergebnisse zeigten jedoch eine genetische Verteilung der Sumatra-Kaskadenfrösche in nördliche und südliche Linien. Gemäss meiner Untersuchung glaube ich, dass die "*Paleodrainage-Hypothesis*" für bestimmte Tiergruppen, insbesondere diejenigen, die in ihrem Lebenszyklus nicht vollständig auf Flusslebensräume beschränkt sind (z. B. Raniden mit gastromyzophoren Kaulquappen), wahrscheinlich nicht ausschlaggebend ist. Adulte Frösche scheinen im terrestrischen Lebensraum stärkere Ausbreitungsfähigkeiten zu haben als ihre Larvenstadien in den Flüssen, was den Genfluss unabhängig von der Flussgeographie aufrechterhalten könnte. Aufgrund meiner Divergenz Zeit-Analyse haben Kaskadenfrösche in Sumatra lange vor der Bildung der Paläo-Flusssysteme eine Speziation durchlaufen. Das Ergebnis meiner Studie soll dazu beitragen, die geographischen Muster ihrer Diversität vorherzusagen und Forschung an Anuren in der Sunda-Region, Entdeckung weiterer Arten und den Schutz anzuregen.

Zusammenfassend ist meine Studie ein überzeugender Beweis dafür, dass die Vielfalt der Sumatra-Frösche immer noch erheblich unterschätzt wird und neue Entdeckungen zu erwarten sind. Es müssen strategische Sammlungsaktionen unternommen werden, um die unbekannt Vielfalt und die geographischen Muster der Insel aufzuzeigen. In meiner Doktorarbeit habe ich zum Beispiel eine neue *Pulchrana*-Art aus Sumatra beschrieben und die geografische Verbreitung ihrer Schwesterarten (*P. centropeninsularis*) von der Malaiischen Halbinsel bis nach Sumatra vergrößert. Weiter zeigte meine Arbeit, dass eine umfassende geografische und gründliche Probenahme von Adult- und Larvenformen in biologischen Hotspots wie Sumatra, sowie die Integration verschiedener Evidenzen von wesentlicher Bedeutung sind, um die taxonomischen und phylogenetischen Probleme der tropischen Regionen zu lösen, vor allem für kryptische oder sehr ähnliche Arten, wie sie in den Tropen häufig vorkommen. Ausserdem erfordern meine Ergebnisse zur Nord-Süd-Verteilung der Kaskadenfrösche auf der Insel eine Bestätigung durch die Untersuchung weiterer Taxa. Diese Verteilungsmuster könnten Licht auf die geografische Geschichte der Insel werfen, was hilfreich für das Erstellen von Schutzprioritäten in dieser Region ist.

Sistematika filogenetik, keanekaragaman, dan biogeografi katak dengan berudu gastromyzofoora (Amphibia: Ranidae) di Sumatra, Indonesia

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Ringkasan

Pulau Sumatra memiliki tingkat keanekaragaman vertebrata yang sangat luar biasa, termasuk di dalamnya adalah spesies endemik, terutama amfibi. Tercatat sekitar 104 spesies amfibi di pulau ini, yang terdiri atas katak/kodok (Anura) dan sesilian (Gymnophiona). Dalam satu dekade terakhir, cukup banyak spesies baru yang dideskripsi dari Sumatra. Walaupun demikian, para ahli menduga bahwa keanekaragaman amfibi yang sebenarnya di pulau ini masih belum diketahui. Hambatan utama dari masalah ini adalah kurangnya sampling/survey dan terbatasnya data molekuler yang tersedia. Fokus utama disertasi saya terletak pada keanekaragaman dan distribusi katak dari famili Ranidae di Sumatra, khususnya kelompok katak yang memiliki berudu gastromyzofoora. Pada tipe berudu ini terdapat semacam alat penghisap pada bagian abdomen, sebagai mekanisme adaptasi untuk hidup di habitat sungai berarus deras. Kelompok katak dengan tipe berudu ini dikenal secara kolektif sebagai *Cascade Frogs*, dan sebelum penelitian saya dilakukan hanya diketahui untuk genus *Amolops*, *Meristogenys*, dan *Huia*. Hingga penelitian ini dilakukan, hanya *H. sumatrana* saja yang diketahui memiliki tipe larva seperti ini di Sumatra, meskipun terdapat banyak sekali habitat sungai yang berpotensi sebagai tempat hidup untuk katak jenis ini. Penelitian saya bertujuan untuk: 1) mengetahui apakah ada katak lain di Sumatra yang memiliki tipe berudu gastromyzofoora; dan 2) untuk menguji apakah pola distribusi spesies di Sumatra berkaitan erat dengan keberadaan DAS (Daerah Aliran Sungai) purba di pulau ini. Katak dengan berudu gastromyzofoora sangat cocok untuk studi ini karena fase larvanya sangat bergantung pada habitat sungai.

Penemuan spesies baru. Penelitian saya adalah yang pertama menyajikan data comprehensive dari kelompok katak ranid yang dikoleksi sepanjang garis transek longitudinal di Sumatra, khususnya untuk *Cascade Frogs*. Penelitian ini juga yang pertama menggunakan pendekatan molekuler (barcoding) untuk mengukuhkan identitas katak dewasa dengan berudu gastromyzofoora dari pulau ini. Hasil studi saya menunjukkan bahwa *Cascade Frogs* di Sumatra memiliki keanekaragaman yang lebih banyak dibandingkan dengan yang sudah diketahui saat ini. Saya berhasil membuktikan bahwa berudu gastromyzofoora dari Sumatra merupakan berudu dari katak endemik yang sebelumnya dikenal sebagai *Chalcorana crassiovis*, dengan menggunakan sekuens DNA mitokondria (12S dan 16S). Analisis filogenetik dari DNA mitokondria dan DNA inti juga menunjukkan adanya dua garis keturunan lain yang juga berkerabat dekat dengan *C. crassiovis*. Oleh karena itu, dengan bukti-bukti yang ada (molekuler, morfologi, distribusi, dan berudu), genus baru *Sumaterana* diajukan untuk mengelompokkan katak-katak yang dikenal sebagai *C. crassiovis* dan kedua spesies baru tersebut. Selain itu, studi filogenetik saya juga menunjukkan tingkat keanekaragaman genetik dari katak

genus *Huia* yang cukup mengejutkan. Setidaknya ada tiga garis keturunan berbeda dalam kelompok katak *Huia* di pulau Sumatra. Lebih dari itu, analisis filogenetik saya mengindikasikan bahwa dalam famili Ranidae, berudu gastromyzofoora berevolusi melalui dua jalur mandiri, yaitu pada nenek moyang katak *Huia+Sumaterana+Meristogenys* dan pada nenek moyang katak genus *Amolops*.

Pengaruh DAS (Daerah Aliran Sungai) purba terhadap proses diversifikasi katak. DAS purba yang terdapat di daerah Paparan Sunda pada jaman Pleistosen yang juga melalui pulau Sumatra adalah DAS Selat Malaka, DAS Siam, DAS Sunda bagian Utara, dan DAS Sunda bagian Timur. Analisis filogenetik saya tidak menunjukkan bukti yang kuat mengenai keberadaan DAS tersebut yang mempengaruhi proses kladogenesis pada katak dengan berudu gastromyzofoora. Namun, hasil penelitian ini memperlihatkan bahwa secara genetic *Cascade Frogs* di Sumatra terdistribusi ke dalam kelompok utara dan selatan. Berdasarkan penelitian ini, untuk kelompok hewan tertentu, terutama yang siklus hidupnya tidak sepenuhnya terbatas pada habitat sungai (misalnya ranid dengan berudu gastromyzofoora), hipotesis mengenai DAS purba ini tidak berlaku. Katak dewasa kemungkinan memiliki kemampuan menyebar yang lebih baik dibandingkan dengan fase berudu, sehingga dapat mempertahankan *gene flow* secara independen dari geografi sungai. Lebih dari itu, berdasarkan hasil analisis untuk waktu divergensi, diversifikasi *Cascade Frogs* di Sumatra sudah terjadi jauh sebelum DAS purba terbentuk pada masa Pleistosen. Hasil penelitian saya diharapkan dapat membantu memetakan pola geografi dari keanekaragaman katak Sumatra. Selain itu, hasil penelitian ini dapat digunakan sebagai acuan untuk penelitian mengenai penemuan spesies anura lainnya dan untuk konservasi.

Sebagai kesimpulan, penelitian saya adalah bukti nyata bahwa keanekaragaman katak di Sumatra masih sangat jauh dari yang sebenarnya. Dapat diperkirakan bahwa penemuan species baru akan tetap terjadi di masa mendatang. Upaya pengambilan sampel yang strategis sangat diperlukan untuk dapat mengungkap keanekaragaman yang belum diketahui dan memetakan pola geografi spesies yang ada di pulau ini. Contoh lain juga disertakan dalam disertasi saya, yaitu penemuan spesies baru dari genus *Pulchrana* di Sumatra. Selain itu, dalam studi tersebut saya juga memperluas daerah distribusi dari *P. centropeninsularis* yang sebelumnya hanya diketahui dari wilayah Malay Peninsula. Lebih luas lagi, hasil penelitian saya menunjukkan bahwa sampling menyeluruh, baik lokasi maupun sampel (katak dewasa dan berudu) di wilayah hotspots seperti Sumatra, serta dengan mengintegrasikan berbagai bukti, merupakan langkah penting untuk menyelesaikan masalah filogenetik dan taksonomi di daerah tropis. Terutama karena spesies kriptik atau spesies dengan kemiripan morfologi yang tinggi sangat umum ditemukan di wilayah ini. Lebih lanjut, penemuan saya mengenai pembagian wilayah utara-selatan untuk distribusi *Cascade Frogs* di Sumatra perlu dibuktikan untuk taksa yang lain juga. Dengan mengetahui pola distribusi spesies di pulau ini diharapkan dapat menjelaskan sejarah geografi Sumatra yang akan bermanfaat untuk merancang prioritas konservasi di wilayah ini.

CHAPTER 1

General introduction

I Geology and biodiversity of the Sunda region:

I.1 Sundaland as a biodiversity hotspot

The Sunda region or Sundaland is considered the continental core of Southeast Asia (Hall 2014). It was a large, exposed landmass during the Pleistocene that consisted of southern Indochina, the Thai-Malay Peninsula, Sumatra, Java, Borneo, the shallow sea of the Sunda Shelf that connects these islands, and west Sulawesi (Hall 2014). This region is known to be home for an extraordinary number of species and particularly endemics. It is considered one of 35 biodiversity hotspots in the world (Fig. 1) (Mittermeier et al. 2011, Sloan et al. 2014, Conservation International 2018). Sundaland contains at least 2% of total endemic plants and vertebrates worldwide (Myers et al. 2000). Furthermore, compared to other biodiversity hotspots in Southeast Asia (Indo-Burma, Philippines, and Wallacea), Sundaland has higher percentages of endemic species for the six focal taxa described in Table 1: plants 60.00%, birds 18.94%, freshwater fishes 54.34%, amphibians 81.40%, and mammals 55.16% (Mittermeier et al. 2011). Among those species, some charismatic endemic species from the region are the Sumatran tiger *Panthera tigris sumatrae* (Sumatra), Sumatran rhino *Dicerorhinus sumatrensis* (Sumatra), Javan rhino *Rhinoceros sondaicus* (Java), orangutan *Pongo pygmaeus* (Sumatra and Borneo), long-nosed monkey *Nasalis larvatus* (Borneo), and Javan hawk-eagle *Nisaetus bartelsi* (Java). This fascinating species richness and unique distribution pattern of the species within Sundaland were suggested to be strongly influenced by the complex geological history of the region (Morley 2012, de Bruyn et al. 2013).

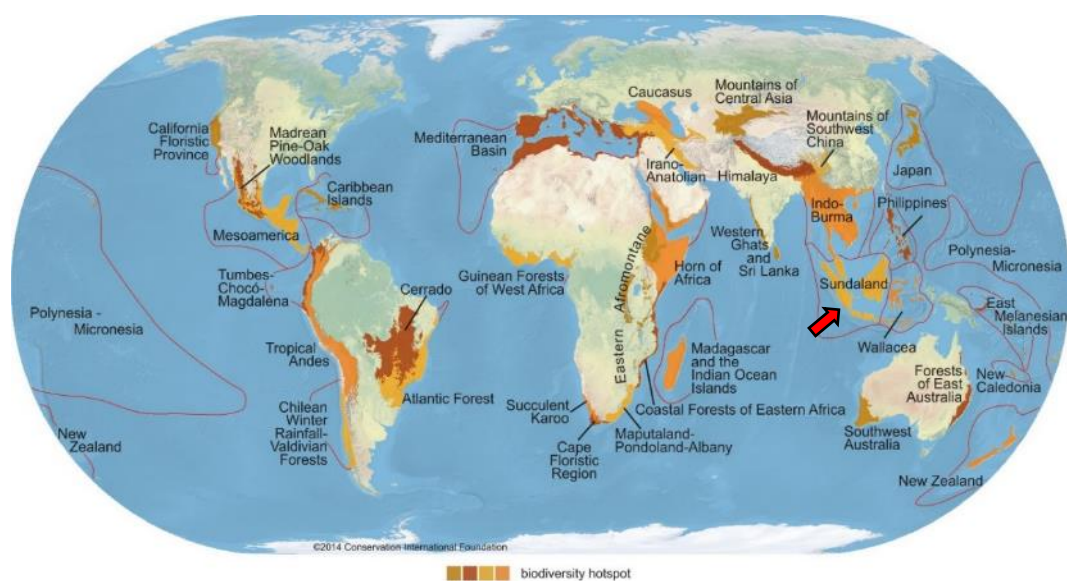


Figure 1 The 35 biodiversity hotspot regions in the world. Sundaland is indicated by a red arrow. (Conservation International 2018)

Table 1 Number of species that occur (O) and are endemic (E) in the Southeast Asia biodiversity hotspots (Mittermeier et al. 2011).

	Number of species occur (O) and endemic (E) in			
	Sundaland	Indo-Burma	Philippines	Wallacea
Plants (Mittermeier et al. 2004)	O: 25,000; E: 15,000	O: 13,500; E: 7,000	O: 9,253; E: 6,091	O: 10,000; E: 1,500
Birds (Mittermeier et al. 2004)	O: 771; E: 146	O: 1,277; E: 73	O: 535; E: 185	O: 650; E: 265
Reptiles (Mittermeier et al. 2004)	O: 449; E: 244	O: 518; E: 204	O: 235; E: 160	O: 222; E: 99
Freshwater fishes (Mittermeier et al. 2004)	O: 950; E: 350	O: 1,262; E: 553	O: 281; E: 67	O: 250; E: 50
Amphibians (Stuart et al. 2008)	O: 258; E: 210	O: 328; E: 193	O: 94; E: 78	O: 49; E: 33
Mammals (Schipper et al. 2008)	O: 397; E: 219	O: 401; E: 100	O: 178; E: 113	O: 244; E: 144

I.2 Geology of the Sundaland

The continental core of Southeast Asia (Sundaland) was initiated in the Late Paleozoic and the Triassic by the assemblage of two landmasses in the western part of the Sundaland continent (Fig. 2), that are known as Sumatra and the Malay Peninsula, respectively, in the present day (Metcalf 2011a-b). From the Triassic until the early Late Cretaceous, subduction of Pacific plates at East Asian margin occurred towards the west. In the Late Triassic, Indochina-East Malaya, the Sukhotai Arc and Sibumasu were amalgamated. As a consequence, from the Jurassic onwards part of today's Sunda Shelf as far south as Sumatra became emergent, including much of Indochina southwards through the Thai-Malay Peninsula (Hall 2014). In the Early Cretaceous, the South West Borneo block (SWB, Fig. 2) amassed to the Sunda region (Ben-Avraham and Emery 1973, Hall 2014). In the early Late Cretaceous, two significant collisions took place in the region (Hall 2014). First, the two other blocks (the East Java-West Sulawesi "EJ-WS" and the Sabah-North West Sulawesi "S-NSW", Fig. 2) moved northwards and attached to the SWB block joining Southeast Asia. A suture from West Java through the Meratus Mountains northwards marked the collision of these landmasses (Hamilton 1979, Parkinson et al. 1998, Hall 2014). Second, the Sumatran margin of western Sundaland collided with the Woyla intra-oceanic arc (Barber et al. 2005, Hall 2014). This event in the early Late Cretaceous was marked by the termination of numerous subductions in the Sunda region (Clements et al. 2011, Hall 2014). During the Cenozoic, Sundaland and Southeast Asia in general, have experienced complex geological events that are very likely to have frequently changed the sea level during this epoch. These events have significantly impacted the distribution of land and sea, climate and vegetation on the region, as well as its biogeographic pattern (Morley 2012, de Bruyn et al. 2013, Hall 2013).



Figure 3 The early formation of the continental core of Sundaland during Late Triassic (Hall 2014 based on Hall 2002 and Metcalfe 2011a)

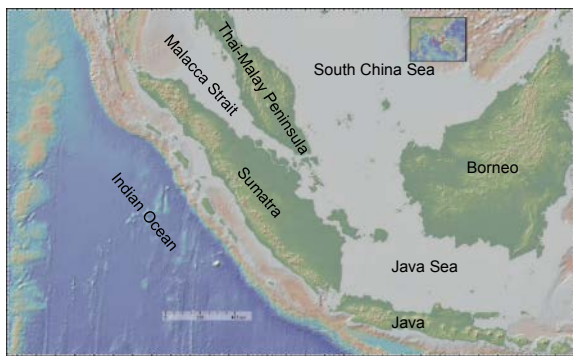


Figure 2 Sumatra Island, Indonesia (GeoMapApp 3.6.8)

I.3 Geography and geology of Sumatra Island

Sumatra island (Fig. 3), which is also known as *Swarnadwipa* (Island of Gold) and *Swarnabhumi* (Land of Gold) in ancient times, is one of the five largest islands in the today's Indonesian archipelago. It is also the sixth largest island in the world. Situated in the most western part of the Greater Sunda islands (0.589724 S 101.3431058 E), this island stretched approximately 473,481 km² (not including the adjacent islands) with the longest axis measuring 1,790 km and a maximum width of 435 km. Sumatra island (including adjacent islands) is currently divided into ten provinces with a population density of 1,199 persons/km² in 2015 (Badan Pusat Statistik 2018). Ten national parks and another 17 conservation areas are currently recorded in this island (KSDAE 2016).

As mentioned earlier, the Sumatra and Malay Peninsula landmasses were the first two landmasses in the Sunda region that were assembled during the early assemblage of Sundaland in the Late Paleozoic and the Triassic (Metcalfe 2011a-b). The Sumatra-Malay Peninsula landmasses were composed by three continental blocks (Fig. 4): the East Malaya block, the Sibumasu block (East Sumatra, Western Malay Peninsula, and Langkawi Island), and the West Sumatra blocks (Barber and Crow 2009). Sumatra itself was only composed by the last two blocks, in addition to Sikuleh and Natal Microcontinental blocks that were part of the Woyla nappe (Fig. 4; Barber and Crow 2009, Hall 2009, 2014). The contact zone between the Sibumasu and the West Sumatra crustal blocks are marked by a zone of highly deformed rocks including schists and gneisses known as MSTZ - the Medial Sumatra Tectonic Zone (Fig. 4). This zone runs the length of Sumatran from the Andaman Sea to Palembang by 1760 km (Hutchinson 1994, Barber 2005, Barber and Crow 2009).

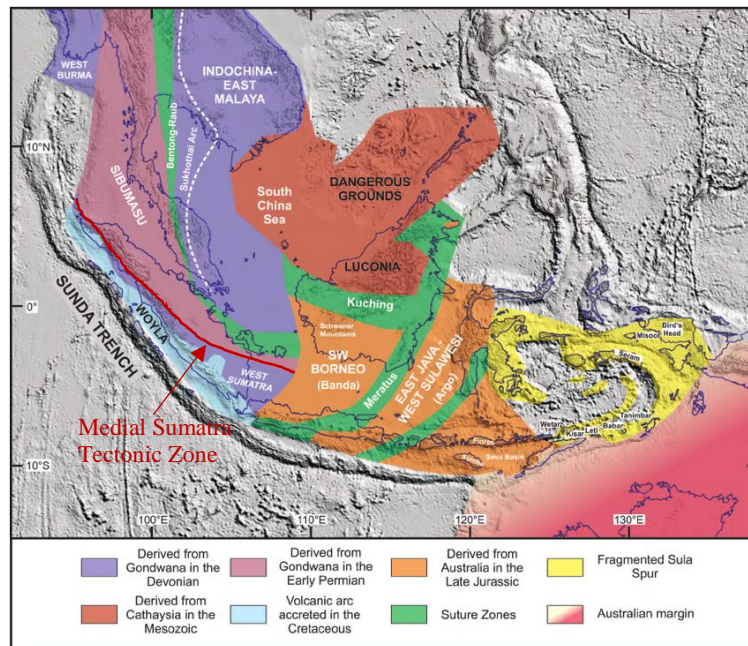


Figure 4 Continental tectonic blocks in Southeast Asia. Sumatra formed by three blocks: Sibumasu, West Sumatra, and Woyla terrain. Medial Sumatra Tectonic Zone is shown by red arrow. (Hall 2014 after Metcalfe 1996, 2011a–b and Barber et al. 2005).

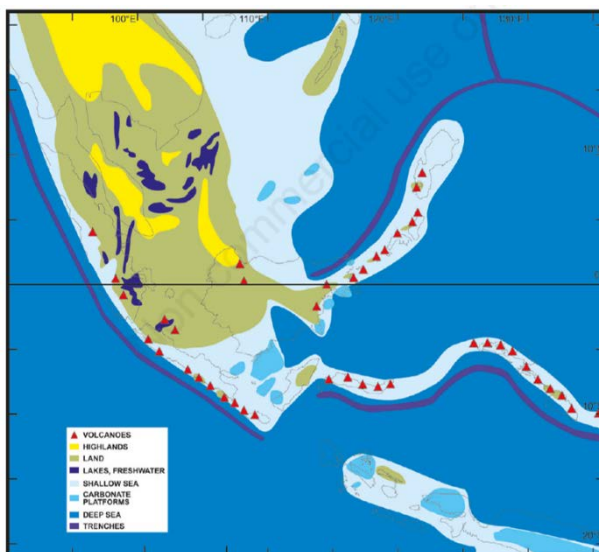


Figure 5 Map of Sundaland in Mid Oligocene. Much of Sundaland had a significantly lower topography than earlier in the Cenozoic, and large freshwater lakes that were not linked to the ocean existed (Hall 2013, Morley and Morley 2013)

The three Sumatran crustal blocks have been hypothesized to have been reorganized during the Mesozoic, most likely by strike-slip faulting at an active margin of this continent (Hall 2009). From the Jurassic onwards, portions of the present Sunda Shelf Islands, as far south as Sumatra were an emergent region. Major parts of this region were probably surrounded by subduction zones, implying that volcanoes and mountains were included in the margins (Hall 2014). Uninterrupted subduction from the Cretaceous into the Cenozoic was assumed in most

reconstructions of the Sunda region (Hall 2013). However, Hall (2013) suggested that there was almost no subduction beneath Sumatra, Java, and Borneo between 90–45 Ma (Late Cretaceous and Mid Eocene). The subduction around Sundaland was terminated at about 90 Ma (Hall 2013), which contributed to a widespread uplift of Sundaland marked by a major regional unconformity (Clements et al. 2011). Then, the subduction around the Sunda region continued at about 45 Ma (Mid Eocene), when Australia began to move north after having separated from Antarctica (Hall 2013). Hall (2013) suggested

that subduction initiation was associated with widespread changes on land and rifting at the Sundaland margins. By the Mid Oligocene, much of Sundaland had a significantly lower topography than earlier in the Cenozoic, and large freshwater lakes existed that were not linked to the ocean (Hall 2013, Morley and Morley 2013; Fig. 5).

Whitten et al. (2000) suggested that the Barisan mountain range (Fig. 3) began to be lifted and formed in the Early Paleocene. Hall (2012, 2013) suggested that between the Eocene and Early Miocene, there were volcanic arcs at the southern margin of Sundaland. Most of these volcanoes formed islands, not continuous nor extensive in area of land (Hall 2013). From the Mid Eocene, volcanic activity in Sumatra became extensive (Crow 2005, Hall 2012, 2013). In the Late Eocene, a possible Toba-scale caldera may have spread its volcanic ashes over the major part of Central Sumatra (Crow 2005, Hall 2012, 2013). Substantial subsidence took place in the Barisan range between the Oligocene and Miocene (Whitten et al 2000). Marine transgression due to regional subsidence has deepening and widening the marine basins in both the fore arc and back arc of Sumatra (Barber et al.2005). As a result, the volcanic Barisan Mountains became a chain of large islands south of the elevated Malay Peninsula (Barber et al. 2005, Hall 2013).

Since the Early Miocene global sea level fell (Hall 2012) and Southeast Asia experienced the wettest climate (Morley 2012). Hall (2012, 2013) suggested that from the Mid Miocene the Sumatran volcanic chain rose and widened due to volcanic activity and strike-slip faulting as well as an effect of region-wide Sundaland deformation after Australia collided with eastern part of Indonesia (Hall 2012, 2013). Furthermore, Hall (2012, 2013) studies demonstrated that the subduction-related deformation of the Indian Plate might also have contributed to the elevation of Sumatra and its fore arc. Consequently, several islands (e.g., Nias, Siberut) were probably temporarily connected to the Sumatran mainland because there was no deep basin between the fore arc high and the coast. Since then, Sumatra has progressively become the large island it is today (Hall 2012, 2013).

II The Paleo-drainage systems across Sundaland

In the Pleistocene, river systems drained sections of Sumatra across the Sunda and Sahul shelves. Voris (2000) proposed four major paleo-drainages systems in Sundaland (Fig. 6) that were later refined by Sathiyamurthi and Voris (2006). What follows are the four paleo-river systems (Fig. 6) that occur in Sumatra (and Java) with notes on their current river systems:

(1) The Malacca Strait River system. It comprises present-day major rivers in the northern part of Sumatra, e.g., Sungai Simpang Kanan, Sungai Panai, Sungai Rokan, Sungai Siak. They ran towards the Malacca Strait.

(2) The Siam River system. Sungai Kampar is the only one found in Sumatra today that was part of this ancient river system. Two hypothesis on where this river system ran have been

discussed: (i) it ran north through the Singapore Strait to join the Johor River, then run north over a large expanse of the Sunda Shelf to the Gulf of Thailand (e.g., Wyrski 1961, Verstappen 1975, Ollier 1985); (ii) it flowed south-east along the coast of Sumatra, then north to join the North Sunda River avoiding the Siam River system (e.g., Heaney 1991, Rainboth 1996).

(3) The North Sunda River system. Today's river known as part of this river system are: Sungai Indragiri, Sungai Kapuas, Sungai Batanghari, and Sungai Musi. This river system ran north from the north-east coast of Sumatra to join the Kapuas River from Borneo and then entered the sea north-east of Natuna Island.

(4) The East Sunda River system. This river system includes the present-day rivers of the north coast of Java and the northern portion of the east coast of Sumatra. It ran to the Java Sea. Another smaller river in south-east Sumatra and the Thousand Islands (Seribu Islands) flowed south through the Sunda Straits to enter the Indian Ocean (Umbgrove 1949, van Bemmelen 1949).

It is hypothesized that these vast river systems served as bridges for numerous faunal exchanges between the Greater Sunda Islands (e.g., Inger and Voris 2001, de Bruyn et al. 2013). Consequently, numerous freshwater riverine faunas inhabiting many of today's rivers that are at present restricted to Indo-China, the Malay Peninsula, or one of the Greater Sunda Islands were connected in the Pleistocene (Voris 2000; Sathiamurthy and Voris 2006).

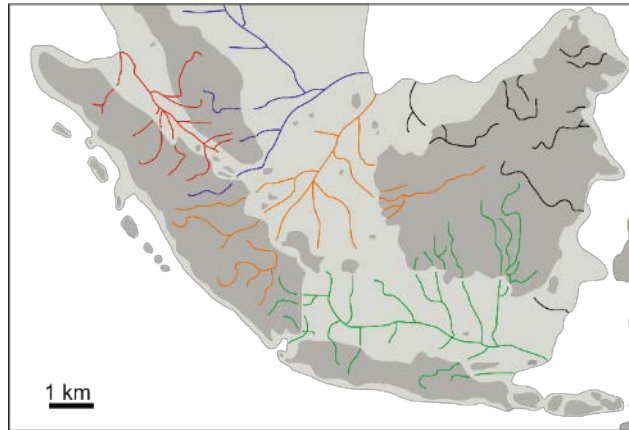


Figure 6 Map (120 m contour) of four major Paleodrainage systems in Southeast Asia: Malacca Strait River system (red), Siam River system (blue), North Sunda River system (orange), and East Sunda River system (green). Light grey is Shelf and dark grey is exposed landmasses. Redraw map from Voris (2000).

III Amphibian diversity and the Sumatran ranids with gastromyzophorous tadpoles

III.1 Amphibian diversity in Sundaland and Sumatra

The complex geological events of Sumatra and Sundaland that were described in the previous section greatly influenced the climate and vegetation in this region. Geological history very likely has significantly shaped the biodiversity of the region (Morley 2012). The formation of the Barisan mountain range (Fig. 3) that stretches along Sumatra's longitudinal axis, for instance, had profoundly shaped the topology of the island. A wide elevational gradient (up to 3,805 m a.s.l.) and tropical climate in this region have created various types of forest ecosystems on this island (Oshawa et al. 1985, Bihari and Lal 1989, Whitten et al. 2000). Numerous types of habitats and microhabitats are available for vertebrate and invertebrate species. Today, Sumatra harbours an extraordinary biodiversity including numerous endemic species (Myers et al. 2000; de Bruyn et al. 2014). This also hold true also for amphibians in particular.

To date, Frost (2018, accessed in November 2018) has recorded a total of 567 species of amphibians in Indonesia with 104 of which have been recorded from Sumatra (Table 2). This number is still underestimated since numerous new species have been described in only the last decade (e.g., Inger et al. 2009; McLeod et al. 2011; Hamidy and Kurniati 2015; Smart et al. 2017, Arifin et al. 2018). In general, the accumulation of amphibian species numbers in the Southeast Asian regions (including Sumatra) has significantly accelerated (Baker and Couvreur 2012). This number is predicted to steadily increase in the near future as more and more sampling efforts continue to be performed along with the utilization of more refined data (integrative approach; Dayrat 2005, Padijal et al. 2010).

The Ranidae, which is also known as true frogs, is one of the largest and most widespread families among frogs (Anura). Within the family of Ranidae, the genera *Abavorana*, *Amnirana*, *Chalcorana*, *Hylarana*, *Huia*, *Pulchrana*, *Odorrana*, and *Sumaterana* occur on Sumatra. Due to its unique topology, particularly along the Bukit Barisan mountain range, countless torrential habitats are available on this island. Thus, it can be expected that many species, particularly species with a high dependency on cascading stream habitats, such as species with gastromyzophorous tadpoles, would inhabit this type of tropical habitat. However, until this study was conducted, the only Sumatran ranid previously known to possess gastromyzophorous larvae was *Huia sumatrana* (Yang 1991, Manthey and Denzer 2014). Although another species of *Huia*

(*H. modigliani*) has been described from the island, its tadpoles remains unknown. Through my study, another Sumatran ranid with this type of tadpole (genus *Sumaterana*) has been recognized (described more detail in Chapter 2).

Table 2 List of amphibian species (N=104) that has been recorded from Sumatra and its adjacent islands (Frost 2018, accessed in November 2018). Star (*) indicated endemic to or only known from the island.

Family	Species
Bufonidae (9 genera, 19 species)	* <i>Ansonia glandulosa</i> Iskandar and Mumpuni, 2004
	<i>Ansonia leptopus</i> (Günther, 1872)
	<i>Duttaphrynus melanostictus</i> (Schneider, 1799)
	* <i>Duttaphrynus sumatranus</i> (Peters, 1871)
	* <i>Duttaphrynus totol</i> (Ohler, 2010)
	* <i>Duttaphrynus valhallae</i> (Meade-Waldo, 1909)
	<i>Ingerophrynus biporcatus</i> (Gravenhorst, 1829)
	* <i>Ingerophrynus claviger</i> (Peters, 1863)
	<i>Ingerophrynus divergens</i> (Peters, 1871)
	<i>Ingerophrynus parvus</i> (Boulenger, 1887)
	<i>Ingerophrynus quadriporcatus</i> (Boulenger, 1887)
	<i>Leptophryne borbonica</i> (Tschudi, 1838)
	<i>Pelophryne signata</i> (Boulenger, 1895)
	<i>Phrynoidis asper</i> (Gravenhorst, 1829)
	<i>Phrynoidis juxtasper</i> (Inger, 1964)
	<i>Pseudobufo subasper</i> Tschudi, 1838
	<i>Rentapia hosii</i> (Boulenger, 1892)
	* <i>Sigalegalephrynus mandailinguensis</i> Smart, Sarker, Arifin, Harvey, Sidik, Hamidy, Kurniawan, and Smith, 2017
	* <i>Sigalegalephrynus minangkabauensis</i> Smart, Sarker, Arifin, Harvey, Sidik, Hamidy, Kurniawan, and Smith, 2017
Dicroglossidae (3 genera, 10 species)	<i>Fejervarya cancrivora</i> (Gravenhorst, 1829)
	<i>Limnonectes blythii</i> (Boulenger, 1920)
	<i>Limnonectes khasianus</i> (Anderson, 1871)
	<i>Limnonectes macrodon</i> (Duméril and Bibron, 1841)
	<i>Limnonectes malesianus</i> (Kiew, 1984)
	* <i>Limnonectes sisikdagu</i> McLeod, Horner, Husted, Barley, and Iskandar, 2011
	<i>Limnonectes shompenorum</i> Das, 1996
	<i>Limnonectes tweediei</i> (Smith, 1935)
	<i>Occidozyga baluensis</i> (Boulenger, 1896)
	<i>Occidozyga sumatrana</i> (Peters, 1877)
Ichthyophiidae (1 genus, 6 species)	* <i>Ichthyophis billitonensis</i> Taylor, 1965
	* <i>Ichthyophis elongatus</i> Taylor, 1965
	<i>Ichthyophis nigroflavus</i> Taylor, 1960
	<i>Ichthyophis paucisulcus</i> Taylor, 1960
	* <i>Ichthyophis paucidentulus</i> Taylor, 1960
	* <i>Ichthyophis sumatranus</i> Taylor, 1960
Microhylidae (7 genera, 18 species)	<i>Glyphoglossus volzi</i> (Van Kampen, 1905)
	<i>Kaloula baleata</i> (Müller, 1836)
	<i>Kaloula pulchra</i> Gray, 1831
	<i>Kalophrynus minusculus</i> Iskandar, 1998
	<i>Kalophrynus pleurostigma</i> Tschudi, 1838
	<i>Leptobrachium hasseltii</i> Tschudi, 1838
	<i>Leptobrachium hendricksoni</i> Taylor, 1962
	* <i>Leptobrachium waysepuntiense</i> Hamidy and Matsui, 2010
	* <i>Megophrys lancip</i> Munir, Hamidy, Farajallah, and Smith, 2018
	<i>Megophrys montana</i> (Kuhl and Van Hasselt, 1822)
	<i>Megophrys nasuta</i> (Schlegel, 1858)
	* <i>Megophrys parallela</i> Inger and Iskandar, 2005
	<i>Microhyla berdmorei</i> (Blyth, 1856)
	<i>Microhyla heymonsi</i> Vogt, 1911
	<i>Microhyla palmipes</i> Boulenger, 1897
	<i>Microhyla superciliaris</i> Parker, 1928
<i>Micryletta inornata</i> (Boulenger, 1890)	

	<i>Phrynella pulchra</i> Boulenger, 1887
Ranidae (7 genera, 20 species)	<i>Amnirana nicobariensis</i> (Stoliczka, 1870)
	<i>Chalcorana chalconota</i> (Schlegel, 1837)
	* <i>Chalcorana parvaccola</i> (Inger, Stuart, and Iskandar, 2009)
	* <i>Chalcorana rufipes</i> (Inger, Stuart, and Iskandar, 2009)
	* <i>Huia modiglianii</i> (Doria, Salvidio, and Tavano, 1999)
	* <i>Huia sumatrana</i> Yang, 1991
	<i>Hylarana erythraea</i> (Schlegel, 1837)
	*" <i>Hylarana</i> " <i>persimilis</i> (Van Kampen, 1923)
	<i>Odorrana hosii</i> (Boulenger, 1891)
	<i>Pulchrana centropeninsularis</i> (Chan, Brown, Lim, Ahmad, and Grismer, 2014)
	<i>Pulchrana baramica</i> (Boettger, 1900)
	* <i>Pulchrana debussyi</i> (Van Kampen, 1910)
	* <i>Pulchrana fantastica</i> Arifin, Cahyadi, Smart, Jankowski, and Haas, 2018
	<i>Pulchrana glandulosa</i> (Boulenger, 1882)
	* <i>Pulchrana siberu</i> (Dring, McCarthy, and Whitten, 1990)
	<i>Pulchrana signata</i> (Günther, 1872)
	* <i>Pulchrana rawa</i> (Matsui, Mumpuni, and Hamidy, 2012)
	* <i>Sumaterana crassiovis</i> (Boulenger, 1920)
	* <i>Sumaterana dabulescens</i> Arifin, Smart, Hertwig, Smith, Iskandar, and Haas, 2018
	* <i>Sumaterana montana</i> Arifin, Smart, Hertwig, Smith, Iskandar, and Haas, 2018
Rhacophoridae (7 genera, 31 species)	* <i>Chiromantis baladika</i> Riyanto and Kurniati, 2014
	* <i>Chiromantis nauli</i> Riyanto and Kurniati, 2014
	<i>Kurixalus appendiculatus</i> (Günther, 1858)
	<i>Nyctixalus pictus</i> (Peters, 1871)
	* <i>Philautus amabilis</i> Wostl, Riyanto, Hamidy, Kurniawan, Smith, and Harvey, 2017
	* <i>Philautus cornutus</i> (Boulenger, 1920)
	<i>Philautus kerangae</i> Dring, 1987
	<i>Philautus larutensis</i> (Boulenger, 1900)
	* <i>Philautus polymorphus</i> Wostl, Riyanto, Hamidy, Kurniawan, Smith, and Harvey, 2017
	<i>Philautus refugii</i> Inger and Stuebing, 1996
	* <i>Philautus thamyridion</i> Wostl, Riyanto, Hamidy, Kurniawan, Smith, and Harvey, 2017
	* <i>Philautus ventrimaculatus</i> Wostl, Riyanto, Hamidy, Kurniawan, Smith, and Harvey, 2017
	<i>Polypedates colletti</i> (Boulenger, 1890)
	<i>Polypedates leucomystax</i> (Gravenhorst, 1829)
	<i>Polypedates macrotis</i> (Boulenger, 1891)
	<i>Polypedates pseudotilophus</i> Matsui, Hamidy, and Kuraishi, 2014
	* <i>Rhacophorus achantharrhena</i> Harvey, Pemberton, and Smith, 2002
	<i>Rhacophorus angulirostris</i> Ahl, 1927
	* <i>Rhacophorus barisani</i> Harvey, Pemberton, and Smith, 2002
	* <i>Rhacophorus bengkuensis</i> Streicher, Hamidy, Harvey, Anders, Shaney, Kurniawan, and Smith, 2014
	* <i>Rhacophorus bifasciatus</i> Van Kampen, 1923
	* <i>Rhacophorus catamitus</i> Harvey, Pemberton, and Smith, 2002
	* <i>Rhacophorus indonesiensis</i> Hamidy and Kurniati, 2015
	* <i>Rhacophorus modestus</i> Boulenger, 1920
	<i>Rhacophorus nigropalmatus</i> Boulenger, 1895
	<i>Rhacophorus norhayati</i> Chan and Grismer, 2010
	<i>Rhacophorus pardalis</i> Günther, 1858
	* <i>Rhacophorus poecilnotus</i> Boulenger, 1920
	* <i>Rhacophorus pseudacutirostris</i> Dehling, 2011
	<i>Theloderma asperum</i> (Boulenger, 1886)
	<i>Theloderma leporosum</i> Tschudi, 1838

II.2 Gastromyzophorous tadpoles

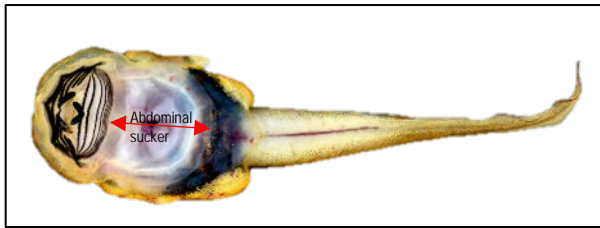


Figure 7 Morphology of the gastromyzophorous tadpole (ventral view, *Sumaterana crassiovis*, Lampung province).



Figure 8 Gastromyzophorous tadpole of *Sumaterana crassiovis* in its natural habitat (Aceh province).

In anuran larvae, the term “gastromyzophorous tadpole” (Fig.7) was introduced to delineate Bornean ranids tadpoles that inhabited cascading streams and have a gastric sucker apparatus (Inger 1966). The gastric sucker is an adaptation of tadpoles to cling to rocks in the current (Fig. 8) and can be used as a defining characteristics for an ecomorphological guild (Altig and Johnston 1989, McDiarmid and Altig 1999, Gan et al. 2015).

The body profile of a gastromyzophorous larva is streamlined with an extended sloping snout. With their adhesive abdominal sucker they hang

on to rocks even in fast-flowing, turbulent water of cascades (Fig.8, Nodzenski and Inger 1990, Gan et al. 2015). This sucker occupies large parts of the ventral surface of the body immediately posterior to the oral disk (Fig. 7). The sucker has raised thickened lateral and posterior rims that seal against the substrate. The oral disk is broadly expanded to almost full body width. Spots or bands of brown skin, composed of keratinized epithelium can be seen on the ventral surface of this sucker. This feature probably helps to enhance friction when the sucker engages with the rock surface (Inger 1985, Gan et al. 2015). The sucker and oral disk act together to press the body to the substrate through suction. The tadpoles use their strongly developed jaws to drag themselves forwards by losing the suction momentarily. While wandering over the rock surface, they scrap off the algae and other organic rock overgrowth using their jaws and keratodont rows of the oral disk (Inger 1966, Altig and Johnston 1898, Haas pers. comm.). This feeding behavior restricts taxa with gastromyzophorous larvae to certain habitats and microhabitats. In Borneo, for example, *Meristogenys* tadpoles typically live in clear rocky streams with considerable swiftness and adequate light reaching those rocks to form organic overgrowth for the tadpoles to graze on (Haas pers. comm.).

Among anurans, gastromyzophorous tadpoles are relatively rare. Only some Bufonids species (e.g., *Atelopus* Duméril and Bibron, 1841, *Rhinella* Fitzinger, 1826; Boistel et al.

2005, Matsui et al. 2007, Aguayo et al. 2009, Rueda-Solano 2015) and some Asian ranids (e.g. *Amolops* Cope, 1865, *Huia* Yang, 1991, *Meristogenys* Yang, 1991, *Rana sauteri* Boulenger, 1909, Kuramoto et al. 1984, Yang 1991, Malkmus et al. 2002, Ngo et al. 2006, Stuart 2008, Gan et al. 2015; and the recently described genus *Sumaterana* Arifin et al. 2018) have been known to possess this type of larvae. Gastromyzophorous tadpoles of *Rana sauteri* (Kuramoto et al. 1984) are significantly different in anatomy and biogeography compared to gastromyzophorous tadpoles of *Amolops*, *Huia*, *Meristogenys*, and *Sumaterana* (Kuramoto et al. 1984, Gan et al. 2015, Arifin et al. 2018). Gan et al. (2015) have summarized the morphological differences (particularly in the abdominal sucker and the musculus diaphragmatopraecordialis) between *R. sauteri* and other Asian gastromyzophorous tadpoles (*Amolops*, *Huia*, and *Meristogenys*). They concluded that the morphological evidence in combination with current phylogenetic hypotheses suggest a separate origins of gastromyzophorous tadpoles in *R. sauteri* and different adaptive scenarios.

III.3 Geographical distribution and species account

According to Frost (2018), the Asian anuran genera in the family Ranidae with gastromyzophorous tadpoles (*Amolops*, *Huia*, *Meristogenys*, and the recently described *Sumaterana*) are widely distributed in Asia, spanning from the Nepal-Himalayan region towards the eastern and southern part of Asia, with a total of 76 species recorded for the four genera. The adult frogs of this group were mainly recorded along swift rocky hillside or mountain streams in forested areas. They can easily be observed at night on rocks or vegetation in the vicinity of streams (Malkmus et al. 2002). Malkmus et al. (2002) also reported that eggs of *Meristogenys* are glued to rock surfaces to prevent them being washed away. Due to their dependency to cascading stream habitats, the term Cascade Frogs was occasionally used informally for frog species that lived in these habitat types. The term was applied, particularly, but not exclusively, to species of the Ranidae that possess gastromyzophorous tadpoles (see Bain et al. 2003, Stuart et al. 2005, Zhang et al. 2012). In this thesis, I will use and restrict the term Cascade Frogs to refer collectively to Asian frogs of the genera *Amolops*, *Huia*, *Meristogenys*, and *Sumaterana* (all Ranidae) that possess an abdominal sucker apparatus in their larval form.

Frost (2018) recorded 55 species of *Amolops*, which are widely distributed in the mainland of Asia, from Nepal and northern India, western and southern China to Peninsular Malaysia. *Meristogenys* is endemic to Borneo, with a total of 13 species recorded. Although the distribution range of *Meristogenys* is restricted to the island of Borneo, most of the species were mainly described and documented in the Malaysian

part of Borneo (e.g., Inger and Stuebing 2009, Matsui et al. 2010, Shimada et al. 2011). The Indonesian part (Kalimantan) has been less explored to date. The genus *Huia* has been documented in Thailand, Sumatra, Java, and Borneo (Frost 2018). Surprisingly, *Huia* has the lowest number of species (five species; Frost 2018) compared to the other Cascade Frogs genera, despite its vast geographical range. Through broad sampling in my study, *Huia* is indicated to be more diverse than it is currently known (see Chapter 4). The fourth genus of the Cascade Frogs, *Sumaterana*, was recognized for the first time through this study (see Chapter 2, Arifin et al. 2018). This genus is endemic to Sumatra and Arifin et al. (2018) presented evidence that newly discovered gastromyzophorous tadpoles belonged to this taxon. The genus currently comprises three species.

III.4 Taxonomy and systematics of the Cascade Frogs

The taxonomic and systematic status of the Cascade Frogs has been controversial for quite some time. After its original description by Cope (1865), the genus *Amolops* was distinguished from *Staurois* and others genera by the possession of gastromyzophorous larvae (Inger 1966) and the presence of poisonous glands on dorsal and ventral regions of the tadpoles (Yang 1991). Based on larvae and adult morphology, Yang (1991) split this group of frogs into three genera: *Amolops* (at that time 20 species, type species - *A. afghanus*), *Huia* (4 species, type species - *H. cavitympanum*), and *Meristogenys* (8 species, type species - *M. jerboa*). Since then, the number of species has been increasing and various changes in the taxonomic arrangement of the Cascade Frogs have been proposed, including the addition of the fourth genus *Sumaterana* that was delimited through my study. For more details on the taxonomic history see Frost 2018).

Yet, the proposed hypotheses did not solidify the position of the Cascade Frogs in phylogenetic systematic. The genus *Amolops*, despite its astonishing similarity in larval morphology, was suggested to be more closely related to other ranids that do not possess gastromyzophorous tadpoles, than to *Huia*, *Meristogenys*, and *Sumaterana* (Stuart 2008, Wiens et al. 2009, Kurabayashi et al. 2010, Pyron and Wiens 2011, Arifin et al. 2018). Furthermore, among the four recognized genera, the phylogenetic position of *Huia* in particular seemed very problematic. Until recently, this genus appears as paraphylum in phylogenetic analyses whereas the clade of *Amolops*, *Meristogenys*, and *Sumaterana*, respectively, form solid monophyletic groups. The type species of *Huia* (*H. cavitympanum*) is a sister taxon of the clade of Bornean endemic *Meristogenys*, and not to other species in the genus *Huia* (Stuart 2008, Wiens et al. 2009, Pyron and Wiens 2011, Arifin et al. 2018). Previous to my investigation (Arifin et al. 2018), other studies

only included one sample for each *Huia* species in their analysis (except none for *H. modiglianii*), which is clearly insufficient and inadequate with respect to the wide geographical range of this genus (the Malay Peninsula, Sumatra, Java, and Borneo). *Huia modiglianii*, the second species of *Huia* on Sumatra, only known from the type locality (Si Rambe) and Bantjan Batu in the north of Lake Toba (Doria et al. 1999). The position of this species is also questionable as it has never been included in any molecular analyses and its original description seems ambiguous (Manthey and Denzer 2014). Apart from the *Huia* problem, the genera *Huia*, *Meristogenys*, and *Sumaterana* were not forming a monophyletic group, as one would have been expected from their highly similar gastromyzophorous tadpoles. *Clinotarsus*, which does not possess gastromyzophorous tadpoles (e.g., Grosjean et al 2003, Grosjean et al. 2015), was nested within this assemblage in various phylogenetic analyses (Fig. 9; Stuart 2008, Wiens et al. 2009, Pyron and Wiens 2011).

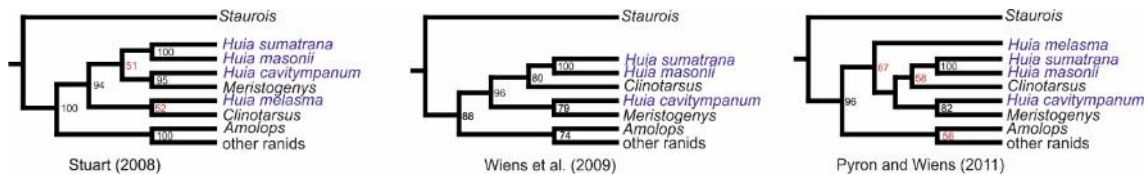


Figure 9 Simplified phylogenetic trees (Maximum Likelihood tree with bootstrap values; red represent low support value following Hillis and Bull 1993) from several studies shows that ranid frogs of the genus *Huia* (in blue) is a paraphyletic group within the family Ranidae.

IV Integrative taxonomy

Taxonomy, the science of characterizing, classifying, and naming taxa, is a fundamental discipline in exploring and understanding biodiversity on earth. Thus, a proper species delimitation is significantly essential to build hypotheses on assigning specimens to particular species (Schlick-Steiner et al. 2010), especially in the biodiversity hotspot regions. These areas (e.g., Sumatra, Madagascar, Amazon) are very rich in species diversity and endemics, but its diversity is still underestimated (see previous section). Countless species (e.g., amphibians) tend to exhibit cryptic or morphologically similar species (Bossuyt and Milinkovitch 2002, Bickford et al. 2007). As consequence, many of these species were often misidentified and treated as single species (Bain et al. 2003, Stuart et al. 2006, Funk et al. 2012). In addition, many studies (e.g., Stuart et al. 2006, Arifin et al. 2018) showed that a lack of dense geographic sampling and a lack of molecular data are the main problems in revealing biodiversity in these hotspot areas.

Biodiversity inventories (thorough and broad sampling) is a very critical step in elucidating true diversity in the tropics. However, delimiting species based on only morphological characters is significantly inadequate and can be misleading in identifying taxa with similar morphology that were previously known as a single species (Stuart et al. 2006). The necessity of finding another sources of evidence (integrative taxonomy; Padial et al. 2010, Schlick-Steiner et al. 2010), such as molecular genetics, bioacoustics, ecology, distribution, shall be considered (Stuart et al. 2006) as cross-validation of criteria to delineate species from others (Schlick-Steiner et al. 2010).

Integrative taxonomy was introduced to refer to taxonomic approaches that integrates all available data sources to delimit species (Padial et al. 2010, Schlick-Steiner et al. 2010, Yeates et al. 2011). Although molecular approaches is a powerful methodology to solve various phylogenetic problems, including species delimitation (e.g., Del-Prado et al. 2010, Yang and Rannala 2010, Fujita et al. 2011), species will be better delimited if we know what caused their origin and determined their evolutionary trajectories (Padial et al. 2010). Thus, a consensus from the combination of molecular data and morphology as well as other evidence, such as bioacoustics, ecology, behavior, geographical distribution, is recommended to accurately and convincingly validated the identity of certain species in taxonomy (Padial et al. 2010, Schlick-Steiner et al. 2010). In my study, I employed integrative taxonomy approaches to delimit new ranid frogs from Sumatra (see Chapter 2 and 3).

V Objectives and outline of the thesis

In this thesis, I assess the systematics and diversity of the Sumatran Cascade Frogs. Then, I evaluate the correlation between species distribution patterns in Sumatra with the occurrence of the Pleistocene river systems in this island. The Sumatran Cascade Frogs are very suitable for such a study because they have specialized larvae (gastromyzophorous tadpoles) that are highly dependent on torrential stream habitats and distributed widely in the island. Spatially dense and thorough sampling was conducted across the longitudinal axis of Sumatra, and molecular approaches as well as the integrative taxonomy approaches were employed in this study.

This thesis is divided into five chapters to answer my research questions. Chapter 1 gives a general introduction on the background of this study, such as the complex geological history of Sumatra and Sundaland, as well as the paleo-drainage systems during the Pleistocene in the region. An introduction on the amphibian diversity in this region, particularly the Sumatran frogs of the family Ranidae with gastromyzophorous

tadpoles is also given in this chapter. Chapter 2–4 covers the core objectives of this study that were:

- (1) to conduct thorough and dense amphibian sampling in Sumatra that shows the importance of this approach with the application of integrative taxonomy to reveal diversity and solve phylogenetic problem of difficult taxa,
- (2) to assess and describe the diversity of Sumatran frogs, within the family Ranidae, particularly one with gastromyzophorous tadpoles, and
- (3) to unravel diversification pattern of the Sumatran frogs and its main potential drivers in correlation with the occurrence of paleo-drainage system in Sumatra during Pleistocene.

In Chapter 2–3, I present the new discovered taxa from the island of Sumatra. Despite rich in amphibian diversity, Sumatran amphibian diversity is still poorly understood to date. The main problems have been the lack of thorough sampling across the region and lack of molecular data (see “Taxonomy and systematics of the Cascade Frogs”). My study (Chapter 2) shows that integrative taxonomy methods (Padial et al. 2010) and thorough sampling successfully revealed new ranid taxa with gastromyzophorous tadpoles. Larval forms are as important as adult morphology in solving phylogenetic controversies. Chapter 3 is another example of newly discovered taxa in Sumatra. Both discoveries suggest that true amphibian diversity in Sumatra is still underestimated. In Chapter 4, the role of the Pleistocene paleo-drainages system in Sumatra for species diversification is addressed. At the same time this analysis shows that the genus *Huia* contains more diversity than previously known. The two genera of the Sumatran Cascade Frogs (*Sumaterana* and *Huia*) were analyzed biogeographically because their larvae are highly dependent on cascading stream habitats potentially restricting their dispersal potential. Furthermore, these taxa are distributed widely on the island of Sumatra. It has been hypothesized in other organisms that the ancient Sundaland paleo-drainage system played a significant role in diversification and I performed analyses to test that for the frogs in question.

The last chapter of this thesis (Chapter 5) provides a general discussion on amphibian diversity and distribution on Sumatra and possible scenarios for their diversification process.

References

- Aguayo R, Lavilla EO, Candiotti VMF, Camacho T (2009) Living in fast-flowing water: morphology of the gastromyzophorous tadpole of the bufonid *Rhinella quechua* (R. veraguensis Group). *Journal of Morphology* 270: 1431–1442. <https://doi.org/10.1002/jmor.10768>
- Altig R (2006) Discussions of the origin and evolution of the oral apparatus of anuran tadpoles. *Acta Herpetologica* 1(2): 95–105.
- Altig R, Johnston GF (1989) Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetological Monographs* 3(1989): 81–109. <https://doi.org/10.2307/1466987>
- Arifin U, Smart U, Hertwig ST, Smith EN, Iskandar DT, Haas A (2018) Molecular phylogenetic analysis of a taxonomically unstable ranid from Sumatra, Indonesia, reveals a new genus with gastromyzophorous tadpoles and two new species. *Zoosystematics and Evolution*, 94, 163–193.
- Bain RH, Lathrop A, Murphy RW, Orlov NL, Cuc HT (2003) Cryptic species of a cascade frog from Southeast Asia: taxonomic revisions and descriptions of six new species. *American Museum Novitates* 1–60.
- Baker WJ, Couvreur TLP (2012) Biogeography and distribution patterns of Southeast Asian palms. *Biotic evolution and environmental change in Southeast Asia* (82): 164–190.
- Barber AJ, Crow MJ (2009) Structure of Sumatra and its implications for the tectonic assembly of Southeast Asia and the destruction of Paleotethys. *Island Arc*, 18(1), 3–20.
- Barber AJ, Crow MJ, Milsom J (Eds 2005) *Sumatra: geology, resources and tectonic evolution*. Geological Society of London.
- Ben-Avraham Z, Emery KO (1973) Structural framework of Sunda shelf. *AAPG Bulletin*, 57(12), 2323–2366.
- Bickford DP, Lohman DJ, Sodhi NS, Ng PKL, Meier R, Winker K, Ingram KK, Das I (2007) Cryptic species as a window on diversity and conservation. *Trends Ecology and Evolution* 22: 148–155. doi:10.1016/j.tree.2006.11.004
- Bihari M, Lal CB (1989) Species composition, density and basal cover of tropical rainforests of central Sumatra. *Tropical Ecology* 30(1): 118–137.
- Boistel R, Grosjean S, Lötters S (2005) Tadpole of *Atelopus franciscus* from French Guyana, with comments on other larvae of the genus (Anura: Bufonidae). *Journal of Herpetology* 39(1): 148–153. [https://doi.org/10.1670/0022-1511\(2005\)039\[0147:TOAFFF\]2.0.CO;2](https://doi.org/10.1670/0022-1511(2005)039[0147:TOAFFF]2.0.CO;2)
- Bossuyt F, Milinkovitch M (2002) Convergent adaptive radiations in Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. *PNAS* 97: 6585–6590. <https://doi.org/10.1073/pnas.97.12.6585>
- Boulenger GA (1909) Descriptions of four new frogs and a new snake discovered by Mr. H. Sauter in Formosa. *Annals and Magazine of Natural History Series* 8 4: 492–495. <https://doi.org/10.1080/00222930908692704>
- Clements B, Burgess PM, Hall R, Cottam MA (2011) Subsidence and uplift by slab-related mantle dynamics: a driving mechanism for the Late Cretaceous and Cenozoic

- evolution of continental SE Asia?. Geological Society, London, Special Publications, 355(1), 37–51.
- Conservation International (2018) Biodiversity hotspots regions. (Accessed on November 2018)
- Cope ED (1865) Sketch of the primary groups of Batrachia s. Salientia. Natural History Review. New Series 5: 97–120.
- Dayrat B (2005) Towards integrative taxonomy. Biological journal of the Linnean society, 85(3), 407–417.
- De Bruyn M, Rüber L, Nylinder S, Stelbrink B, Lovejoy NR, Lavoué S, Tan HH, Nugroho E, Wowor D, Ng PKL, Siti Azizah MN, Rintelen TV, Hall R, Carvalho G (2013). Paleo-drainage basin connectivity predicts evolutionary relationships across three Southeast Asian biodiversity hotspots. Systematic Biology, 62(3), 398–410.
- De Bruyn M, Stelbrink B, Morley RJ, Hall R, Carvalho GR, Cannon CH, van den Bergh G, Meijaard E, Metcalfe I, Boitani L, Maiorano L (2014) Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity. Systematic Biology 63(6): 879–901.
- Del-Prado R, Cubas P, Lumbsch HT, Divakar PK, Blanco O, de Paz GA, Molina MC, Crespo A (2010) Genetic distances within and among species in monophyletic lineages of Parmeliaceae (Ascomycota) as a tool for taxon delimitation. Molecular Phylogenetics and Evolution, 56(1), 125–133.
- Doria D, Salvido S, Tavano ML (1999) Description of *Amolops (Huia) modiglianii*, new species from Sumatra (Amphibia, Anura, Ranidae). Annali del Museo Civico di Storia Naturele “G. Doria”. VII, 317.
- Duméril AMC, G Bibron (1841) Erpétologie Générale ou Histoire Naturelle Complète des Reptiles. Volume 8. Paris: Librairie Encyclopedique de Roret.
- Fitzinger LJJ (1826) Neue Classification der Reptilien nach ihren Natürlichen Verwandtschaften nebst einer Verwandtschafts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des K. K. Zoologisch Museum’s zu Wien. Wien: J. G. Heubner.
- Frost DR (2018). Amphibian Species of the World: an Online Reference. Version 6.0 (Accessed on November 2018). Electronic Database accessible at <http://research.amnh.org/herpetology/amphibia/index.html>. American Museum of Natural History, New York, USA.
- Fujita MK, Leaché AD, Burbrink FT, McGuire JA, Moritz C (2012) Coalescent-based species delimitation in an integrative taxonomy. Trends in ecology & evolution, 27(9), 480–488.
- Funk WC, Caminer M, Ron SR (2012) High levels of cryptic species diversity uncovered in Amazonian frogs. Proceeding of the Royal Society Biology, 279(1734), 1806–1814.
- Gan L, Hertwig ST, Das I, Haas A (2015) The anatomy and structural connectivity of the abdominal sucker in the tadpoles of *Huia cavitympanum*, with comparisons to *Meristogenys jerboa* (Lissamphibia: Anura: Ranidae). Journal of Zoological Systematics and Evolutionary Research 54(1): 1–14.
- Grosjean S, Perez M, Ohler A (2003) Morphology and buccopharyngeal anatomy of the tadpole of *Rana (Nasirana) alticola* (Anura: Ranidae). Raffles Bulletin of Zoology, 51(1), 101–107.

- Grosjean S, Bordoloi S, Chuaynkern Y, Chakravarty P, Ohler A (2015) When young are more conspicuous than adults: a new ranid species (Anura: Ranidae) revealed by its tadpole. *Zootaxa*, 4058(4), 471–498.
- Hall R (2009) Southeast Asia's changing palaeogeography. *Blumea-Biodiversity, Evolution and Biogeography of Plants*, 54(1-2), 148–161.
- Hall R (2013) The palaeogeography of Sundaland and Wallacea since the Late Jurassic. *Journal of Limnology*, 72(s2), 1.
- Hall R (2014) The origin of Sundaland. *Proceeding of Sundaland Resources*. Palembang, South Sumatra, 17–18.
- Hamidy A, Kurniati H (2015) A new species of tree frog genus *Rhacophorus* from Sumatra, Indonesia (Amphibia, Anura). *Zootaxa* 3947(1): 049–066. <https://doi.org/10.11646/zootaxa.3947.1.3>
- Hamilton WB (1979) Tectonics of the Indonesian region (No. 1078). US Govt. Print. Off.
- Hutchison CS (1994) Gondwana and Cathaysian blocks, Palaeozoic Sutures and Cenozoic Tectonics in Southeast Asia, *Geologische Rundschau*, v. 82, 388-405.
- Heaney LR (1991) A synopsis of climatic and vegetational change in Southeast Asia. In *Tropical Forests and Climate* (pp. 53–61). Springer, Dordrecht.
- Inger RF (1966) The systematics and zoogeography of the Amphibia of Borneo. *Fieldiana Zoology* 52: 1–402.
- Inger RF (1985) Tadpoles of the forested regions of Borneo. *Fieldiana* 26: 1–89.
- Inger RF, Voris HK (2001) The biogeographical relations of the frogs and snakes of Sundaland. *Journal of Biogeography*, 28(7), 863-891.
- Inger RF, Stuebing RB (2009) New species and new records of Bornean frogs (Amphibia: Anura). *The Raffles Bulletin of Zoology* 57(2): 527–535.
- Inger RF, Stuart BL, Iskandar DT (2009) Systematics of a widespread Southeast Asian frog, *Rana chalconota* (Amphibia: Anura: Ranidae). *Zoological Journal of Linnean Society* 155(1): 123–147. <https://doi.org/10.1111/j.1096-3642.2008.00440.x>
- Kurabayashi A, Yoshikawa N, Sato N, Hayashi Y, Oumi S, Fujii T, Sumida M (2010) Complete mitochondrial DNA sequence of the endangered frog *Odorrana ishikawae* (family Ranidae) and unexpected diversity of mt gene arrangements in ranids. *Molecular Phylogenetics and Evolution* 56(2): 543–553.
- Kuramoto M, Wang CS, Yü HT (1984) Breeding, larval morphology and experimental hybridization of Taiwanese Brown Frogs, *Rana longicrus* and *R. sauteri*. *Journal of Herpetology* 18(4): 387–395. <https://doi.org/10.2307/1564101>
- Manthey U, Denzer W (2014) Südostasiatische Anuren im Fokus Spezies der Gattung *Huia* (sensu lato) Yang, 1991 (Amphibia: Anura: Ranidae). *Sauria* 36(4): 31–48.
- Malkmus R, Manthey U, Vogel G, Hoffmann P, Kosuch J (2002) Amphibians and Reptiles of Mount Kinabalu (North Borneo). A. R. G. Gantner K G, Koeltz Scientific Books, Koenigstein.
- Matsui M, Yambun P, Sudin A (2007) Taxonomic relationships of *Ansonia anotis* (Inger, Tan and Yambun 2001) and *Pedostibes maculatus* (Mocquard 1890), with a description of a new genus (Amphibia, Bufonidae). *Zoological Science* 24: 1159–1166. <https://doi.org/10.2108/zsj.24.1159>

- Matsui M, Shimada T, Sudin A (2010) A New Species of *Meristogenys* (Amphibia, Anura, Ranidae) from Sabah, Borneo. *Zoological Science* 27: 61–66. <https://doi.org/10.2108/zsj.27.61>
- McDiarmid RW, Altig A (1999) Tadpole: The Biology of Anuran Larvae (pp. 453). The University of Chicago Press.
- Mcleod DS, Horner SJ, Husted C, Barley A, Iskandar D (2011) Same-same, but different”: an unusual new species of the *Limnonectes kuhlii* complex from West Sumatra (Anura: Dicroglossidae). *Zootaxa* 2883(1): 52–64.
- Metcalfe I (2011a) Palaeozoic–Mesozoic history of SE Asia. Geological Society, London, Special Publications, 355(1), 7–35.
- Metcalfe I (2011b) Tectonic framework and Phanerozoic evolution of Sundaland. *Gondwana Research*, 19(1), 3–21.
- Mittermeier RA, Turner WR, Larsen FW, Brooks TM, & Gascon C (2011) Global biodiversity conservation: the critical role of hotspots. In *Biodiversity hotspots* (pp. 3–22). Springer, Berlin, Heidelberg.
- Morley RJ (2012) A review of the Cenozoic palaeoclimate history of Southeast Asia. *Biotic evolution and environmental change in Southeast Asia*, 79–114.
- Morley RJ, Morley HP (2013) Mid Cenozoic freshwater wetlands of the Sunda region. *Journal of Limnology*, 72(s2), 2.
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403(6772): 853.
- Ngo A, Murphy RW, Liu W, Lathrop A, Orlov NL (2006) The phylogenetic relationships of the Chinese and Vietnamese waterfall frogs of the genus *Amolops*. *Amphibia-reptilia* 27(1): 81–92.
- Nodzenski E, Inger RF (1990) Uncoupling of related structural changes in metamorphosing torrent-dwelling tadpoles. *Copeia* 1990(4): 1047–1054. <https://doi.org/10.2307/1446488>
- Ohsawa M, Nainggolan PHJ, Tanaka N, Anwar C (1985) Altitudinal zonation of forest vegetation on Mount Kerinci, Sumatra: with comparisons to zonation in the temperate region of east Asia. *Journal of Tropical Ecology* 1(3): 193–216.
- Ollier CD (1985) The geological background to prehistory in island Southeast Asia. *Modern Quaternary Research South East Asia*, 9, 25–42.
- Padial JM, Miralles A, De la Riva I, Vences M (2010) The integrative future of taxonomy. *Frontiers in Zoology* 7(16): 1–14. <https://doi.org/10.1186/1742-9994-7-16>.
- Parkinson CD, Miyazaki K, Wakita K, Barber AJ, Carswell DA (1998) An overview and tectonic synthesis of the pre-Tertiary very-high-pressure metamorphic and associated rocks of Java, Sulawesi and Kalimantan, Indonesia. *Island Arc*, 7(1-2), 184–200.
- Pfenninger, M., & Schwenk, K. (2007). Cryptic animal species are homogeneously distributed among taxa and biogeographical regions. *BMC Evolutionary Biology*, 7(1), 121.
- Pyron A, Wiens JJ (2011) A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians.

- Molecular Phylogenetics and Evolution 61(2): 543–583.
<https://doi.org/10.1016/j.ympev.2011.06.012>
- Rainboth WJ (1996) Fishes of the Cambodian Mekong. Food & Agriculture Org..
- Rueda-Solano LA, Vargas-Salinas F, Rivera-Correa M (2015) The highland tadpole of the harlequin frog *Atelopus carrikeri* (Anura: Bufonidae) with an analysis of its microhabitat preferences. *Salamandra* 51: 25–32.
- Sathiamurthy E, Voris HK (2006) Maps of Holocene sea level transgression and submerged lakes on the Sunda Shelf. *Tropical Natural History*, (2), 1–44.
- Schlick-Steiner BC, Steiner FM, Seifert B, Stauffer C, Christian E, Crozier RH (2010) Integrative taxonomy: a multisource approach to exploring biodiversity. *Annual Review of Entomology* 55: 421–438.
- Shimada T, Matsui M, Yambun P, Sudin A (2011) A taxonomic study of Whitehead's torrent frog, *Meristogenys whiteheadi*, with descriptions of two new species (Amphibia: Ranidae). *Zoological Journal of Linnean Society* 161: 157–183.
<https://doi.org/10.1111/j.1096-3642.2010.00641.x>
- Sloan S, Jenkins CN, Joppa LN, Gaveau DL, Laurance WF (2014) Remaining natural vegetation in the global biodiversity hotspots. *Biological Conservation*, 177, 12–24.
- Smart U, Sarker GC, Arifin U, Harvey MB, Sidik I, Hamidy A, Kurniawan N, Smith EN (2017) A new genus and two new species of arboreal toads from the highlands of Sumatra with a phylogeny of Sundaland toad genera. *Herpetologica* 73: 63–75.
<https://doi.org/10.1655/Herpetologica-D-16-00041>.
- Stuart BL, Orlov NL, Chan-ard T (2005) A new cascade frog (Amphibia: Ranidae) from Laos and Vietnam. *Raffles Bulletin Zoology* 53(1): 125–131.
- Stuart BL, Inger RF, Voris HK (2006) High level of cryptic species diversity revealed by sympatric lineages of Southeast Asian forest frogs. *Biology letters*, 2(3), 470–474.
- Stuart BL (2008) The phylogenetic problem of *Huia* (Amphibia: Ranidae). *Molecular Phylogenetic and Evolution* 46(1): 49–60.
<https://doi.org/10.1016/j.ympev.2007.09.016>
- Umbgrove JHF (1949) Structural history of the East Indies. CUP Archive.
- van Bemmelen RW (1949) The geology of Indonesia. 1, A. General geology of Indonesia and adjacent archipelagoes. US Government Printing Office.
- Verstappen HT (1975) On palaeo-climates and landform development in Malaysia. *Modern Quaternary Research in Southeast Asia*.
- Voris HK (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography*, 27(5), 1153–1167.
- Whitten T (2000) The Ecology of Sumatra, vol. 1. Periplus Edition, Jakarta, Indonesia.
- Wiens JJ, Sukumaran J, Pyron RA, Brown RM (2009) Evolutionary and biogeographic origins of high tropical diversity in Old World frogs (Ranidae). *Evolution: International Journal of Organic Evolution* 63(5): 1217–1231.
- Wyrki K (1961) Physical oceanography of the Southeast Asian waters.

- Yang DT (1991) Phylogenetic systematics of the *Amolops* group of ranid frogs of southeastern Asia and the Greater Sunda Islands. *Fieldiana: Zoology New Series* 63: 1–42. <https://doi.org/10.5962/bhl.title.2854>
- Yang Z, Rannala B (2010) Bayesian species delimitation using multilocus sequence data. *Proceedings of the National Academy of Sciences*, 200913022.
- Yeates DK, Seago A, Nelson L, Cameron SL, Joseph LEO, Trueman JW (2011) Integrative taxonomy, or iterative taxonomy?. *Systematic Entomology* 36(2): 209–217.
- Zhang S, Guo H, Shi F, Wang H, Li L, Jiao X, Wang Y, Yu H (2012) Hainanenins: a novel family of antimicrobial peptides with strong activity from Hainan cascade-frog, *Amolops hainanensis*. *Peptides* 33(2): 251–257.

CHAPTER 2

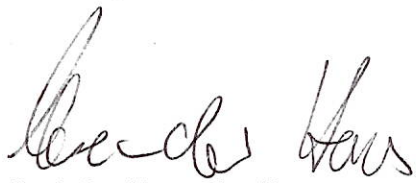
Molecular phylogenetic analysis of a taxonomically unstable ranid from Sumatra, Indonesia, reveals a new genus with gastromyzophorous tadpoles and two new species

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Author contribution

I hereby confirm that Umilaela Arifin conceived, designed, analyzed the data, and wrote the paper.

Hamburg, 04.12.2018

A handwritten signature in black ink, appearing to read 'Alexander Haas', written in a cursive style.

Prof. Dr. Alexander Haas



Molecular phylogenetic analysis of a taxonomically unstable ranid from Sumatra, Indonesia, reveals a new genus with gastromyzophorous tadpoles and two new species

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Abstract

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Key Words

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Huia

Meristogenys

Morfologi

Molekular sistematik

Keanekaragaman spesies

Taksonomi

The presence of an adhesive abdominal sucker (gastromyzophory) allows tadpoles of certain species of anurans to live in fast-flowing streams. Gastromyzophorous tadpoles are rare among anurans, known only in certain American bufonids and Asian ranids. To date, *Huia sumatrana*, which inhabits cascading streams, has been the only Sumatran ranid known to possess gastromyzophorous tadpoles. In the absence of thorough sampling and molecular barcoding of adults and larvae, it has remained to be confirmed whether other Sumatran ranid species living in similar habitats, i.e., *Chalcorana crassiovis*, possesses this larval type. Moreover, the taxonomic status of this species has long been uncertain and its taxonomic position within the Ranidae, previously based exclusively on morphological characters, has remained unresolved. To study the diversity and relationships of these frogs and to establish the identity of newly collected gastromyzophorous tadpoles from Sumatra, we compared genetic sequences of *C. crassiovis*-like taxa from a wide range of sites on Sumatra. We conducted bayesian and maximum likelihood phylogenetic analyses on a concatenated dataset of mitochondrial (12S rRNA, 16S rRNA, and tRNA^{Met}) and nuclear (RAG1 and TYR) gene fragments. Our analyses recovered *C. crassiovis* to be related to *Clinotarsus*, *Huia*, and *Meristogenys*. The DNA barcodes of the gastromyzophorous tadpoles matched adults from the same sites. Herein, we provide a re-description of adult *C. crassiovis* and propose “*C. kampeni*” as a synonym of this species. The molecular evidence, morphological features, and distribution suggest the presence of two related new species. The two new species and *C. crassiovis* together represent a distinct phylogenetic clade possessing unique molecular and morphological synapomorphies, thus warranting a new genus.

Abstrak

Pada beberapa jenis katak tertentu yang hidup di sungai berarus deras, di bagian abdomen berudunya terdapat semacam alat perekat sebagai mekanisme adaptasi pada kondisi habitat tempat tinggalnya. Tipe berudu seperti ini dikenal dengan nama *gastromyzophorous* dan sangat jarang ditemukan, hanya diketahui pada beberapa jenis bufonid di Amerika dan katak ranid di Asia. Hingga saat ini, hanya *Huia sumatrana*, dengan habitat sungai berarus deras, yang diketahui memiliki tipe berudu seperti ini di Sumatra. Tanpa survey menyeluruh dan tanpa *DNA barcoding* untuk katak dewasa dan kecebong, dugaan men-

genai keberadaan katak jenis lain dengan tipe berudu serupa di pulau ini, misalnya *Chalcorana crassiovis*, masih harus dibuktikan. Di sisi lain, status taksonomi jenis ini hingga kini masih belum dapat dipastikan, dan posisi taksonominya dalam famili Ranidae hanya berdasarkan karakter morfologi saja. Oleh karena itu, untuk mengetahui keanekaragaman dan hubungan kekerabatan dari katak-katak jenis tersebut, serta untuk memastikan identitas koleksi berudu *gastromyzophorous* dari Sumatra, kami membandingkan data genetik dari semua taxa yang mirip dengan *C. crassiovis* dari berbagai lokasi di Sumatra. Kami merekonstruksi pohon filogeni dengan menganalisis sekuens DNA dari gabungan fragmen gen mitokondria (12S rRNA, 16S rRNA, dan tRNA^{val}) dan gen inti (RAG1 dan TYR) menggunakan metode Bayesian dan Maximum Likelihood. Hasil penelitian kami membuktikan bahwa *C. crassiovis* berkerabat dekat dengan *Clinotarsus*, *Huia*, dan *Meristogenys*. Sekuens DNA dari berudu *gastromyzophorous* memiliki kecocokan dengan sekuens DNA katak dewasa dari lokasi yang sama. Dalam paper ini, kami menyajikan deskripsi ulang untuk *C. crassiovis* dan menyarankan agar "*C. kampeni*" menjadi junior synonym dari *C. crassiovis*. Bukti molekuler, karakter morfologi, dan kisaran distribusi menunjukkan bahwa terdapat dua jenis baru yang berkerabat dengan *C. crassiovis*. Ketiganya menunjukkan perbedaan filogenetik yang signifikan, yang dibuktikan dengan adanya synapomorphy pada karakter molekuler dan morfologi yang unik. Oleh sebab itu dibentuk genus baru untuk ketiga jenis ini.

Introduction

A fascinating aspect of Southeast Asian ranid frogs is that some of them possess tadpoles with large abdominal suckers. The presence of this adhesive structure has been referred to as gastromyzophory (Inger 1966). Altig and Johnston (1989) described gastromyzophorous tadpoles as an ecomorphological guild. These tadpoles are adapted to live in fast-flowing streams (McDiarmid and Altig 1999, Altig 2006). Their body profile is streamlined with an extended sloping snout. Their adhesive abdominal sucker allows them to cling to rocks even in the fast-flowing, turbulent water of cascades (Nodzinski and Inger 1990, Gan et al. 2015). The abdominal sucker occupies almost the entire ventral surface of the body immediately posterior to the oral disk; both act together to press the body to the substrate through suction. The sucker has raised thickened lateral and posterior rims that seal against the substrate; the oral disk itself is broadly expanded to almost full body width. On the ventral surface of this sucker, there are spots or bands of brown skin, i.e., keratinized epithelium, probably enhancing friction when the sucker engages with the rock surface (Inger 1985, Gan et al. 2015). The tadpoles are able to loosen the suction momentarily to drag themselves forward by action of their strongly developed jaws; algae and other organic rock overgrowth is scraped off by the jaws and keratodont rows of the oral disk while wandering over the rock surface (Inger 1966, AH pers. observ.). According to our field observations on Bornean *Meristogenys* tadpoles (AH unpubl.), this feeding mode restricts taxa with gastromyzophorous tadpoles to certain habitats and microhabitats: clear rocky streams with considerable water velocity and enough light reaching those rocks to form organic overgrowth for the tadpoles to graze on.

Members of the gastromyzophorous tadpole guild are relatively rare among anurans. They are known only in certain bufonids (e.g., Rao and Yang 1994, Boistel et al. 2005, Matsui et al. 2007, Aguayo et al. 2009, Rueda-Solano et al. 2015) and some Asian ranids: species of *Amolops* Cope, 1865, *Huia* Yang, 1991, *Meristogenys* Yang, 1991, and *Rana sauteri* Boulenger, 1909 (Kuramoto et al. 1984, Yang 1991, Malkmus et al. 2002, Matsui et al. 2006, Ngo et al. 2006, Shimada et al. 2007, Stuart 2008, Gan et al. 2015).

In Asia, *Amolops*, *Huia*, and *Meristogenys* are all genera for which the tadpoles are known to have the gastromyzophorous type (Inger 1966, Yang 1991, Shimada et al. 2015): a total of 69 species are currently listed for these genera (Frost 2017). All adult frogs of this group were mainly recorded along swift rocky hill or mountain streams in forested areas. These frogs usually like to perch themselves on rocks or vegetation in the vicinity of streams. In case of *Meristogenys*, it has been reported that eggs are glued to rock surfaces to keep them from being washed away (Malkmus et al. 2002). In Sumatra, this aforementioned habitat for ranid species with gastromyzophorous tadpoles is very abundant due to the mountainous topography, which stretches longitudinally along the island. To date, *Huia sumatrana* Yang, 1991 has been the only Sumatran ranid positively known to possess gastromyzophorous tadpoles (Yang 1991, Manthey and Denzer 2014). The tadpoles of *H. modigliani* (Doria, Salvidio & Tavano, 1999), a species also recorded from Sumatra, remain unknown. In an extensive field effort, we focused on sampling riverine ranids from fast-flowing or torrential streams. We suspected that there might be species, other than *H. sumatrana*, that inhabit torrential stream habitats in Sumatra and also possess gastromyzophorous larvae. In fact, one of us had found unidentified gastromyzophorous tadpoles in Su-

matra in previous fieldwork (DI unpubl.). It has been known that particularly *Odorrana hosii* (Boulenger, 1891), *Chalcorana crassiovis* (Boulenger, 1920), and/or *C. kampeni* (Boulenger, 1920), are Sumatran ranid species that occur in rocky, fast flowing streams, along with *H. sumatrana*. Potentially, as inferred from the preferred habitat of adults, these taxa could all be candidates for possessing gastromyzophorous tadpoles. The tadpoles of *O. hosii*, however, show that such habitats offer various microhabitats options. The tadpole of *O. hosii* have no abdominal sucker and live in relatively quiet, leaf litter filled side-pools (Inger 1966, Grossmann and Manthey 1997, AH pers. observ.). In case of *C. crassiovis* and/or *C. kampeni*, no information regarding tadpoles is hitherto available and the possibility of a gastromyzophorous tadpoles has remained unverified until now.

Chalcorana crassiovis (Boulenger, 1920) was originally described as *Rana crassiovis* Boulenger, 1920 based on two specimens (BMNH 1947.2.3.99 and BMNH 1947.2.4.1) collected from Kerinci, Sumatra, Indonesia at ~1219 m (4,000 ft.) a.s.l. In the same publication describing *C. crassiovis*, Boulenger (1920) also re-described *Rana pantherina* van Kampen, 1910 as *R. kampeni*. The short original description of *R. pantherina* by van Kampen (1910) included a figure of one specimen. Boulenger (1920) based his description of *C. kampeni* on a specimen (ZMA unregistered number) collected at Bandar Baru, Batak Mts., Kabupaten (=Regency) Dili Serdang, Provinsi (=Province) Sumatera Utara at ± 900 m a.s.l. Van Kampen (1923) later recorded another population of *C. kampeni* from Serepai and Sungai Kring in Kerinci. Van Tujil (1995) declared the holotype of *C. kampeni* as lost.

Inger and Iskandar (2005) were the first to report on a large series of *Chalcorana crassiovis* from along the banks of Batang Tarusan, Provinsi Sumatera Barat and provide a re-description of *C. crassiovis* on the basis of these samples. The original description of *C. kampeni* was very similar to that of *C. crassiovis* leading Inger and Iskandar (2005) to doubt the validity of *C. kampeni* and to conclude that it may be conspecific with *C. crassiovis*. Inger and Iskandar (2005) considered the larger tympanum of *C. kampeni* only a sexual dimorphism within *C. crassiovis*; judging by its small reported size (36.5 mm, van Kampen 1910), the *C. kampeni* type specimen was probably a male. Despite the conclusion of Inger and Iskandar (2005), the two taxa have not been synonymized and some authors have maintained the name *C. kampeni* and applied it to all known populations previously referred to as *Rana kampeni* (e.g., Frost et al. 2006, Che et al. 2007, Oliver et al. 2015).

To date, no studies have included *Chalcorana crassiovis* (or *C. kampeni*) in a molecular phylogenetic context, and few have included Sumatran congeners (Inger et al. 2009, Pyron and Wiens 2011, Oliver et al. 2015, Chan and Brown 2017). Sound phylogenetic hypotheses based on robust sampling of the *Chalcorana* group remain to be proposed. This is significant given the ensuing debates over the relationships among the Asian Ranidae in recent decades. After its original description by Bou-

lenger (1920) as *Rana crassiovis*, this species has been placed in various genera (i.e., *Hydrophylax* (Frost et al. 2006), *Hylarana* (Che et al. 2007), and *Chalcorana* (Oliver et al. 2015)) on the basis of secondary taxonomic implications from analyses of other, putatively related taxa (Frost 2017). This past history of various placements clearly shows that *C. crassiovis* needs to be analyzed in a larger phylogenetic context amongst ranids. Phylogenetic analyses of new data have the potential to significantly contribute to the ongoing discussion and ultimately lead to more stable taxonomic amendments.

Considering the confusing and unstable taxonomic history of *Chalcorana crassiovis* and its relatives, it became clear that a thorough resampling and molecular analysis of cascade-dwelling frogs of Sumatra was necessary. Herein, we present our analyses of newly sampled material of *C. crassiovis*. The objectives of this study were: 1) to examine the phylogenetic relationships and taxonomic status of *C. crassiovis* and morphologically similar taxa based on new molecular data; 2) to evaluate the phylogenetic position and taxonomy of material topotypic with *C. kampeni*; 3) to assess material from extensive sampling along the longitudinal axis of Sumatra in an effort to elucidate the diversity and distribution of this group of frogs; 4) to assign samples of collected gastromyzophorous tadpoles to specific species based on molecular evidence.

Materials and methods

Sampling strategy

We conducted rapid biological sampling (Ribeiro-Junior et al. 2008) at sites across Sumatra between 2013–2016. All specimens examined were collected during these sampling activities, and additional specimens were collected during 2008 and 2012 (Fig. 1). Rapid sampling entails visiting many sites but with limited time at each site in order to gather as much data as possible from as many sites as possible. This approach is cost effective and indispensable for sampling potentially cryptic species (Ribeiro-Junior et al. 2008). We collected frogs that were morphologically similar to *Chalcorana crassiovis* at their torrential stream habitats along with any gastromyzophorous tadpoles found in the same streams. The sampling included specimens from the reported type locality of the enigmatic taxon *C. kampeni*. Its type locality, when originally described as *Rana pantherina* van Kampen, 1910 was Bandar Baru, a village in the Kabupaten Deli Serdang, Provinsi Sumatera Utara. We collected stream frogs that are morphologically similar to *C. crassiovis* from the hillside streams of Bandar Baru and consider our materials (Appendix 1) topotypic to the original types of *C. kampeni*. The type locality of *C. crassiovis* is “Korinchi, Sumatra, 4,000 feet” (Boulenger 1920). Today, the modern spelling, “Kerinci” is applied to Mt. Kerinci as well as the Kabupaten Kerinci area; the original description does not provide hints as to where exactly the type specimens were collected from within that area. We visited Mt. Ker-

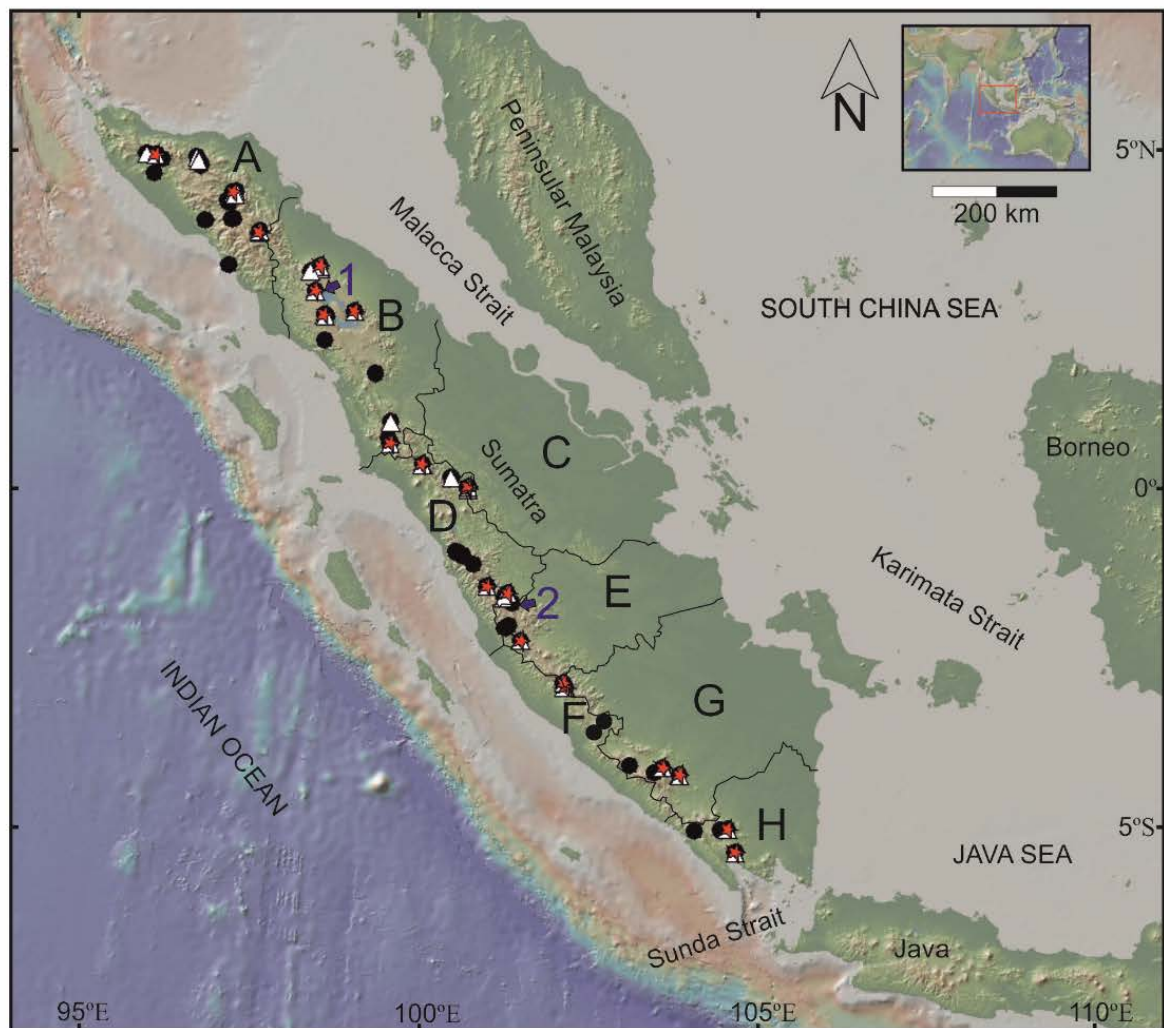


Figure 1. Sampling localities of adult and larva of *Chalcorana crassiovis* specimens for this study. Black circles represent localities of specimens which were examined. White triangles represent localities of specimens which were examined and measured. Red stars represent localities of specimens which were examined, measured, and sequenced. Type locality of *C. kampeni* shown by number 1 (Bandar Baru), number 2 (Kerinci) for *C. crassiovis*. Provinces are shown by alphabet: A Aceh, B Sumatera Utara, C Riau, D Sumatera Barat, E Jambi, F Bengkulu, G Sumatera Selatan, H Lampung. Borders between provinces are represented by black lines. The map was prepared using GeoMapApp (Ryan et al. 2009).

inci but could not find frogs of the group in question, so our nearest samplings were approximately 10 km north and northeast of Mt. Kerinci and several localities were still within the Kabupaten Kerinci area (Appendix 1).

We followed the general legal guidelines of Germany (Tierschutzgesetz, <https://www.gesetze-im-internet.de/tierschg/BJNR012770972.html>) for handling and euthanizing the specimens. Each frog was anesthetized slowly and ultimately euthanized in an aqueous solution of chlorobutanol. Tissue samples of muscle or liver tissue were preserved in either ethanol (96%), RNA later (Sigma Aldrich, USA) or Lysis buffer (0.5 M Tris / 0.25% EDTA / 2.5% SDS, pH 8.2) for DNA analyses. Specimens were fixed in 4% neutral-buffered formalin and then transferred to 70% ethanol for long term storage. All specimens examined in

this study are deposited at one of these following museum: The Natural History Museum (BMNH), London, United Kingdom; the Museum Zoologicum Bogoriense (MZB), Bogor, Indonesia; the Zoologisches Museum Hamburg (ZMH), Hamburg, Germany; the Museum of the University of Texas Arlington (UTA), Arlington, USA; and the Museum of Vertebrate Zoology (MVZ), Berkeley, USA.

In order to uncover the true diversity of *Chalcorana crassiovis*, we acquired DNA sequences from tissue samples of adults ($n = 20$) from 19 localities across Sumatra. We selected the 20 specimens after a preliminary assessment of the qualitative morphological features of all specimens ($n = 329$) that were examined. Additionally, we included a subsample of four Sumatran gastromyzophorous tadpoles in the genetic analysis for identification. We

followed the results of previously published studies (Yang 1991, Frost et al. 2006, Oliver et al. 2015) to select potentially related species to compose a diverse and sufficiently comprehensive ingroup in order to test the phylogenetic relationships of our *C. crassiovis* samples. *Staurois* was chosen as the outgroup taxon (Pyron and Wiens 2011). We selected sequence data of *C. chalconota* (Schlegel, 1837), *C. megalonesa* (Inger, Stuart & Iskandar, 2009), *Hydrophylax malabaricus* (Tschudi, 1838), *Hydr. leptoglossa* (Cope, 1868), *Hylarana erythraea* (Schlegel, 1837), *Hyl. macrodactyla* Günther, 1858, *Clinotarsus alticola* (Boulenger, 1882), *Cli. penelope* Grosjean, Bordoloi, Chuaynkern, Chakravarty & Ohler, 2015, and *Staurois guttatus* (Günther, 1858), particularly to serve as generic representatives. We applied the name *Cli. penelope* for one sample that was originally loaned under the name *Cli. alticola* (FMNH 268338), because it was identical with available sequences (16S) of *Cli. penelope* (Genbank accession numbers KR827723 [MNHN 2000.4633] and KR827724 [MNHN 930P]; Grosjean et al. 2015).

We added DNA sequences of *Amolops afghanus* (Günther, 1858), *A. indoburmanensis* Dever, Fuiten, Konu & Wilkinson, 2012, *A. marmoratus* (Blyth, 1855), *A. panhai* Matsui & Nabhitabhata, 2006, *Huia sumatrana* Yang, 1991, *H. cavitympanum* (Boulenger, 1893), *H. masonii* (Boulenger, 1884), *H. melasma* Stuart & Chan-ard, 2005, *Meristogenys jerboa* (Günther, 1872) and *M. kinabaluensis* (Inger, 1966) because these taxa have reliably recognizable gastromyzophorous larvae. Finally, we included *Odorrana hosii* (Boulenger, 1891) and *O. livida* (Blyth, 1856) as additional species. *Odorrana hosii* lives syntopically in the same streams with *C. crassiovis*. Sequences of *M. jerboa*, *C. megalonesa*, *Hyl. macrodactyla*, *Hydr. malabaricus*, *Hydr. leptoglossa*, and *O. livida* were obtained from Genbank. The remaining ingroup sequences were generated by this project. The list of voucher specimens ($n = 46$) comprising the genetic data set is provided in Suppl. material 1.

Laboratory protocols

We extracted DNA from tissue samples (liver, muscle) using Crystal DNA mini Kit (Biolab), PeqGOLD Tissue Kit (Peqlab), or Qiagen DNeasy Blood and Tissue Kit. We then amplified mitochondrial genes (12S rRNA, 16S rRNA, and tRNA^{val}) and nuclear genes (recombination-activating gene 1, RAG1, tyrosinase exon 1, TYR) for all frog samples. For tadpoles, we sequenced the 12S rRNA and 16S rRNA (which include tRNA^{val}) genes as barcode tool to associate them with adults. Primer information and PCR annealing temperatures applied for this study are provided in Table 1. We cleaned the PCR products using ExoSAP-ITTM and let a contractor (Macrogen, LGC, or Microsynth) sequenced the purified forward and reverse strands. We used GENEIOUS v 8.0 (Kearse et al. 2012, Biomatters Inc., www.geneious.com) to check sequence quality of both strands by comparison to their respective chromatograms, and to assemble and edit if necessary. Furthermore, we aligned sequences for each

gene loci using MAFFT v7.017 (Katoh and Standley 2013, module implemented in GENEIOUS v 8.0) with default setting. We eliminated poorly aligned positions and divergent regions of an alignment of each DNA loci using GBLOCK 0.91b (Castresana 2000, Talavera and Castresana 2007) which included in the online software <http://www.phylogeny.fr> (Dereeper et al. 2008), with setting for a less stringent selection (allows smaller final block and allows gap positions within the final block).

Phylogenetic analyses

We ran PARTITION FINDER v.1.1 (Lanfear et al. 2012) on our concatenated dataset using Bayesian Information Criterion (BIC) to find the best models by testing a variety of models and partitioning strategies for each loci. Four partitions were proposed by the analysis: 12S rRNA, 16S rRNA, and tRNA^{val}: GTR+I+G; RAG1 codon 1, RAG1 codon 2, and TYR codon 1: HKY+I; RAG1 codon 3: HKY+G; TYR codon 3: K80+G. We then employed Maximum Likelihood (ML) and Bayesian Inference (BI) to infer phylogenetic trees. To explore partitions, we constructed trees using individual loci, concatenated sequences for mitochondrial loci only, concatenated sequences for nuclear loci only, and concatenated sequences for combined mitochondrial and nuclear loci; the later was used for optimal tree reconstruction (Kluge 1989, 2004). ML tree search included 1000 bootstrap replicates in RAXML v. 8 (Stamatakis 2014) and was performed using the CIPRES Science Gateway V 3.3 (Miller et al. 2010, www.phylo.org/sub.sections/portal/), with default parameters. We also used the CIPRES Science Gateway to find optimal phylogenetic trees with MR. BAYES v 3.2.6 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003) in two independent runs, each with four chains, and running for 50 million generations with sampling every 1000 generations. Convergence was assessed by examining all parameters and the effective sample sizes in TRACER v.1.6 (Rambaut et al. 2014) after discarding the first 25% of samples as burn in. We viewed trees that resulted from RAXML and MR. BAYES in FIGTREE v.1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>) and prepared the tree in Fig. 2 using CORELDRAW X6. Nodal support with Bootstrap values (BS) ≥ 70 for ML tree (Hillis and Bull 1993) and Posterior Probability value (PP) ≥ 0.95 for Bayesian analyses (Huelsenbeck and Ronquist 2001) are herein considered as strong support (Huelsenbeck and Ranala 2004, Mulcahy et al. 2011). We also calculated genetic *p*-distances using MEGA 7.0.25 (Kumar et al. 2016) from 16S ribosomal subunit.

Adult and tadpole morphology

We measured a total of 175 adult *Chalcorana crassiovis* group frogs (males = 133, females = 42). These represent a subsample of all specimens examined ($n = 329$, Appendix 1). Measurements were taken with digital calipers with 0.01 mm reading accuracy. The subsample of 175 specimens included the sequenced specimens (except for MVZ271526, tissue only). Measurements were taken by UA, following current standards for morphological mea-

Table 1. Gene markers, primer sequences, annealing temperatures and sequence length information.

Markers	Sequence	Annealing temp (°C)	Length (bps)	Citation
12S	12SZ-L: AAAGGTTTGGTCTAGCCTT 12SK-H: TCCRGTAIRCCTACCDTGTTACGA	52	825	Goebel et al. (1999)
16S+ tRNA ^{val}	12sm: GGCAAGTCGTAACATGGTAAG 16sd: CTCGGTCTGAACTCAGATCACGTAG	51	1406	Pauly et al. (2004), Oliver et al. (2015)
RAG1	Rag1 1F: GCMTTGTSCCRGGGTATCA Rag1 2R: TCAATGGACGGAAGGGTTTCAATAA	50	801	Oliver et al. (2015)
TYR	Tyr1A: AGGTCCTCTTRAGCAAGGAATG Tyr1G: TGCTGGGCRTCTCTCCARTCCA	57	579	Oliver et al. (2015)

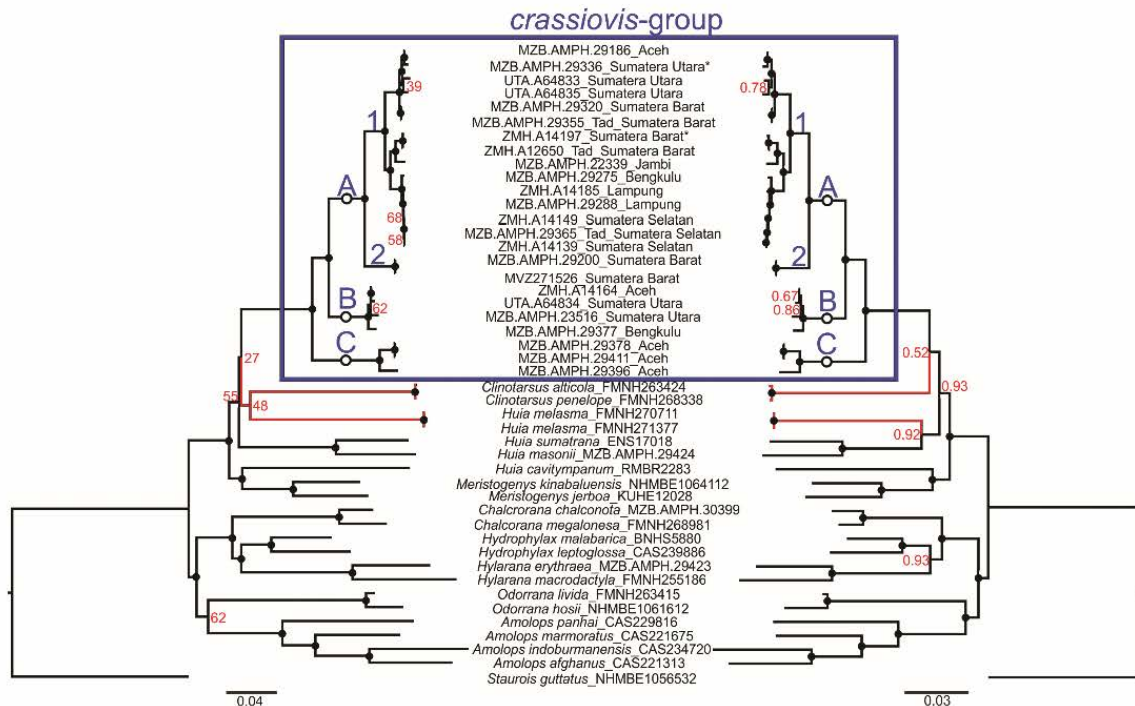


Figure 2. Bayesian (on the right) and Maximum Likelihood (on the left) trees showing the phylogenetic relationship of the *crassiovis*-group. A, B, C are distinct lineages within *crassiovis*-group. Black circles represent well supported nodes (PP ≥ 0.95 and BS ≥ 70). Red branches represent relationship between *Clinotarsus* and *Huia melasma*. Tadpole sequences named with specimen number_Tad_locality (province). Adult sequences named with specimen number_locality (province). MZB.AMPH.29336 and ZMH.A14197 were collected from the type locality of *C. kampeni* and *C. crassiovis*, respectively.

measurements of frogs (e.g., Matsui et al. 2010, Shimada et al. 2011, Waser et al. 2016, and Watters et al. 2016). All acronyms and definitions of measured distances are explained in Table 2 and illustrated in Suppl. material 2A. We determined sex by the presence of nuptial pads and vocal sacs in males, and their absence and presence of eggs, respectively, in females. We analyzed sexes separately to control for bias resulting from sexual dimorphism.

We collected tadpoles from rocks in fast flowing water using a fishnet and followed the procedures suggested in Haas and Das (2011). We preserved tail tissues of the photographed specimens in either 96% ethanol or RNAlater. We fixed and stored the remaining specimens from the series in neutral-buffered formalin solution (4%). We staged the tadpoles (n = 29) according to the table in Gosner (1960). The range of Gosner stages was 25–42, with the majority

of specimens at Stage 25 (n = 12). We assigned the 25 tadpoles that were not sequenced to the respective clade of the genetically examined tadpoles based on their morphological similarity. Standard measurements for tadpoles (Altig 2007, Shimada et al. 2007, Haas and Das 2011, Oberhummer et al. 2014) were taken from digital images with a calibrated digital microscope VHX5000 KEYENCE Corporation, Japan (Table 3 and Suppl. material 2B) by UA. We slightly edited all images in this study using Adobe PHOTOSHOP CS6 (contrast adjustment, background, cleanup, cropping, sharpening). We prepared image plates with CORELDRAW X6.

We followed the morphological terminology of Duellman (2001) and Kok and Kalamandeen (2008). For webbing we used the formula in Guayasamin et al. (2006). We adopted the suggestions for glands cluster definitions from Shimada et al. (2015).

Table 2. Standard measurement for adult specimens used in this study. See Suppl. materials 2A for illustration.

Acronym	Characters	Explanation
SVL	Snout Vent Length	From tip of snout to vent
HL	Head Length	From tip of snout to angle of jaw
HW	Head Width	Maximum width of the head at angle of jaw
SL	Snout Length	From tip of snout to the anterior corner of eye
SN	Snout Narial distance	From tip of snout to center of nares
ED	Eye Diameter	Maximum distance between anterior and posterior corners of eye
EN	Eye Narial distance	From center of naris to anterior circumference of eye
IND	Internarial Distance	Distance between centers of nares
IOD	Interorbital Distance	Minimum distance between upper eyelids
UEW	Upper Eyelid Width	Maximum transverse width of upper eyelid
TYv	vertical Tympanum diameter	Maximum vertical diameter, from the outer edges of tympanic annulus
TYh	horizontal Tympanum diameter	Maximum horizontal diameter, from the outer edges of tympanic annulus
ET	Eye-Tympanum distance	From posterior corner of eye to the anterior edge of tympanum
LAL	Lower Arm Length	From the tip of the elbow to the proximal edge of the palmar tubercle
HAL	Hand Length	From the proximal edge of the palmar tubercle to the tip of Finger III
FE	Femur Length	From center of vent to lateral of knee
TL	Tibia Length	Distance between anterior point of knee and posterior surface of heel with both tibia and tarsus flexed
FL	Foot Length	From proximal end of inner metatarsal tubercle to tip of Toe IV
IMTL	Inner Metatarsal Tubercle Length	Maximum distance between anterior and posterior tip of inner metatarsal tubercle
F1L	Finger I Length	From the proximal edge of subarticular tubercle of Finger I to the tip of Finger I
F2L	Finger II Length	From the proximal edge of subarticular tubercle of Finger II to the tip of Finger II
F3DW	Finger III Disc Width	Maximum width of Finger III disc
T4DW	Toe IV Disc Width	Maximum width of Toe IV disc

Table 3. Standard measurement for tadpole specimens used in this study. See Suppl. materials 2B for illustration.

Acronym	Character	Explanation
BL	Body Length	From snout to the point where the axis of the tail (horizontal septum of myotomes) meets the body wall
BH	Body Height	Maximum body height at trunk
BW	Body Width	Maximum body width
EN	Eye Narial distance	From center of eye to the center of naris
ED	Eye Diameter	Diameter of eye measured horizontally
ES	Eye Snout distance	From tip of snout to the anterior circumference of the eye
IND	Inter Narial Distance	Distance between center of nares
IOD	Inter Orbital Distance	Minimum distance between eyeballs
LFH	Lower Fin Height	Measured at point of maximum tail height
MTH	Maximum Tail Height	Measured from the maximum point of upper fin to the maximum point of lower fin
NL	Narial Length	Maximum aperture of narial opening in dorsal view
ODW	Oral Disc Width	Maximum width of oral disc
SN	Snout Narial distance	From snout to the center of naris
SS	Snout Spiracle distance	From snout to end of spiracle tube
SUL	Sucker Length	From anterior end to posterior end of abdominal sucker
SUW	Sucker Width	Maximum width of abdominal sucker
SSL	Snout and Sucker Length	From the tip of snout and to posterior end of abdominal sucker
TTL	Total Length	From tip of snout to tip of the tail
TAL	Tail Length	Calculated as: Total Length (TTL) – Body Length (BL)
TMH	Tail Muscle Height	Maximum tail muscle height at body-tail junction
TMW	Tail Muscle Width	Maximum tail muscle width at body-tail junction
UFH	Upper Fin Height	Measured at point of maximum tail height

Results and discussion

Phylogenetic analyses and morphology

We inferred optimal phylogenetic trees from our concatenated dataset (3611 bps) comprising all gene markers (12S rRNA+16S rRNA+tRNA^{val}+RAG1+TYR), of which 12.16% gaps and undetermined characters state. The best log likelihood of ML tree was -25426.240268.

The tree topologies recovered from ML and BI, respectively, were identical, except for the arrangement of *Clinotarsus* and *Huia melasma* (Fig. 2). Our BI tree (Fig. 2 right) suggested *Clinotarsus* to be sister taxon of the *Chalcorana crassiovis* group and *H. melasma* to be the sister taxon of *H. sumatrana*+*H. masonii*. In the ML tree (Fig. 2 left), however, *Clinotarsus*+*H. melasma* and the *C. crassiovis* group were sister taxa. Based on a dataset of two nuclear markers (RAG1+TYR) and lacking *C. crassiovis*, Stuart (2008) suggested *Clinotarsus*+*H. melasma* to be the sister taxon of a clade comprising other *Huia* species from Sumatra, Java, and Borneo, and *Meristogenys*. In contrast, based on a larger dataset, Pyron and Wiens (2011) identified *Clinotarsus* as sister taxon to *H. sumatrana*+*H. masonii*, whereas *H. melasma* was sister taxon to all other species in a clade comprising *Huia*+*Meristogenys*+*Clinotarsus*. However, all of these scenarios for the arrangement of *Clinotarsus* and *H. melasma* within ranid phylogeny had low nodal support. Consequently, we prefer not to draw any phylogenetic conclusions or recommend taxonomic amendments concerning *Clinotarsus* or *H. melasma*.

With the exception of the incongruence in the position of *Clinotarsus* and *Huia melasma*, both the ML and BI trees confirmed the existence of two major clades each with strong nodal support (Fig. 2): *crassiovis*-group+*Huia*+*Meristogenys*+*Clinotarsus* (PP = 1; BS = 100) and *Amolops*+*Odorrana*+*Hylarana*+*Hydrophylax*+*Chalcorana* (PP = 0.97; BS = 75). This result strongly suggests that *C. crassiovis* is not the closest relative of either *C. chalconota* (generotype) or *C. megalonesa*. DNA barcoding (12S rRNA+16S rRNA+tRNA^{val} genes) successfully matched samples of gastromyzophorous tadpoles to adult in the *crassiovis*-group.

Our results further corroborate previous studies (Stuart 2008, Pyron and Wiens 2011) in that the genus *Huia* is paraphyletic in its current composition. Yet, our phylogenetic trees were different from these previous studies concerning other genera. For example, our trees suggest *Odorrana* to be more closely related to *Amolops* (PP = 0.98, BS = 62, Fig. 2) than to *Chalcorana*+*Hylarana*+*Hydrophylax*. Stuart (2008) and Pyron and Wiens (2011) presented evidence that *Odorrana* was as closely related to some *Rana* or *Lithobates*, embedded in a more inclusive assemblage (including, among others, *Chalcorana*, *Hylarana*, and *Hydrophylax*, in current generic assignment). To corroborate that was beyond the scope of our analysis and, thus, we did not include samples of *Rana* and *Lithobates*.

Within the clade of the *crassiovis*-group (Fig. 2), unexpected genetic diversity was revealed along the Sumatran transect. Our phylogenetic tree showed three distinct, well supported clades within our samples that previously would have been all be assigned to *Chalcorana crassiovis*, i.e., Clade A, Clade B, and Clade C (PP = 1, BS = 100). These three clades showed high genetic divergence among each other (Clade A–B: 6.61–8.53%, Clade A–C: 7.46–9.59%, and Clade B–C: 7.74–8.74%, respectively, Suppl. materials 3). Clade A comprises frogs from northern part of Provinsi Aceh to the southern part of Provinsi Lampung, including samples from the type localities of *C. crassiovis* (ZMH.A14197) and of *C. kampeni* (MZB.AMPH.29336), respectively. We found no evidence, that specimens from the type locality of *C. kampeni* were significantly divergent genetically from the remaining lineages in Clade A (uncorrected *p*-distance = 2.56%). Clade B encompass samples from Aceh, Sumatera Utara, and Bengkulu provinces, whereas Clade C consists of samples from the northern part of Provinsi Aceh. Apart from clearly being genetically distinct, we also found morphological features distinguishing both Clades B and Clade C, respectively, from Clade A. The morphology of our specimens in Clade A, however, fit well the description of *C. crassiovis* (*sensu* Inger and Iskandar 2005 assuming synonymy with *C. kampeni*). In the expanded morphological dataset, both quantitative data (morphometric values and body ratio values) and qualitative data (e.g., skin texture and coloration, iris coloration, pattern of rear of thigh, see Fig. 3) clearly clustered the *C. crassiovis* specimens and their respective geographic division into Clades A–C. Morphological analyses are detailed in the taxonomic section below.

Frogs in Clade A share a similar elevational range (425–1545 m a.s.l.) and a similar habitat type (primary forest or good secondary forest) with Clade C (314–1000 m a.s.l.). Clade A also overlaps in elevational range with Clade B (1190–2033 m a.s.l.). In Aceh, we observed specimens of Clade A and Clade B at the same stream (1190 m a.s.l.), as well as frogs of Clade A and Clade C in another stream (1000 m a.s.l.). These observations suggest independent evolution occurring with the syntopic species. Two genetic samples (MZB.AMPH.29200 and MVZ271526) from Cagar Alam (=Nature Reserve) Rimbo Panti, Kecamatan (=District) Panti, Kabupaten (=Regency) Pasaman, Provinsi (=Province) Sumatera Barat, were separated by 4.05–4.90% uncorrected *p*-distance from their nearest relatives (Suppl. materials 3) and were sister to all other samples in Clade A (Fig. 2). Although this could be indicative of a separately evolving lineage, we could not find unambiguous morphological evidence that could separate these two with certainty from that of the remaining samples in Clade A. Some morphological features in the Rimbo Panti specimens, such as rear of thigh pattern and webbing formula (Fig. 4) overlap with other populations in Clade A. Rimbo Panti specimens (n males = 9, n females = 3) are bigger in size (SVL males = 46.45–48.87 mm, females = 78.00–83.99 mm) com-

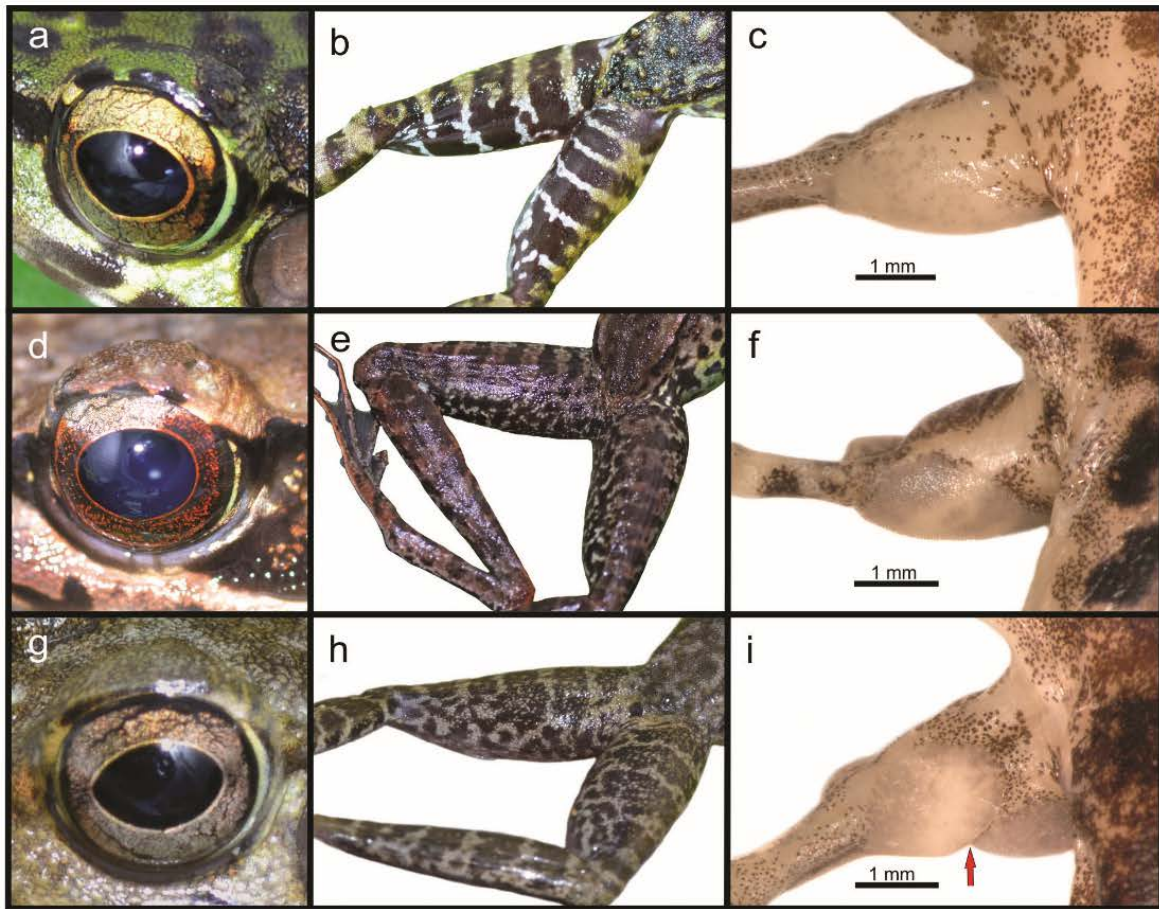


Figure 3. Comparison of three lineages within Clade 1 based on the coloration of iris, the coloration of rear of thigh, and nuptial pad. Clade 1A (a–c), Clade 1B (d–e) and Clade 1C (g–i). Photographs were taken from ZMHA.14197, male, Provinsi Sumatera Barat (a–c); ZMHA.14194, female, Provinsi Bengkulu (d–e); MZB.AMPH.23524, male, Provinsi Sumatera Utara (f); and MZB.AMPH.29396, male, Provinsi Aceh (g–i). Photos by U. Arifin.

pared to the remaining samples of this clade (SVL males = 30.30–41.75 mm, females = 40.98–77.73 mm). However, the specimens of Rimbo Panti were collected at 450 m a.s.l. whereas the smallest body size of the remaining specimens of Clade A were from 1355 m a.s.l. at Gunung Konyit, Kabupaten Kerinci, Provinsi Jambi (SVL males = 30.03–32.81 mm). The rear of thigh of Rimbo Panti specimens is typically mottled, light on dark background (Fig. 4d). The mottling pattern varied among specimens and some specimens are similar in pattern to the specimens from other regions in Clade A. The majority of specimens in Clade A were fully webbed, except for one free phalanx on Toe IV. Six specimens from Rimbo Panti were fully webbed, and six (all males) had webbing only reaching the base of the disc of Toe IV but deeply incised). This webbing pattern is also present in other specimens in Clade A. At present we conservatively consider these differences as interspecific variation, despite the genetic distance.

Three of the four tadpoles sequenced belonged to Clade A and one tadpole belonged to Clade C. Morphological characters such as shape of the jaw sheath and number of

keratodont rows showed distinct separation Clades A and C (see below) and were in accordance with the genetically justified assignment.

Taxonomic Amendments: Genus and Species Descriptions

Herein we adopt the Unified Species Concept (de Queiroz 2005) and consider Clades A–C as independently evolving units. Evidence for this assumption is provided by substantial genetic divergence (6.61–9.59%, Suppl. materials 3), robustly supported reciprocal monophyly in phylogenetic analyses, adult and tadpole morphology, geographical distribution, and syntopic occurrence. We believe that the establishment of a new genus for the *crassiovis*-group is in place because 1) the group is monophyletic; 2) the group is biogeographically well delimited (endemic to Sumatra); 3) the branch length (Fig. 2) that separates the *crassiovis*-group from any potential relative is substantial and on par with nodes that define other genera in ranids, indicating similar ages of origin. The new genus is comprised of three species, two of which are new to science (Fig. 2).

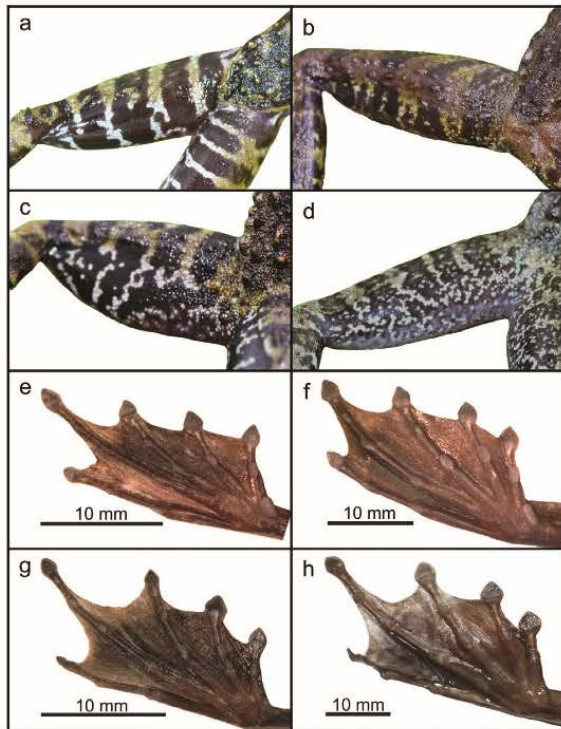


Figure 4. Variation of rear of thigh pattern and webbing on toes of the specimens within Clade 1A. Photographs were taken from ZMH.A14197, male, Provinsi Sumatera Barat (a, g); MZB.AMPH.29196, female, Provinsi Aceh (b); MZB.AMPH.29320, male, Provinsi Sumatera Barat (c); MZB.AMPH.29200, male, Provinsi Sumatera Barat (d-e); ZMH.A14170, female, Provinsi Sumatera Barat (f); ZMH.A14185, female, Provinsi Lampung (h). Photos by U. Arifin

Sumaterana gen. n.

<http://zoobank.org/1BC968B1-5D37-4D67-9413-8A4FA811DC83>

Fig. 5a-c

Type species. *Rana crassiovis* Boulenger, 1920, Syn-types: two adult females, BMNH1947.2.3.99 and BMNH1947.2.4.1.

Diagnosis. *Sumaterana* gen. n. belongs to a group of ranid torrent frogs, along with *Huia* and *Meristogenys* that possess gastromyzophorous larvae (Inger 1966, Inger and Gritis 1983, Inger 1986, Yang 1991). *Sumaterana* gen. n. species can be diagnosed by a combination of: (1) gastromyzophorous tadpole; (2) larval upper jaw sheaths thick, smooth, broadly arched, with thinner medial section; (3) lower jaw sheaths undivided, smooth, and V-shaped; (4) Labial Tooth Row Formula (LTRF): 8(5–9)/8(1) to 9(5–9)/9(1); (5) infraorbital and postorbital gland clusters present; (6) adult frogs medium sized (SVL males = 27.94–48.87 mm; females = 40.98–83.99 mm); (7) dorsum finely granulated, with or without scattered tubercles; (8) supratympanic fold present (skin fold above the tympanum, starting behind the eye); (9) posttympanic fold absent (vertical skin fold immediately posterior to tympanum); (10) dorsolateral fold absent or present; (11) tibia length

58.08–79.67% SVL; (12) outer metatarsal tubercle absent; (13) inner metatarsal tubercle present; (14) Finger I relatively shorter or subequal to Finger II; (15) width of finger discs larger or subequal to width of toe discs; (16) vocal sacs and nuptial pads present; (17) humeral gland absent.

Comparison. *Sumaterana* gen. n., *Huia*, *Meristogenys*, and *Amolops* can be distinguished from *Chalcorana*, *Clinotarsus*, *Hydrophylax*, *Hylarana*, *Odorrana*, and all other ranids (except, *Rana sauteri*, Kuramoto et al. 1984) by having gastromyzophorous tadpoles. Although *R. sauteri* has gastromyzophorous tadpoles (Kuramoto et al. 1984), Gan et al. (2015) pointed out that *R. sauteri* larvae differs from the gastromyzophorous tadpole of *Huia* and *Meristogenys* in significant features of the sucker (see below). *Amolops* and *R. sauteri* seem only distantly related to *Huia* and *Meristogenys* (Pyron and Wiens 2011; this study), and independent evolution in gastromyzophorous tadpoles must be assumed. We corroborate and expand the conclusion of Manthey and Denzer (2014) that the tadpoles of *Sumaterana* gen. n., *Amolops*, *Huia*, and *Meristogenys* can be distinguished by the shape of their jaw sheaths. The jaw sheath of *Sumaterana* gen. n. is characterized by (followed by *Amolops*; *Huia*; *Meristogenys* features in parentheses): the upper jaw sheath thick, broadly arched, with thinner medial section (thick, broadly arched, without the medial thinning; M-shaped or \wedge -shaped; divided; Yang 1991, Manthey and Denzer 2014); lower jaw sheath V-shaped (V-shaped; V-shaped; divided or undivided; Yang 1991, Manthey and Denzer 2014). The number of keratodont rows on the lower lip is eight to nine in *Sumaterana* gen. n. (three to five rows in *Amolops*, except for *A. cremnobatus* with six rows (Inger and Kottelat 1998); six rows or more in *Huia* (Manthey and Denzer 2014); four rows or more in *Meristogenys* (Inger and Stuebing 2009, Manthey and Denzer 2014, Shimada et al. 2015). *Sumaterana* gen. n. has two glandular clusters, infraorbital and postorbital (postorbital and abdominal clusters in *Amolops* (Yang 1991, Inger and Kottelat 1998, Liu et al. 2000, Matsui and Nabhitabhata 2006, Ngo et al. 2006), except for *A. cremnobatus*, postorbital and midlateral clusters (Inger and Kottelat 1998); a combination of infraorbital, postorbital, prespiracular, midlateral, and variably caudal/fin clusters in *Meristogenys* (e.g., Yang 1991, Matsui et al. 2010, Shimada et al. 2011, Shimada et al. 2015); and a combination of caudal/fin, postorbital, midlateral, and infraorbital clusters in *Huia* (Yang 1991; UA pers. observ.).

Adult *Sumaterana* gen. n. can be distinguished from *Huia*, *Meristogenys*, and *Amolops* by: lacking posttympanic fold (present in *Huia*, *Meristogenys* and *Amolops*; Yang 1991; UA unpubl. data); the disc of Finger III wider or almost equal to that of Toe IV (subequal in *Huia*, less or equal to in *Meristogenys*, wider in *Amolops*; Yang 1991); Finger I length shorter or subequal to that of Finger II (Finger I \geq Finger II in *Huia*, Finger I $>$ Finger II in *Meristogenys*, Finger I \leq Finger II in *Amolops*; Yang 1991); lacking an outer metatarsal tubercle (present in *Huia* except for



Figure 5. *Sumaterana* gen. n. species: (a) *S. crassiovis* comb. n., ZMHLA14197, male, Provinsi Sumatera Barat; (b) *S. dabulescens* sp. n., MZB.AMPH.29396, male, holotype, Provinsi Aceh; (c) *S. montana* sp. n., ZMHLA14194, female, paratype, Provinsi Bengkulu. Photos by U. Arifin.

II. cavitympanum, present in *Meristogenys* except for *M. kinabaluensis*; Yang 1991); tibia length relative to SVL 58.08–78.39% (> 70% in *Huia* and in *Meristogenys*; Yang 1991); furthermore, *Sumaterana* gen. n. differs from *Huia* by having a translucent but non-transparent tympanum; tympanum not encased by dark Π -shaped marking (Manthey and Denzer 2014); and dorsolateral folds less distinct or absent. *Sumaterana* gen. n. differs from *Amolops* by having diamond-shaped finger and toe tips (rounded in *Amolops*) and relatively smaller fingers and toe discs.

Etymology. *Sumaterana* is a compound generic epithet created from the Indonesian proper noun Sumatera, the Indonesian name for the island of Sumatra, and *rana*, the feminine Latin word for frog. Sumatera itself is named after the kingdom of Samudra Pasai, which was located along the coast of Aceh, Sumatra from the 13th to the 16th centuries CE. Samudra is a Sanskrit word that means gathering of the seas, a place where the Andaman, Java, and South China seas meet the Indian Ocean. *Rana*, was also the very first generic name to be assigned to a member of the *S. crassiovis* group, endemic to the island of Sumatra.

Common name. Sumatran Cascade Frogs (English) and Katak Jeram Sumatra (Bahasa Indonesia).

Phylogenetic definition and content. *Sumaterana* gen. n. is a node-based genus that consists of three known species: *Sumaterana crassiovis* comb. n. (Fig. 2 Clade A, Fig. 5a), *S. montana* sp. n. (Fig. 2 Clade B, Fig. 5c), and *S. dabulescens* sp. n. (Fig. 2 Clade C, Fig. 5b), and their most recent common ancestor. *Chalcorana kampeni* is considered a junior synonym of *S. crassiovis* comb. n. based on Inger and Iskandar (2005) and the new molecular evidence. The monophyletic clade of *Sumaterana* gen. n. is restricted to the island of Sumatra, Indonesia. Our phylogenetic analyses and morphological examination supports these taxonomic recognitions (uncorrected *p*-distances in Suppl. materials 3).

Distribution and habitat. Species of *Sumaterana* gen. n. inhabit riparian habitats in primary or secondary forest in Sumatra, Indonesia. Inhabited streams are typically

fast flowing, 5 m wide or less, dominated by big rocks (diameter > 1 m). The known elevational range is from 314–2033 m a.s.l. Adult frogs of these genus usually perched on rocks or vegetation at the stream. Tadpoles of these frogs can be found in groups attached to the top or sides of rocks in fast moving water.

Sumaterana crassiovis comb. n.

Figs 2 Clade A, 5a, 6a

Rana pantherina Van Kampen, 1910.
Rana crassiovis Boulenger, 1920.
Rana (Hylorana) kampeni Boulenger, 1920.
Rana (Hylorana) crassiovis Boulenger, 1920.
Rana (Hylarana) kampeni Van Kampen, 1923.
Rana (Hylarana) crassiovis Van Kampen, 1923.
Rana (Chalcorana) kampeni Dubois, 1992.
Rana (Chalcorana) crassiovis Dubois, 1992.
Hydrophylax kampeni Frost et al., 2006.
Hydrophylax crassiovis Frost et al., 2006.
Hylarana kampeni Che et al., 2007.
Hylarana crassiovis Che et al., 2007.
Chalcorana kampeni Fei et al., 2010; Oliver et al., 2015.
Chalcorana crassiovis Fei et al., 2010; Oliver et al., 2015.

Syntypes. Two adult females (BMNH1947.2.3.99 and BMNH1947.2.4.1-Fig. 7), Kerinci, Sumatra, Indonesia, 4000 feet (~1219 m a.s.l.), coll. Robinson-Kloss Expedition on the Batrachians. Based on the lack of morphological distinguishing characters (Inger and Iskandar 2005) and low genetic divergence (2.56%, Suppl. materials 3) of topotypic specimens (this study), we consider *C. kampeni* a junior synonym of *S. crassiovis* comb. n..

Referred specimens (283). 262 adults (128 of them: 96 males and 32 females; were measured) and 21 tadpoles collected from Aceh up to Lampung (Appendix 1).

Description. Specimens were assigned to *Sumaterana crassiovis* comb. n. based on comparison of material from Kabupaten Kerinci. *Sumaterana crassiovis* comb. n. is described by the following combination of characters: a medium sized species, SVL in males 30.03–48.87 mm,

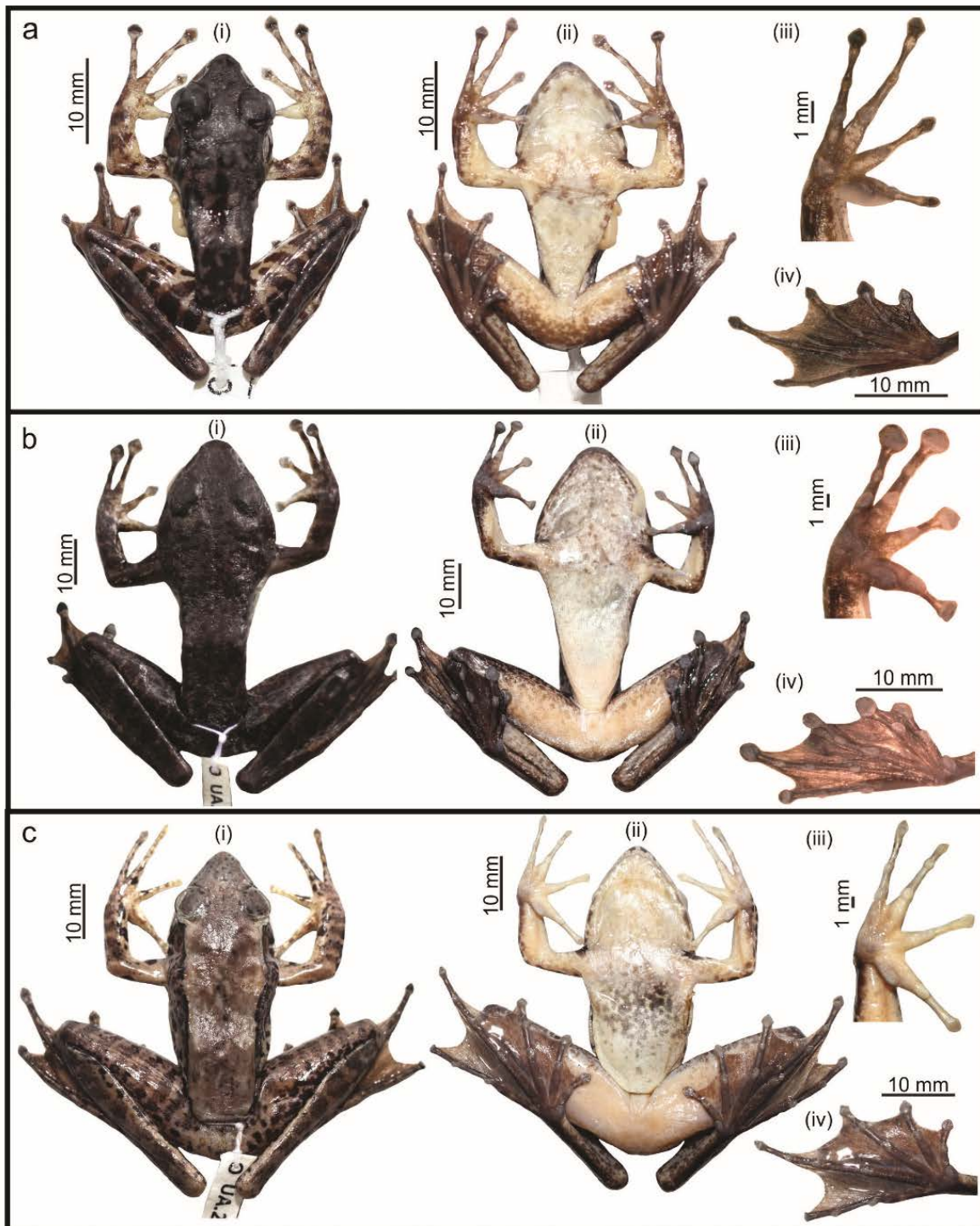


Figure 6. Morphological comparison of (i) dorsal, (ii) ventral, (iii) palmar, and (iv) plantar regions of *Sumaterana* gen. n. species. (a) *S. crassiovis* comb. n., ZMILA14197, male, Provinsi Sumatera Barat; (b) *S. dabulescens* sp. n., ZMILA14159, female, paratype, Provinsi Aceh; (c) *S. montana* sp. n., ZMHA14194, female, paratype, Provinsi Bengkulu. Photos by U. Arifin.

females 40.98–83.99 mm; head width subequal to head length; snout rounded, obtusely pointed in dorsal view, slightly protruding in lateral view; nostril closer to snout than to eye; vomerine teeth present, in oblique groups, be-

tween choanae; tongue lanceolate; loreal area deeply concave; canthus rostralis sharp, constricted behind nostrils; rictal ridge present; tympanum distinct, translucent (not transparent); interorbital distance 75.96–124.80% width

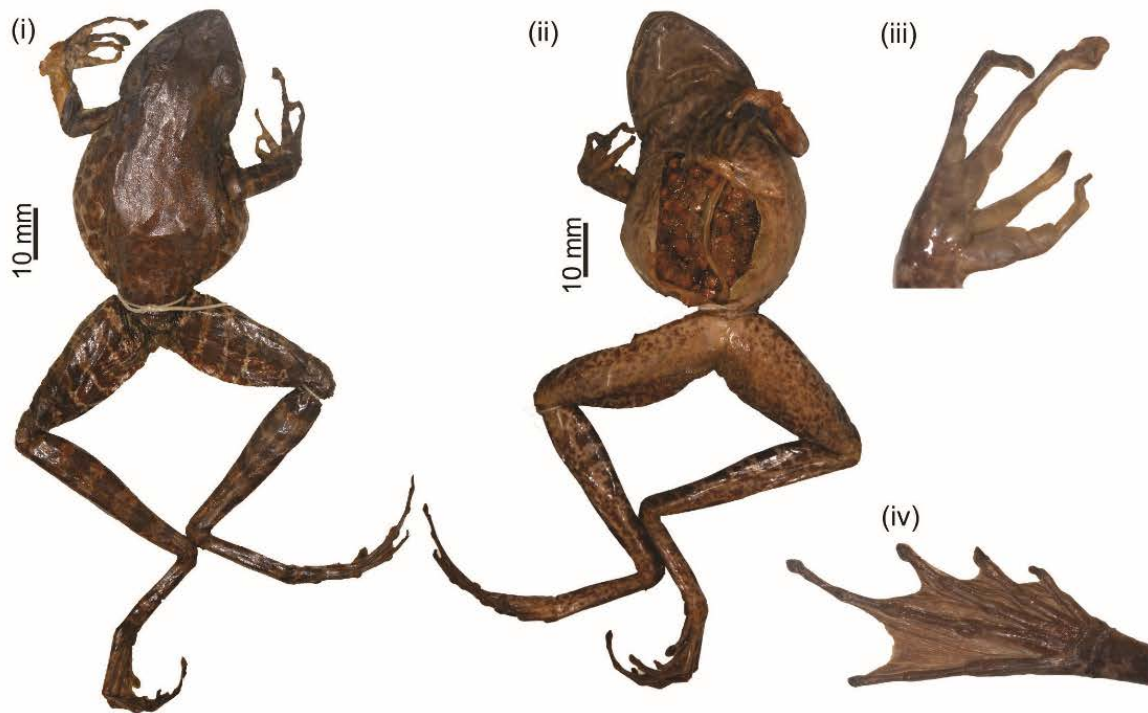


Figure 7. Pictures of dorsal (i), ventral (ii), palmar (iii), and plantar (iv) regions of the type species of *Sumaterana crassiovis* comb. n. (BMNH1947.2.4.1, female). Photos by U. Arifin.

of upper eyelid in females, 68.26–120.31% width of upper eyelid in males; pineal spot visible; dorsolateral fold absent; supratympanic fold thick, posttympanic fold absent; dorsum finely granulated with scattered tubercles, variable in size and density; flanks coarsely granulated with few tubercles; venter smooth, granulated posteriorly; rear of thigh usually barred as continuation of thigh dorsal pattern; arm slender, lower arm length 19.03–24.18% SVL in females and 19.58–25.46% SVL in males; hand length 31.54–36.98% SVL in females and 31.77–39.23% SVL in males; fingers long, without webbing; fingertips expanded into discs, diamond-shaped, with circummarginal groove; Finger I < Finger II, Finger III longest; fringes present on the outer phalanges of all fingers; subarticular tubercles distinct; width of Finger III disc > width of Toe IV disc; hindlimbs long, articulation of the heels reaching beyond tip of snout, when limb aligned to body; relative femur length 85.39–94.32% tibia length in females, 85.82–95.02% tibia length in males; length of tibia 60.17–70.52% SVL in females, 58.78–76.44% in males; toes slender and long; tip of toe extended into disc, diamond-shaped, with circummarginal grooves; toe lengths: I < II < III < V < IV, Toe V only slightly longer than Toe III; Toes I, II, III, and V fully webbed, webbing of Toe IV usually one phalanx free (I(1^{1/2}–1^{1/2})II(1^{1/2}–1^{1/2})III(1^{1/2}–2^{1/2})IV(2^{1/2}–1^{1/2})V); subarticular tubercles distinct; inner metatarsal tubercle distinct, oval, 92.07–212.77% T4DW in males and 98.80–150.00% in females; outer metatarsal tubercle absent; tarsal fold absent. (Measurements: Tables 4–5).

Coloration. Dorsal skin background green in life, with dark blotches around tubercles, lighter areas on the dorsum forming irregular network pattern; dark line connects the eye and the snout; the upper and lower lips with dark blotches on a light background; iris golden yellow, reddish anteriorly and posteriorly, with a dark netting pattern; tympanum pale brown, encircled by a dark line; flanks lighter than dorsum, lighter ventrad and with dark spots; venter whitish, throat and chest with or without dark marking; distinct cross-bars on dorsal limbs; the rear of thigh with dark vertical bars (usually a continuation from dorsal surface and separated by narrow lighter areas) or mottling (dark marking on lighter background); ventral legs are dusted with brown pigment; webbing color brown. In preservative, dorsal background light brown; flanks becoming gray; iris changed to gray.

Variation. (1) number of tubercles on dorsum and flanks: few to dense; (2) size of tubercles on dorsum: small and round to larger and elongated; (3) dorsolateral fold absent, but row of few small tubercles form incomplete dorsolateral series, dorsal to the posterior of trunk (not in continuation of tympanic fold); (4) dorsal coloration: dark blotches on green background vary from few and isolated, to dense, and forming irregular green background network between the dark blotches; (5) flank color yellowish-green to green (as dorsum), lighter ventrad, with distinct spots; (6) upper and lower lips: whitish to greenish, with dark markings, small distinct bars to wide and connected, lip

Table 4. Morphometric values from all specimens of *Sumaterana* gen. n. examined in this study. Information given for each character as follows: average±st.deviation (first line), min–max (second line).

Character	<i>S. crassiovis</i> comb. n.		<i>S. montana</i> sp. n.		<i>S. dabulescens</i> sp. n.	
	(males, n = 96)	(females, n = 32)	(males, n = 10)	(females, n = 7)	(males, n = 27)	(females, n = 3)
SVL	37.58±4.01	67.43±10.42	29.98±1.14	55.07±2.58	37.65±1.45	57.30±7.58
	30.03–48.87	40.98–83.99	27.94–31.56	51.61–59.60	34.69–40.86	48.03–66.60
HL	14.73±1.76	26.84±4.04	12.01±0.40	21.61±0.99	14.86±0.53	24.13±2.71
	11.92–19.66	16.44–32.44	11.53–12.83	20.42–25.35	13.81–15.73	20.79–27.43
HW	13.52±1.66	24.43±3.72	10.88±0.53	19.61±1.09	14.00±0.59	23.03±2.78
	10.96–18.61	14.14–29.68	9.74–11.79	18.04–21.65	12.99–15.20	19.41–26.18
SL	5.85±0.71	10.80±1.66	4.99±0.38	8.76±0.59	5.82±0.22	9.55±0.98
	4.52–7.82	6.76–13.61	4.47–5.53	7.83–9.59	5.22–6.26	8.35–10.74
SN	2.26±0.26	3.92±0.64	2.15±0.35	3.95±0.60	2.21±0.14	3.39±0.40
	1.78–2.99	2.50–5.82	1.73–2.77	3.11–4.80	1.94–2.47	2.88–3.85
EN	3.45±0.35	6.30±0.95	2.70±0.24	4.86±0.31	3.38±0.13	5.33±0.46
	2.62–4.44	4.17–8.16	2.29–3.14	4.58–5.55	3.10–3.62	4.71–5.80
IND	3.78±0.44	6.52±0.94	3.50±0.33	6.10±0.75	3.79±0.19	5.95±0.50
	3.03–5.17	3.79–7.90	3.06–4.01	5.04–7.58	3.44–4.26	5.25–6.40
IOD	3.49±0.34	6.13±0.88	3.23±0.19	5.21±0.40	3.41±0.16	4.93±0.70
	2.90–4.53	4.05–7.99	2.96–3.51	4.72–5.94	3.02–3.76	4.03–5.74
UEW	4.07±0.62	6.84±1.10	2.96±0.18	5.21±0.40	4.02±0.34	5.63±0.56
	2.72–6.05	4.18–8.48	2.72–3.22	4.65–6.00	3.41–4.67	4.90–6.26
ED	5.62±0.61	9.10±1.42	4.41±0.35	7.23±0.59	5.40±0.37	7.96±1.06
	4.59–7.70	5.68–11.40	3.80–4.97	6.64–8.29	4.76–6.39	6.63–9.22
TY _v	3.23±0.37	3.86±0.59	3.08±0.31	3.69±0.14	3.21±0.23	2.99±0.58
	2.39–3.97	2.46–4.82	2.43–3.40	3.50–3.92	2.88–3.86	2.26–3.67
TY _h	3.22±0.36	3.84±0.63	3.02±0.30	3.43±0.14	3.12±0.28	2.78±0.17
	2.39–4.29	2.46–4.82	2.44–3.50	3.19–3.57	2.27–3.70	2.58–3.00
ET	1.14±0.29	2.74±0.64	0.92±0.12	2.14±0.17	1.20±0.11	2.07±0.19
	0.74–2.90	1.44–4.01	0.70–1.17	1.87–2.31	1.01–1.50	1.90–2.33
LAL	8.26±0.75	14.43±2.03	7.05±0.31	11.63±0.74	8.11±0.31	12.23±1.23
	6.89–10.06	9.00–17.13	6.49–7.58	10.08–12.45	7.74–9.11	10.71–13.73
HAL	13.14±1.34	23.27±3.34	10.85±0.46	18.70±0.98	12.48±0.42	18.25±1.58
	10.77–16.82	14.90–30.32	10.26–11.72	17.41–20.79	11.62–13.33	16.11–19.87
FE	22.33±2.10	40.35±5.89	19.75±0.96	35.94±1.49	22.42±0.81	32.44±4.06
	19.29–28.55	24.25–50.36	18.16–21.14	33.97–38.66	21.18–24.29	27.55–37.50
TL	24.52±2.61	44.61±6.31	22.17±0.90	40.69±1.13	23.74±0.72	36.01±3.32
	20.74–31.85	27.83–55.96	20.96–24.20	38.29–42.08	22.30–25.30	31.46–39.28
FL	20.68±2.34	38.11±5.57	18.82±0.51	34.85±1.53	19.63±1.31	30.27±3.27
	16.26–27.71	23.64–49.14	18.19–19.53	32.30–37.54	14.41–22.04	25.94–33.85
IMTL	1.75±0.27	3.20±0.57	1.50±0.13	2.70±0.30	1.83±0.16	2.74±0.26
	1.28–2.62	1.72–4.29	1.30–1.70	2.30–3.27	1.51–2.10	2.38–2.96
F1L	3.88±0.51	7.77±1.34	3.46±0.18	6.78±0.55	3.78±0.18	5.62±1.50
	3.02–5.30	4.62–10.90	3.19–3.84	6.07–7.73	3.28–4.05	3.52–6.96
F2L	4.85±0.59	8.89±1.39	3.66±0.19	6.99±0.53	4.55±0.22	7.03±0.80
	3.92–6.74	5.85–11.79	3.30–3.96	6.26–8.00	4.17–5.19	6.01–7.97
F3DW	2.00±0.35	3.62±0.62	1.16±0.20	1.82±0.25	2.03±0.16	3.00±0.48
	1.29–3.01	2.26–5.06	0.93–1.54	1.40–2.13	1.64–2.27	2.33–3.46
T4DW	1.36±0.30	2.71±0.46	1.08±0.21	1.82±0.17	1.58±0.13	2.43±0.32
	0.92–2.26	1.72–3.47	0.78–1.40	1.63–2.20	1.30–1.77	1.99–2.76

markings absent or very thin in few individuals; (7) ventral dark markings: from none (ventral side whitish) to dark on throat and reaching venter, pale to dark; (8) rear of thigh with dark bars, complete or broken, or occasionally dark mottling on whitish/grayish background (Fig. 4a–d); (9) iris: golden to pale yellow, from faint and thin to dense and dark netting; (10) number of cross bars: 3–4 on lower arm (from elbow to wrist), 4–7 on thigh; (11) Toe IV:

from one phalanx free of webbing to webbing reaching intercalary tubercle of Toe IV (Fig. 4e–h). See Fig. 8 for images of *Sumaterana crassiovis* comb. n. from different localities and for morphometric variation Tables 4–5.

Sexual dimorphism. Males significantly smaller than females. Tympanum diameter 45.27–71.68% ED in males, 33.33–48.51% ED in females. Male with distinct undi-

Table 5. Morphometric ratios from all specimens of *Sumaterana* gen. n. examined in this study. Information given for each character as follows: average±st.deviation (first line), min–max (second line).

Character	<i>S. crassiovis</i> comb. n.		<i>S. montana</i> sp. n.		<i>S. dabulefscens</i> sp. n.	
	(males, n = 96)	(females, n = 32)	(males, n = 10)	(females, n = 7)	(males, n = 27)	(females, n = 3)
HW/HL	91.80%±2.75% 86.44%–100.30%	90.97%±2.85% 84.36%–97.32%	90.61%±3.99% 82.85%–95.08%	90.72%±2.30% 87.54%–94.49%	94.21%±2.01% 88.32%–96.87%	95.37%±1.61% 93.36%–97.31%
SL/ED	104.32%±8.80% 77.76%–125.45%	119.03%±7.66% 106.07%–138.71%	113.90%±13.48% 94.66%–145.53%	121.99%±14.12% 103.02%–144.43%	108.08%±7.18% 94.05%–120.59%	120.50%±3.99% 116.49%–125.94%
EN/SN	153.27%±12.86% 119.60%–187.64%	162.54%±10.76% 141.08%–187.96%	127.22%±14.95% 107.60%–157.23%	125.25%±16.53% 100.00%–150.80%	153.19%±9.46% 140.27%–177.84%	157.58%±5.31% 150.65%–163.54%
IND/IOD	108.15%±6.51% 95.83%–143.79%	105.48%±6.82% 91.11%–121.35%	108.01%±5.99% 99.71%–121.88%	116.74%±8.06% 106.78%–128.66%	111.38%±5.47% 102.65%–121.94%	121.74%±7.76% 111.50%–130.27%
IOD/UEW	86.87%±9.24% 68.26%–120.31%	91.20%±9.72% 75.96%–124.80%	109.33%±3.46% 102.17%–114.14%	98.60%±6.15% 89.33%–105.48%	84.68%±7.10% 72.38%–100.00%	87.24%±3.88% 82.24%–91.69%
TYv/ED	57.76%±5.57% 46.53%–71.68%	42.59%±3.72% 36.75%–56.83%	74.01%±10.69% 52.31%–89.47%	50.57%±6.19% 43.91%–60.47%	59.63%±4.62% 51.82%–72.94%	37.90%±2.88% 28.18%–45.70%
TYh/ED	57.45%±5.37% 45.27%–71.68%	42.33%±3.80% 33.33%–56.83%	73.07%±11.60% 52.31%–92.89%	46.46%±4.08% 41.54%–54.67%	58.61%±4.30% 51.82%–69.36%	35.29%±2.68% 32.54%–38.91%
F1L/F2L	80.08%±4.24% 70.56%–90.80%	86.72%±3.25% 78.97%–93.54%	94.55%±4.18% 87.67%–101.82%	97.05%±2.62% 93.46%–100.89%	83.41%±4.24% 78.03%–94.16%	78.45%±14.09% 58.57%–89.47%
F3DW/T4DW	148.51%±15.60% 113.73%–197.03%	133.13%±9.69% 112.08%–160.09%	108.13%±8.45% 91.04%–120.00%	93.19%±11.74% 73.68%–108.12%	128.79%±8.42% 105.13%–144.53%	122.94%±4.16% 117.09%–126.38%
FE/TL	91.16%±2.33% 85.82%–95.02%	90.39%±1.87% 85.39%–94.32%	89.10%±2.63% 85.17%–94.12%	88.33%±2.47% 85.09%–93.45%	94.43%±1.96% 89.40%–97.55%	89.85%±4.00% 86.51%–95.47%
HL/SVL	39.17%±1.20% 36.22%–42.03%	39.88%±1.24% 37.52%–43.53%	40.09%±1.51% 37.83%–42.88%	38.84%±1.03% 37.16%–40.28%	39.49%±1.13% 37.66%–42.67%	42.22%±0.86% 41.19%–43.29%
HW/SVL	35.96%±1.46% 33.06%–39.40%	36.27%±1.36% 33.57%–39.68%	36.31%±1.91% 33.66%–39.33%	35.22%±0.59% 34.16%–35.97%	37.20%±1.11% 34.95%–39.01%	40.26%±0.72% 39.31%–41.05%
SL/SVL	15.56%±0.61% 13.99%–17.05%	16.01%±0.65% 14.70%–17.53%	16.65%±1.23% 14.95%–18.73%	15.74%±0.88% 14.42%–17.04%	15.49%±0.59% 14.46%–16.55%	16.73%±0.52% 16.13%–17.38%
SN/SVL	6.02%±0.41% 4.81%–7.50%	5.77%±0.24% 5.31%–6.13%	7.18%±1.11% 5.66%–8.86%	7.09%±0.98% 6.01%–8.66%	5.89%±0.38% 5.04%–6.62%	5.93%±0.11% 5.78%–6.02%
EN/SVL	9.18%±0.47% 8.27%–10.75%	9.37%±0.63% 8.41%–11.02%	9.00%±0.73% 7.44%–10.17%	8.72%±0.25% 8.30%–9.07%	9.00%±0.40% 8.32%–9.64%	9.36%±0.47% 8.71%–9.81%
IND/SVL	10.06%±0.61% 8.67%–12.62%	9.69%±0.68% 8.05%–10.81%	11.66%±1.01% 10.62%–13.52%	10.91%±0.73% 9.75%–11.96%	10.04%±0.43% 9.23%–11.02%	10.46%±0.60% 9.61%–10.93%
IOD/SVL	9.31%±0.46% 8.04%–10.75%	9.21%±0.64% 7.26%–10.33%	10.78%±0.51% 10.10%–11.91%	9.36%±0.42% 8.78%–9.96%	9.03%±0.49% 8.17%–10.13%	8.60%±0.16% 8.39%–8.78%
UEW/SVL	10.81%±0.98% 7.73%–12.90%	10.15%±0.68% 7.73%–11.24%	9.87%±0.59% 8.90%–10.85%	9.50%±0.32% 8.99%–9.90%	10.72%±0.81% 9.18%–12.17%	9.87%±0.34% 9.40%–10.20%
ED/SVL	14.99%±1.06% 12.82%–19.09%	13.50%±0.84% 11.92%–15.40%	14.72%±1.06% 12.16%–16.10%	13.00%±1.02% 11.80%–14.73%	14.37%±0.85% 12.64%–15.84%	13.88%±0.09% 13.80%–14.00%
TYv/SVL	8.67%±0.83% 6.80%–10.79%	5.72%±0.45% 4.83%–6.63%	10.80%±1.12% 8.42%–12.96%	6.81%±0.39% 6.42%–7.54%	8.55%±0.52% 7.78%–9.67%	5.26%±0.98% 3.95%–6.31%
TYh/SVL	8.62%±0.80% 6.42%–10.47%	5.68%±0.42% 4.84%–6.64%	10.73%±1.24% 8.42%–12.36%	6.28%±0.36% 5.68%–6.88%	8.41%±0.55% 7.65%–10.21%	4.90%±0.36% 4.50%–5.37%
ET/SVL	3.03%±0.79% 2.23%–9.66%	3.98%±0.52% 3.12%–5.08%	3.05%±0.36% 2.38%–3.79%	3.83%±0.19% 3.62%–4.14%	3.18%±0.24% 2.78%–3.79%	3.65%±0.35% 3.32%–4.14%
LAL/SVL	22.05%±1.22% 19.58%–25.46%	21.41%±1.12% 19.03%–24.18%	23.53%±0.70% 22.48%–24.48%	20.92%±1.52% 19.44%–24.12%	21.61%±0.83% 20.04%–23.05%	21.44%±0.69% 20.62%–22.30%
HAL/SVL	35.01%±1.51% 31.77%–39.23%	34.47%±1.49% 31.54%–36.98%	36.20%±1.35% 34.17%–38.93%	33.61%±1.47% 30.93%–35.85%	33.26%±1.18% 31.08%–36.00%	32.06%±1.60% 29.83%–33.54%
FE/SVL	59.54%±2.76% 53.83%–67.33%	59.84%±2.37% 54.62%–63.19%	65.86%±1.38% 63.23%–68.32%	64.63%±2.85% 60.35%–67.80%	59.65%±2.52% 54.95%–64.69%	56.67%±0.49% 56.31%–57.36%
TL/SVL	65.32%±2.72% 58.78%–75.37%	66.22%±2.71% 60.17%–70.52%	73.97%±2.34% 70.88%–78.39%	73.29%±4.83% 65.28%–79.67%	63.17%±2.51% 58.08%–68.81%	63.20%±2.99% 58.98%–65.50%
FL/SVL	55.06%±2.44% 49.18%–63.85%	56.46%±2.27% 50.91%–60.23%	62.82%±1.71% 59.52%–65.32%	62.69%±3.42% 57.38%–67.51%	52.25%±3.14% 39.59%–56.93%	53.01%±1.54% 50.83%–54.18%
IMTL/T4DW	131.80%±22.06% 92.07%–212.77%	117.46%±14.34% 98.80%–150.00%	144.27%±33.28% 97.86%–212.82%	139.17%±19.24% 111.36%–171.78%	115.89%±10.10% 98.75%–138.69%	113.49%±6.59% 104.35%–119.60%



Figure 8. Morphological variation within *Sumaterana crassiovis* comb. n. (a) MZB.AMPH.29196, female, Provinsi Aceh, (b) Provinsi Sumatera Utara, (c) MZB.AMPH.29200, male, Provinsi Sumatera Barat, (d) ZMH.A.14197, male, Provinsi Sumatera Barat, (e) MZB.AMPH.29320, male, Provinsi Sumatera Barat, (f) MZB.AMPH.29277, young male, Provinsi Bengkulu, (g) ZMH.A.14151, male, Provinsi Sumatera Selatan, (h) ZMH.A.14185 and MZB.AMPH.29296, male and female, Provinsi Lampung. Photos by U. Arifin, except for (b) by A. Irawan.

vided nuptial pads, covering base of the first finger to subarticular tubercle in dorsal and medial surface, paired subgular vocal sacs, humeral glands absent.

Common name. We propose Kerinci Cascade Frogs as the common English name (to replace the old spelling in “*Korinchi Frog*”, Iskandar and Mumpuni 2004) and Katak Jeram Kerinci as the Indonesian name.

Distribution and ecological remarks. This species is widespread on the island of Sumatra, ranging from the northern part of Provinsi Aceh to Kabupaten Pasawaran, the southern part of Provinsi Lampung (Fig. 9). Elevational range 425–1545 m a.s.l. This species is abundant along rocky streams (usually 1–5 m wide) in primary or good secondary forest. The inhabited streams are typically rocky with boulders (usually diameter > 1 m) and with rock formations along the stream, water current velocity 0.2–1.1 m/s (Fig. 10). Males of this species commonly can be observed perching on rocks or vegetation at the stream banks. Females were rarely observed near the streams. It seems that they approach the streams only during breeding activities. Tadpoles were often found in groups, on rocks in the stream, overflowed with water in cascading sections.

Tadpoles. Tadpoles were identified (100%) using 12S rRNA+16S rRNA+tRNA^{val} barcoding with adult samples from the type locality. We examined total of 21 tadpoles. Stage 25: MZB.AMPH.29362 (n = 1), ZMH.A12649 (n = 3), MZB.AMPH.29363 (n = 1), MZB.AMPH.29364 (n = 1), Stage 26: MZB.AMPH.29362 (n = 2), MZB.AMPH.29356 (n = 1), ZMH.A12649 (n = 2), MZB.AMPH.29365 (n = 1), Stage 31: MZB.AMPH.29362 (n = 1), Stage 32: MZB.AMPH.29362 (n = 1), Stage 35: MZB.AMPH.29362 (n = 1), ZMH.A12650 (n = 1), Stage 36: MZB.AMPH.29355 (n = 1), ZMH.A12649 (n = 1), Stage 39: MZB.AMPH.29360 (n = 1), Stage 42: MZB.AMPH.29361 (n = 1). One selected tadpole from the lot had 100% match (12S rRNA+16S rRNA+tRNA^{val}) to an adult *Sumaterana crassiovis* comb. n. from the type locality. We refer to ZMH.A12650 (stage 35, Fig. 11a–c) for tadpole description.

Head and trunk approximately oval in dorsal view and dorsoventrally depressed and streamlined, in lateral view; maximum body width 64.40% body length; snout expanded and broadly rounded with emargination laterally setting off snout from body; eyes positioned dorsolaterally, oriented laterally; ED = 2.31 mm; IND/IOD = 48.22%; SN/EN = 44.82%; nostril open without raised rim; positioned anterodorsally and anterolaterally directed; two glands clusters present, infraorbital glands (five on each side) and postorbital glands (one on each side); oral disc ventral, a groove separating upper lip from snout, ODW/BW = 66.33%; oral disc marginal papillae short, arranged in single row; marginal papillae of upper lip present only on sides, on lower lip in uninterrupted row; two short submarginal papillae in lateral area of upper lip; LTRF: 9(6–9)/9(1); upper jaw sheath broad and heavily keratinized, smooth, undivided, thick but with distinct thinner medial

section; lower jaw sheath undivided, V-shaped, smooth, and thick; both jaw sheaths finely serrated along their edges; very large abdominal sucker adjoining oral disc posteriorly, SUL/BL = 76.61%, SUW/BW = 89.03%; spiracle sinistral, tube long and posterior half free from body wall, opening directed posteriorly or posterodorsally; anal tube median, free from tail fin, directed posteriorly; strongly muscular tail: TAL/BL = 165.71%, TMH/BH = 71.87%, TMH/MTH = 63.00%; upper fin convex; maximum upper fin height is 30.57% maximum tail height at 49.19% of tail length; tail tip pointed.

In life (Fig. 11a–c), dorsum light brown, orangeish anteriorly and posteriorly to eyes; trunk darker than head; tail muscle light brown with fine-orange stippling; lower flanks region whitish; lateral tail vein very obvious, including dorsal branching along myosepta; upper and lower fins mostly transparent without iridophores; iris black, with dense gold to orange iridescent stippling; abdomen whitish laterally and densely stippled with fine-orange iridophores medially; abdominal sucker mostly transparent with white iridocytes in the center. In preservation, upper side gray with dark stippling; dense-dark stippling laterally; iris black; lens gray; ventral side uniformly transparent with some grey pigments in the anterior region of snout and lateral parts.

Sumaterana montana sp. n.

<http://zoobank.org/72D3A049-2C2F-43FC-B38A-483C295BEC08>

Figs 2 Clade B, 5c, 6c

Holotype. MZB.AMPH.29377 (female), Gunung Baru, Desa (=village) Seblat Ulu, Taman Nasional (=National Park) Kerinci-Seblat, Kabupaten Lebong, Provinsi Bengkulu, Sumatra, Indonesia (02.88413°S, 102.13073°E), 2033 m a.s.l., 4 May 2014, 20:44, coll. U. Arifin.

Paratypes (10). ZMH.A14194 (female, Fig. 5c and Fig. 6c), approx. 300 m from the holotype locality (02.88525°S, 102.12993°E), 2000 m a.s.l., 3 May 2014, 22:04, coll. U. Arifin and G. Cahyadi. MZB.AMPH.23516 (male) and MZB.AMPH.23517 (female), 02.55397°N, 098.59806°E, 1774 m a.s.l.; MZB.AMPH.23518 (female), UTA.A64829 (female), MZB.AMPH.23519 (male), MZB.AMPH.23520 (male), UTA.A64830 (male), UTA.A64831 (male), UTA.A64832 (male), 2.54691°N, 98.61414°E, 1780 m a.s.l.; vicinity of Tele, Kecamatan Samosir, Kabupaten Toba-Samosir, Provinsi Sumatera Utara, Indonesia, 20 January 2014, coll. E. N. Smith, M. I. Lubis, K. A. O’Connell, and E. Wostl.

Referred specimens (16). See Appendix 1.

Diagnosis. (1) medium sized frog, SVL males (n = 10) 27.94–31.56 mm and females (n = 7) 50.11–63.37 mm; (2) dorsum skin finely granulated, color generally brown with scattered light spots; (3) tympanum distinct and translucent, slightly deep, supratympanic fold present, posttympanic fold absent; (4) dorsolateral fold present, thin, continuation of supratympanic fold to the level of pelvic joint, uninterrupted

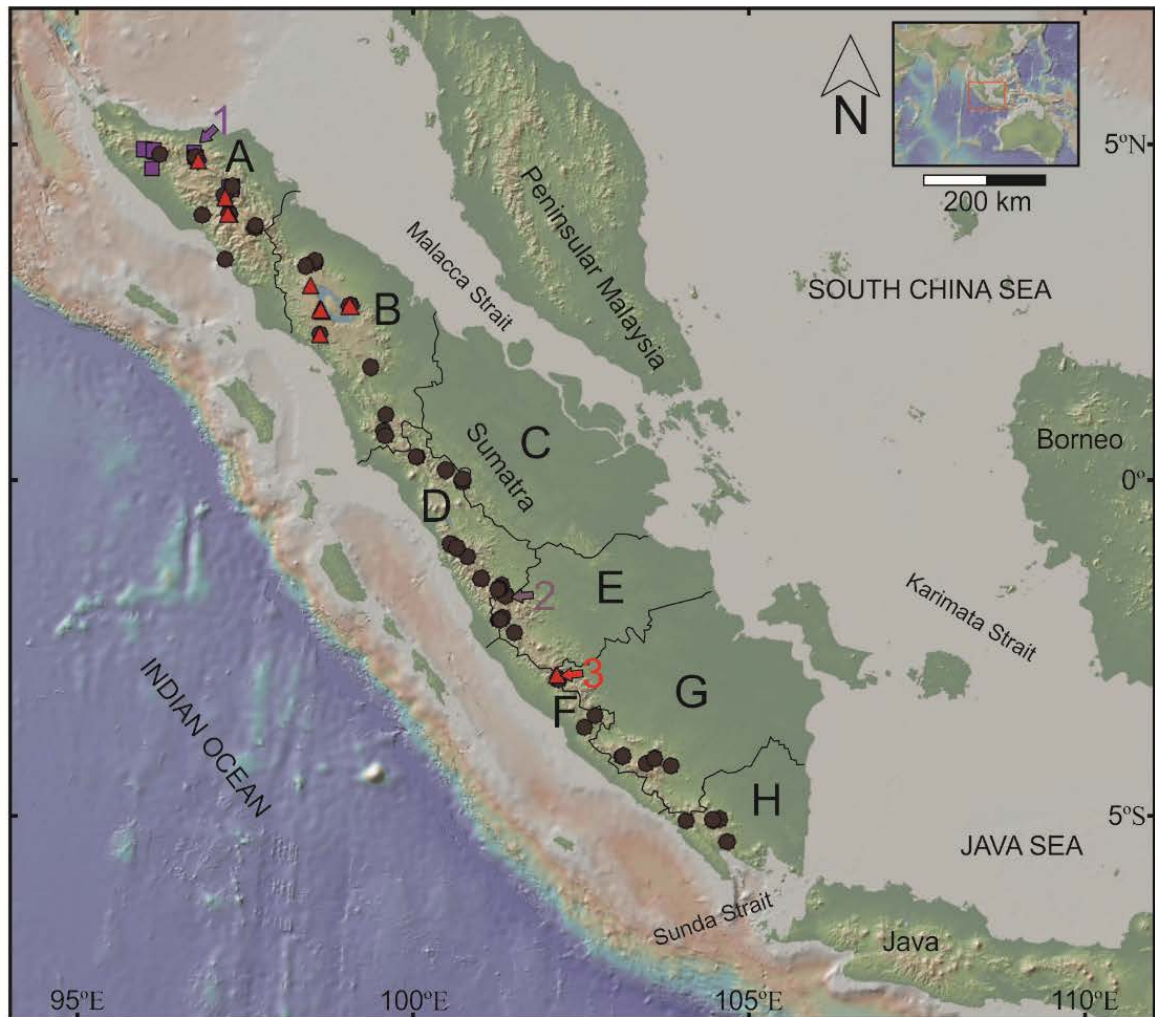


Figure 9. Geographical distribution of *Sumaterana dabulescens* sp. n. (purple squares; type locality purple arrow [1]: Jamat, Taman Buru Linge Isaq), *S. crassiovis* comb. n. (brown circles; type locality brown arrow [2]: Kerinci), and *S. montana* sp. n. (red triangles; type locality red [3]: Gunung Baru, Taman Nasional Kerinci-Seblat). The map was prepared using GeoMap.App (Ryan et al. 2009).

or broken; (5) venter smooth, white or yellowish; (6) tibia length 69.63–79.67% SVL; (7) Finger I 87.67–10.18% Finger II; (8) width of disc of Finger III 73.68–120.00% width of disc of Toe IV; (9) rear of thigh mottled; (10) approx. a quarter of the upper part of iris golden brown and the remaining iris with dense bright red stippling on black background; (11) webbing formula: I(0⁺–1^{1/2})II(0⁺–2)III(0⁺–3⁺)IV(3⁺–0⁺)V; (12) outer metatarsal tubercle absent, inner metatarsal tubercle present; (13) males with paired vocal sacs, undivided nuptial pad, humeral gland absent.

Comparisons. *Sumaterana montana* sp. n. differs from *S. crassiovis* comb. n. (character in parentheses) in these characters: dorsum color brown with scattered light blotches (green background with dark markings on tubercles, lighter area forming irregular network pattern); iris golden brown in the upper quadrant, below with dense bright red stippling on black background (golden yellow

with reddish color in the anterior and posterior sector and dark netting pattern); rear of thigh mottled, light spots on dark background (usually with vertical dark bars on lighter background, as continuation of dorsal thigh); dorsal texture shagreened, generally without tubercles (finely granulated with scattered tubercles); length of Finger I \approx Finger II (Finger I < Finger II); disc width of Finger III \approx disc width of Toe IV (disc width of Finger III > disc width of Toe IV); dorsolateral fold present, thin (absent); webbing formula: I(0⁺–1^{1/2})II(0⁺–2)III(0⁺–3⁺)IV(3⁺–0⁺)V (I(1⁺–1⁺)II(1⁺–1⁺)III(1⁺–2⁺)IV(2⁺–1⁺)V).

Description of holotype. Adult female, gravid; body relatively slender, head width 91.93% head length; snout rounded, slightly pointed in dorsal view, and slightly protruding in lateral view; vomerine teeth present, in oblique groups, between choanae; loreal area deeply concave; canthus rostralis sharp, constricted behind nostrils; rictal ridge

present; eye-nostril distance 133.41% of snout-nostril distance; interorbital distance 99.00% width of upper eyelid; tympanum distinct, translucent, slightly set deep, diameter < 50% ED (TYv/ED = 49.31%, TYh/ED = 44.91%); supratympanic fold present, posttympanic fold absent; pineal spot visible; dorsolateral fold thin, starting in line with supratympanic fold anteriorly to the level of pelvic joint; dorsum and flank skin shagreened; venter skin smooth. Arm slender, lower arm length 19.44% SVL; hand length 32.81% SVL; fingers long, without webbing, tip extended into discs, diamond-like shaped, with circummarginal groove; length of Finger I 96.63% Finger II, Finger III longest; flaps present on the outer phalanges of all fingers; subarticular tubercles distinctive; disc width of Finger III 94.42% disc width of Toe IV. Hindlimbs long, articulation of the heels reach far beyond the tip of snout when limb aligned with body, relative length of femur, foot, and tibia to SVL: 61.01%, 69.63%, and 59.24%, respectively; toe lengths: I < II < III < V < IV, Toe V only slightly longer than Toe III; toe tip extended into diamond-shaped discs; circummarginal groove present; webbing formula: I(0+—1^v)II(0+—2)III(0+—3^v)IV(3—0^v)V; subarticular tubercle distinct; inner metatarsal tubercle distinct, oval, 152.09% T4DW; outer metatarsal tubercle absent; tarsal fold absent.

Holotype coloration. In life, dorsum and upper head brown with scattered light spots; dark dorsolateral line from eye to groin; flanks brown lighting up ventrad, with yellowish color in the posterior region, and many round dark spots; venter yellowish, dark markings on throat up to half of abdomen; golden brown color in at the upper quarter sector of iris, the remaining parts of iris with dense red stippling on black background; a series of dark spots encircled base of upper eye lid; dark brown line from eye to nostril (along canthus rostralis) towards snout tip, not connected to counterpart at tip of snout; dark brown area between eye and tympanum; tympanum pale brown with darker spot in the center; upper lip background brown, lighter posteriorly, with dark brown spots; lower lip brown with few light spots; arm with four dark cross-bars, from elbow to wrist; dorsal face of thigh and tibia brown, each with 6 dark bars; yellow spots on groin; rear of thigh mottled, whitish and yellow spots on brown background; ventral skin of thigh dusted brown on cream background, denser on both lateral side of posterior region; webbing color brown. Color in preservative similar to life coloration; dorsum brown and markings remain the same; yellowish color on flanks and venter changed into white; iris color became gray.

Holotype measurements (mm). SVL 59.60, HL 23.35, HW 21.65, SL 9.14, SN 4.16, EN 5.55, IND 7.58, IOD 5.94, ED 7.95, UEW 6.00, TYv 3.92, TYh 3.57, ET 2.31, LAL 12.32, HAL 20.79, FE 38.66, TL 41.50, FL 37.54, IMTL 3.27, F1L 7.59, F2L 7.73, F3DW 2.03, T4DW 2.15.

Variation. (1) dorsum color background: light pale brown to dark brown; (2) lighter spots on dorsum, none to dense;

variable size; (3) dorsolateral fold: continuous or interrupted, variable thickness; (4) yellowish posterior of flank; pale to brighter; (5) tubercles on flanks: none to many; (6) round dark spots on flanks, few to many; size: small to big; (7) dark marking on throat, chest, and ventrum: none to present and reaching the belly; (8) cross bars on limbs, 3–4 (arm, from elbow to wrist), 5–6 (thigh); variable thickness; (9) mottled pattern on rear of thigh: small, yellow and creamy spots to blotches, on brown background. (Metrics: Tables 4–5).

Sexual dimorphism. Males smaller than females. Tympanum diameter 52.31–92.89% ED in males and 41.54–60.47% ED in females. Adult males with single, undivided nuptial pad covering base of the first finger to subarticular tubercle on dorsal and medial surface. Paired subgular vocal sacs visible, humeral glands absent.

Etymology. The specific epithet is the Latin adjective *montana* in allusion to the distribution of this species at high elevations of the Bukit Barisan mountain range of Sumatra.

Common name. We propose Mountain Cascade Frogs as common English name and Katak Jeram Gunung in Bahasa Indonesia.

Distribution and natural history. Only known from high elevations of northern (Provinsi Aceh and Provinsi Sumatera Utara) and mid (Provinsi Bengkulu) Sumatra (Fig. 9). Known elevation was from 1190–2033 m a.s.l.. The holotype was perching on moss on a root of a dead tree, about 120 cm above a small creek (50 cm wide), ~50 m from Camp 4.5 of Gunung Baru, Desa Ulu Seblat, Taman Nasional Kerinci-Seblat, Kabupaten Lebong, Provinsi Bengkulu (~2000 m a.s.l.). The paratype ZMH.A14194 was observed sitting on the branch, about 300 m away, at the same creek where the holotype was collected, 200 cm above the ground. Accompanying fauna included species of *Rhacophorus* and *Philautus*. Paratypes from the vicinity of Tele, Kecamatan Samosir, Kabupaten Toba-Samosir, Provinsi Sumatera Utara were collected along the stream in the rainforest with patches of coffee plantation. The two specimens of *Sumaterana montana* sp. n. from the stream at Marpunge, Taman Nasional Gunung Leuser, Kabupaten Gayo Lues, Provinsi Aceh were found within low vegetation in the middle of the stream, *S. crassiovis* were abundant syntopically. Specimens from Gunung Sibuatan, Kabupaten Karo, Provinsi Sumatera Utara were found on the stream bank about 1–4 m away from water.

Tadpoles. Unknown.

Sumaterana dabulescens sp. n.

<http://zoobank.org/A4E2A0F3-E0DA-43A1-BEEC-0340026C3BCB>
Figs 2 Clade C, 5b, 6b

Holotype. MZB.AMPH.29396 (male, Fig. 5b), Desa Jamat, Taman Buru Linge Isaq, Kabupaten Aceh Ten-



Figure 10. (a–b) Typical cascading stream habitat of *Sumaterana crassiovis* comb. n. at Taman Nasional Gunung Leuser, Provinsi Aceh. *Sumaterana dabulescens* sp. n. inhabits similar stream habitats. (c) Specimen of *S. dabulescens* sp. n. on a rock near a small cascade in its natural habitat at Taman Buru Linge Isaq, Provinsi Aceh. Photos by U. Arifin.

gah, Provinsi Aceh, Sumatra, Indonesia (04.36482°N, 097.24783°E), 440 m a.s.l., 6 March 2014, 20:02, coll. U. Arifin and G. Cahyadi.

Paratypes (24). ZMH.A14159 (female, Fig. 6b) and MZB.AMPH.29398 (female) and five males MZB.AMPH.29400 (male), MZB.AMPH.29402 (male), ZMH.A14161–62 (males), ZMH.A12667 (male), same data as holotype, (20:00–21:31, except ZMH.A12667 at 13:00). UTA.A64917 (male), stream at Enang-Enang Resort, road of Takengon-Bierut, Provinsi Aceh, (04.88649°N, 096.72689°E, 604 m a.s.l.), 7 August 2015, 20:00–21:00, coll. E. N. Smith and F. Akhsani. UTA.A64919 (male), Kabupaten Bener Meriah, Provinsi Aceh, (04.82623°N, 096.74841°E), 924 m a.s.l., 6 August 2015, coll. I. Sidik and F. Akhsani. UTA.A64921 (male), 04.93841°N, 095.98375°E, 314 m a.s.l., UTA.A64922 (male) and UTA.A64923 (male), 04.93852°N, 095.98294°E, 323 m a.s.l., UTA.A64924 (male), 04.93869°N, 095.98250°E, 333 m a.s.l., Kruong Meuriam, Kecamatan Tangse, Kabupaten Pidie, Provinsi Aceh, 6 June 2016, I. Sidik and W. Trilaksono. MZB.AMPH.29381 (male), MZB.AMPH.29383 (male), MZB.AMPH.29385 (male), MZB.AMPH.29387 (male), MZB.AMPH.29389 (male), ZMH.A14154–58 (males), ZMH.A12668 (male), Kecamatan

Mane, Kabupaten Pidie, Provinsi Aceh, (4.92091°N, 96.12275°E), 761 m a.s.l., 20 March 2014, coll. U. Arifin and G. Cahyadi.

Referred specimens (22). 13 adults, one juvenile, and 8 tadpoles (Appendix 1).

Diagnosis. (1) medium sized frog, SVL males ($n = 27$) 34.69–40.86 mm and females ($n = 3$) 48.03–66.60 mm; (2) dorsum finely granulated with scattered round, distinct tubercles; generally gray with dark gray spots on tubercles; (3) tympanum distinct and translucent (not transparent), supratympanic fold present, posttympanic fold absent; (4) dorsolateral fold absent; (5) venter smooth, granulated posteriorly, white; (6) tibia length 58.08–68.81% SVL; (7) Finger I 58.57–94.16 Finger II; (8) width of disc of Finger III 105.13–144.53% width of disc of Toe IV; (9) rear of thigh mottled; dark blotches on light background; (10) iris silver-gray with dark netting, slightly yellow to orange golden in the upper part; (11) all toes fully webbed to base of discs (I(1^{+/−}–1^{+/−})II(1^{+/−}–1^{+/−})III(1^{+/−}–1^{+/−})IV(1^{+/−}–1^{+/−})V); (12) outer metatarsal tubercle absent, inner metatarsal tubercle present; (13) males with paired vocal sacs, divided nuptial pad, humeral gland absent.

Comparison. *Sumaterana dabulescens* sp. n. differs from *S. crassiovis* comb. n. and *S. montana* sp. n. (character in parentheses: *S. crassiovis* comb. n.; *S. montana* sp. n.) by gray dorsum with dark markings on tubercles, lighter area forming irregular network pattern (green background with dark markings on tubercles, lighter area forming irregular network pattern; brown background with lighter spots, Fig. 5); iris color in life silver gray with dark reticulation, slightly yellow to golden in the upper part (golden yellow with reddish color in the anterior and posterior sector and dark netting pattern; golden brown in the upper quadrant of the iris, remaining iris with dense bright red stippling on black background; Fig. 3); rear of thigh mottled, dark blotches on light background (generally barred, dark bars on light background; mottled, light spots on dark background; Fig. 3); dorsal skin texture coarsely granulated with scattered round tubercle, vary in size and density (finely granulated with scattered tubercles, vary in size, shape, and density; shagreened, without tubercles); dorso-lateral fold absent (absent; present, thin); length of Finger I < Finger II (Finger I < Finger II; Finger I ≈ Finger II); nuptial pad on male divided (undivided; undivided; Fig. 3); webbing full on all toes (I(1⁺—1⁺)II(1⁺—1⁺)III(1⁺—2⁺)IV(2⁺—1⁺)V; I(1—1^{1/2})II(0—2)III(0—3)IV(3—0)V).

Description of holotype. Male, vocal sacs distinct and paired; nuptial pad distinct, divided, covering dorso-medial face of proximal Finger I to level of subarticular tubercle; humeral gland absent; body relatively slender; head width 90.11% head length; in dorsal view, snout obtusely pointed, in lateral view acutely projecting; canthus rostralis sharp, constricted behind nostrils; loreal area deeply concave; vomerine teeth present, in oblique groups, between choanae; tongue lanceolate; rictal ridge present; eye-nostril distance 177.84% snout-nostril distance; interorbital distance 89.27% width of upper eyelid; tympanum distinct, translucent, diameter > 50% ED (TYv/ED = 64.85; TYh/ED = 69.36%); supratympanic fold distinct, posttympanic fold absent; pineal spot visible; dorsolateral fold absent; dorsum and flanks finely granulated with scattered rounded tubercles on the dorsal region up to the upper part of the flanks; venter skin smooth, finely granulated in the posterior region; hindlimb long, articulation of the heels reach far beyond the tip of snout when limb aligned with body; thigh length 94.90% tibia; tibia 64.02% SVL; fingers slender, without webbing; Finger I 94.16% Finger II, Finger III longest; skin flaps present on the outer phalanges of all fingers; subarticular tubercles on fingers and toes distinct; disc width of Finger III 105.13% disc width of Toe IV; discs of toes and fingers diamond-shaped, both with circum-marginal grooves; toe lengths: I < II < III < V < IV, Toe V slightly longer than Toe III; toes fully webbed; inner metatarsal tubercle distinct, oval, 118.59% T4DW; outer metatarsal tubercle absent; tarsal fold absent.

Holotype coloration. In life, dorsum and flanks generally gray; scattered tubercles on the dorsum and the upper part of flanks usually embedded in dark color; lighter area of

the dorsum form an irregular network; golden color with dark spot between eye and nostril; upper lip grayish-white with dark spots (right: 4; left: 4); lower lip whitish with dark spots (right: 3; left: 2); iris silver-gray with dark netting, golden orange in the upper part; tympanum gray with light spot in the center; venter, chest, and throat fully whitish; forearm with four distinct dark cross-bars; hind limbs with thick dark cross-bars dorsally (thigh: 5; tibia: 5); rear of thigh with dark mottling on light gray background; legs light brownish ventrally; webbing brown. Dorsal coloration turned from gray with dark spots into uniformly dark brown in preserved specimens; flanks remained gray, lighter ventrad; iris color changed to uniform gray; no color change in the dark markings or pattern.

Holotype measurements (mm). SVL 36.13, HL 14.87, HW 13.40, SL 5.67, SN 1.94, EN 3.45, IND 3.88, IOD 3.66, ED 5.32, UEW 4.10, TYv 3.45, TYh 3.69, ETD 1.19, LAL 7.76, HAL 12.80, FE 21.95, TL 23.13, FL 19.19, IML 1.85, FIL 4.03, F2L 4.28, F3DW 1.64, T4DW 1.56.

Variation. (1) dorsum generally with round tubercles, lighter spots vary from few to dense; (2) number of dark-round tubercles on dorsum and flanks: few to many tubercles; (3) size of dark round tubercles on dorsum and flanks: small to big tubercle; (4) life coloration of dorsum background: lighter grey or slightly grayish-green to dark gray; (5) iris upper sector: light yellow to orange; (6) dark netting of iris: loose to dense; (7) throat, chest, and venter with or without marking, ranging from none to marking reaching venter; (8) marking on upper and lower lip: variable in size; (9) number of cross bars on limbs: 2–4 (arm between wrist and elbow), 4–7 (thigh); (10) thickness of cross bars on limbs: variable; (11) composition of dark color on lighter background of mottling pattern on rear of thigh: dense to less dense dark pattern on lighter background. Metrics in Tables 4–5.

Sexual dimorphism. Males smaller than females. Tympanum diameter 38.54–72.94% ED in males and 28.18–45.70% ED in females. Adult males with divided nuptial pads and vocal sacs, covering dorso-medial face of proximal Finger I to level of subarticular tubercle, humeral gland absent.

Etymology. The species epithet *dabulescens* is an artificial construct of “dabul”, “gray” in Gayo language, combined with the Latin ending “-escense”, here in the sense of “tending to be”, in allusion to the gray appearance of this species. The Gayo are a local tribe in the Aceh region of Sumatra and after which the Gayo highlands have been named.

Common name. We propose Gayo Cascade Frogs as the English common name and Katak Jeram Gayo as name in Bahasa Indonesia.

Distribution and natural history. Provinsi Aceh, particularly localities in the northern and middle part of Aceh:

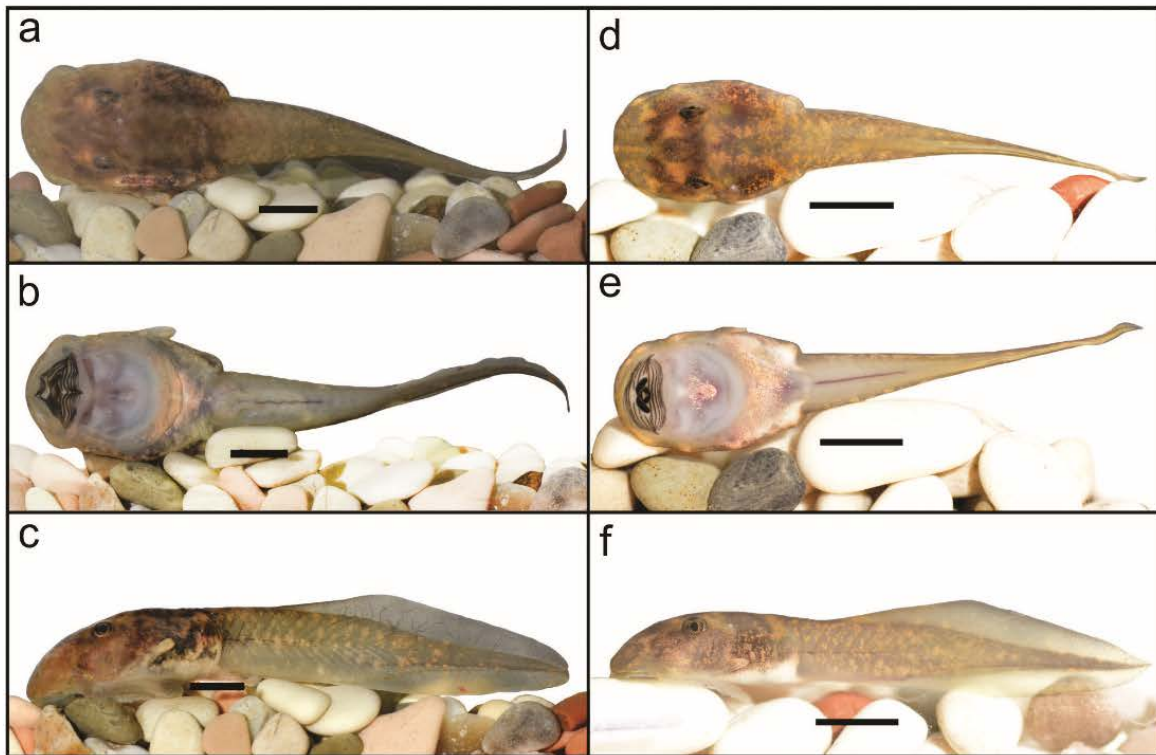


Figure 11. Tadpoles of *Sumaterana crassiovis* comb. n., ZMH.A12650, Provinsi Sumatera Barat (a–c) and *S. dabulescens* sp. n., MZB.AMPH.29411, Provinsi Aceh (d–f) showing dorsal, ventral, and lateral view. Scale 5 mm. Photos by U. Arifin.

Kecamatan Mane, Kabupaten Pidie; Krung Meuriam, Kecamatan Tangse, Kabupaten Pidie; Kabupaten Bener Meriah; Road Takengon-Bierut, Enang-Enang Resort, Kabupaten Aceh Tengah, and Taman Buru Linge-Isaq, Kecamatan Takengon, Kabupaten Aceh Tengah (Fig. 9). Known elevation for this species was 314–1000 m a.s.l.. The holotype was caught 100 cm above water level on a rock wall at the stream slope. The paratypes were perching on vegetation above the stream (15–200 cm above water) or on rocks in the stream or at the stream bank. The other specimens were collected from rocks or vegetation either in stream or approx. 30–100 cm away from the water (e.g., Fig. 10c). Tadpoles were collected between 23:00–24:00 from rocks (diameter ~1 m) in a fast flowing stream (4 m wide), local protected forest, Kecamatan Mane, Kabupaten Pidie.

Tadpoles. We examined eight tadpoles of *Sumaterana dabulescens* sp. n.. Stage 25: UA20140336 (n = 5), ZMH.A12655 (n = 1), Stage 28: MZB.AMPH.29411 (n = 1), Stage 37: MZB.AMPH.29413 (n = 1). Tadpole assignment to species was justified by 100% genetic match (12S rRNA+16S rRNA+tRNA^{val}) of the selected tadpole to an adult from the same locality (Fig. 2). For the following description we refer to MZB.AMPH.29413 (Stage 37) because this specimen has the most advanced developmental stage in the series: in dorsal view, body slightly rectangular, snout broadly rounded, body rounded at both posterior corners; in lateral view, dorsoventrally depressed, streamlined; maximum body width

65.51% body length; eyes dorsolateral, oriented laterally; ED = 1.61 mm; IND/IOD = 48.01%; SN/ES = 45.23%; nostrils directed anterolaterally; nostril opens without raised rim; infraorbital gland cluster (left: 6 glands; right: 3) and postorbital gland cluster (two in each side) present; oral disc ventral, a groove separating upper lip from snout, oral disc width 68.00% body width; edge of oral sucker protruding snout contour in dorsal view; oral disc marginal papillae short, arranged in a single row; on upper lip marginal papillae present only on lateral parts, on lower lip in uninterrupted row; two short submarginal papillae in lateral area of upper lip; I.TRF: 8(5–8)/8(1); upper jaw sheaths broad, heavily keratinized, smooth, undivided, thick but medial part conspicuously thinner than lateral parts; lower jaw sheaths undivided, smooth, V-shaped, thick; both jaw sheaths finely serrated along their edges; very large abdominal sucker in posterior continuation of oral disc, SUL/BL = 70.47%, SUW/BW = 82.94%; spiracle sinistral, tube long, posterior half free from body wall; spiracle directed posterodorsally; anal tube median, free from tail fin, directed posteriorly; strong muscular tail: TMH/BH = 76.19%, TMH/MTH = 66.74%; upper fin convex; maximum upper fin height is approx. 34.99% MTH at approx. 49.00% TAL; tail tip pointed.

In life, dorsal coloration of body and tail densely mottled with brown and golden blotches on a grayish background with dense fine dark stippling; lower flanks with a conspicuous wedge-shaped white area; tail muscle dark with dense-dark stippling overlain by yellowish-golden

to orange mottling; lateral tail vein visible in first third of tail, including dorsal branching along myosepta; upper and lower fin mostly transparent, stippled with melanophores, especially towards the fin margin; yellowish-golden stippling also present in the upper and lower fin; iris background color black, with dense golden to orange iridophore stippling; abdomen whitish laterally and densely stippled with golden iridophores medially; golden iridophores stippling also present in the anterior region of the snout and oral disc; abdominal sucker mostly transparent except for the central spot with golden iridocytes and scattered pigment along the rim. In preservative: color of dorsal region became gray with dense darker dots and dark brown mottling; darker region were obvious on the upper flanks and between eyes and naris; iris all black; lens grayish-white; ventrally uniformly transparent with dark pigments in the anterior region of snout, oral disc, and lateral.

Body proportions between Stage 25, Stage 28, and Stage 37 were variable, e.g., BW/BH in Stage

25 (165.01%) > in Stage 28 (160.72%) > in Stage 37 (144.97%); SUW/BW in Stage 25 (89.58%) > in Stage 28 (86.66%) > in Stage 37 (82.94%); TAL/BL in Stage 25 (153.74%) < Stage 37 (174.06%) < in Stage 28 (183.00%); TMH/BH in Stage 25 (61.38%) < in Stage 37 (76.19%) < in Stage 28 (84.71%); TMH/MTH in Stage 25 (60.53%) < in Stage 37 (66.74%) < in Stage 28 (71.00%). Variation: Body shape in the Stage 25 and Stage 28 were oval; the posterior region gradually arched towards the end of the body (e.g. Stage 28; Fig. 11d–f). Color patterns were also variable among the specimens. For example, in life, MZB.AMPH.29411 (Stage 28, Fig. 11d–f) had less mottling on upper side of body and tail than MZB.AMPH.29413 (Stage 37), more extensive golden color in the iris, smaller orange blotches in the tail region, very few golden spots in both upper or lower fin region, golden iridophores and pigments were less in the ventral region. In preservative, MZB.AMPH.29411 is lighter than MZB.AMPH.29413.

Species keys of *Sumaterana* sp. n. in the context of Southeast Asian Ranidae

- 1 Highly stream-adapted, gastromyzophorous tadpoles abdominal sucker present..... 2
 - Abdominal sucker absent *Abavorana*, *Amnirana*, *Chalcorana*, *Clinotarsus*, *Hylarana*, *Odorrana*, *Pulchrana*, *Staurois*
- 2 Expanded, rounded finger and toe tips *Amolops*
 - Expanded finger and toe tips, pointed and diamond shaped..... 3
- 3 Posttympanic and dorsolateral folds well developed, thick dark \square -shaped over tympanum..... *Huia*
 - Posttympanic and dorsolateral folds well developed, no thick dark \square -shaped over tympanum, endemic to Borneo *Meristogenys*
 - Posttympanic fold absent, dorsolateral folds present or absent, no thick dark \square -shaped over the tympanum, endemic to Sumatra..... 4, *Sumaterana*
- 4 Poorly developed dorsolateral folds, F1 subequal to F2 in length, F3DW subequal to T4DW, dorsum shagreened, brown, sometimes slightly tuberculate..... *S. montana*
 - Dorsolateral folds absent, F1 shorter than F2, F3DW wider than T4DW, dorsum green or greyish with darker markings, finely granulated and tuberculate 5
- 5 Undivided nuptial pad in males, green dorsal background in life, rear of thighs with dark bars *S. crassiovis*
 - Divided nuptial pad in males, gray dorsal background in life, rear of thighs with dark mottling or blotches *S. dabulescens*

Conclusive summary

The taxonomic status of the taxon previously known as *Chalcorana crassiovis* has been problematic for a long time. The case was confounded by the description of a morphologically similar species (*C. kampeni*), the loss of the *C. kampeni* type specimen, insufficient sampling, and a lack of evidence beyond morphology (*viz.*, molecular data). After the original description by Boulenger (1920), only Inger and Iskandar (2015) collected substantial numbers of specimens from that taxonomic group. The exclusively morphological evidence in their validated the existence and provided a re-description of *C. crassiovis*, while questioning the existence of *C. kampeni*. Some authors still continue treating *C. crassiovis* and *C. kampeni* as distinct species, by implication of other evidence. Our study is the first to conduct molecular analyses for these doubtful taxa in a phylogenetic

context. Our phylogenetic hypotheses strongly support *C. crassiovis* as a distinct lineage, and a diverse, monophyletic group (Fig. 2) that is not closely related to other species previously assigned to the genus *Chalcorana*. Our comprehensive sampling along the Sumatran transect yielded specimens with astonishing genetic diversity and morphological differences among the clades comprising the *crassiovis*-group (Fig. 2). We recommend all taxa in Clades A–C to be moved to the proposed new genus *Sumaterana* gen. n.. The new genus currently comprises three known species: *S. crassiovis* comb. n., *S. montana* sp. n. and *S. dabulescens* sp. n.. We consider them to represent valid species (*viz.*, independently evolving lineages) as indicated by genetic, morphological, and ecological differences in comparison to other related species (see above). Furthermore, our molecular data reveal the presence of gastromyzophorus larvae in the species belonging to *Sumaterana* gen. n..

Samples from the type localities of *Sumaterana crassiovis* comb. n. and “*Chalcorana kampeni*” were nested in Clade A in the phylogenetic analysis (Fig. 2) with small amounts of genetic divergence (uncorrected *p*-distance 2.56%, Suppl. materials 3). Furthermore, Inger and Iskandar’s (2005) morphological description of *C. crassiovis* and Boulenger’s (1920) original description matched our Clade A samples well, except for small differences. For example, according to Inger and Iskandar (2005) the tubercles on the dorsum were large and rounded, but in our samples some tubercles were also elongated and variable in size. Inger and Iskandar (2005) noted Finger I equal or slightly longer than Finger II, but in our samples Finger I was consistently shorter than Finger II. This may partially be attributed to different methods of finger length comparison. Inger and Iskandar (2005) reported skin flaps on the outer phalanges of the second and third fingers. We observed flaps present on the outer phalanges of all fingers, although not all of them are movable. This character is difficult to express unambiguously in verbal form (i.e., some may consider them fringes rather than flaps) and graded character states can occur on different fingers. Thus, we do not believe our observations contradict Inger and Iskandar (2005). Based on low genetic divergence within Clade A, morphological homogeneity among samples corroborating the original description of the type (Boulenger 1920) and the re-description by Inger and Iskandar (2005), and the inclusion of topotypic specimens of both previously named taxa, we recommend “*C. kampeni*” be considered a junior synonym of *S. crassiovis* comb. n.

In this study we included four known species of *Huia* (*H. cavitympanum*-type species, Borneo; *H. sumatrana*, Sumatra; *H. masonii*, Java; and *H. melasma*, the mainland Asia). Nevertheless, we were unable to solve the phylogenetic problem of *Huia*, which has previously been considered paraphyletic (Stuart 2008, Pyron and Wiens 2011). Our study perpetuates this conundrum as the type species of *Huia* (*H. cavitympanum*) was shown to be the sister taxon to Bornean *Meristogenys* in our analyses, rather than monophyletic with the other *Huia* species in our dataset. One possibility would have been to subsume all members of the assemblage (*Sumaterana* gen. n., *Meristogenys*, *Huia*, and *Clinotarsus*) under one name (*Clinotarsus*, the oldest available name). We did not choose this option in order to ensure taxonomic stability and because valuable biological information associated with the current monophyletic groups would be dissolved in one genus, such as island endemism (*Sumaterana* gen. n./*Meristogenys*), differences in adult and tadpole morphology and tadpole peculiarities (species of today’s *Clinotarsus* with non-gastromyzophorous tadpoles). Because of the low support in parts of his tree, Stuart (2008) refrained from taxonomic amendments concerning *Huia*, and so do we. Much more effort needs to be invested to solve the perplexing phylogenetic uncertainties concerning *Huia*.

Another interesting subject arises from the optimized phylogenies in our analyses (Fig. 2) with respect to the evolution of larval gastromyzophory in Southeast Asian

ranids. Previously all Asian ranid taxa with gastromyzophorous tadpoles were grouped under the genus *Amolops* (Inger 1966). Yang (1991) split the group into *Amolops*, *Huia*, and *Meristogenys* based on adult and tadpole morphological characters. Molecular systematic studies, however, suggested that the assemblage of *Amolops*, *Huia*, and *Meristogenys* was para- or polyphyletic (Frost et al. 2006, Stuart 2008, Pyron and Wiens 2011). Our phylogenetic analyses indicate that gastromyzophorous tadpoles have likely evolved independently, once in the most recent common ancestor of the group *Huia*+*Sumaterana* gen. n.+*Meristogenys* and again in the ancestor of *Amolops*. Tadpoles from both clades are perplexingly similar morphologically (Noble 1929, Gan et al. 2015), yet molecular evidence implies separate origins. Interestingly, although *Clinotarsus* does not possess gastromyzophorous tadpoles, this genus is nested within *Huia*+*Sumaterana* gen. n.+*Meristogenys* (Stuart 2008, Pyron and Wiens 2011, this study). Therefore, it could be hypothesized that larval gastromyzophory might have been lost secondarily in *Clinotarsus*. Further studies are needed to test and understand the evolution of this larval type in these frogs.

A third case of ranids with gastromyzophorous tadpoles has been reported in *Rana sauteri* (Boulenger, 1909). Its tadpoles are clearly more morphologically (Kuramoto et al. 1984) and biogeographically (Taiwan) distant to *Amolops*, *Huia*, and *Meristogenys*. Gan et al. (2015) summarized that in *R. sauteri* the edge of the abdominal sucker was not as sharply defined as in *Amolops*, *Huia*, and *Meristogenys* (sucker is completely free and rim raised), particularly at the posterior. Moreover, the sucker seems to work differently in *R. sauteri*: the musculus diaphragmatopraecordialis is absent in *R. sauteri*, but well developed in *Amolops*, *Huia*, and *Meristogenys* (Gan et al. 2015, Kuramoto et al. 1984). Finally, other body features of *R. sauteri* (relatively narrow oral sucker and extensive dorsal tail fin) underline the morphological differences between this and to other Asian gastromyzophorous tadpoles, implying possible separate origins and different adaptive scenarios.

We are fully aware that phylogenetic and taxonomic problems persist in our studied taxa. These need to be addressed in the future. Broad thorough geographic sampling of adult and larval forms is a prerequisite to solve phylogenetic quandaries with any amphibian taxa, especially in the species rich tropical realm. Moreover, integrating independent sources of evidence (e.g. DNA, morphology, distribution) is an optimal strategy to accurately and convincingly validate the taxonomic position of doubtful amphibian taxa from hyperdiverse hotspots (Dayrat 2005, Padial et al. 2009, Padial et al. 2010). Distantly related frog species that converged onto similar morphotypes (i.e., ecomorphs) are common in tropical biodiversity hotspots (Bossuyt and Milinkovitch 2002) and can confound taxonomic decisions; examples are documented in Stuart (2008).

Our results are also further evidence that the taxonomic diversity of Sumatran frogs is still significantly underestimated (Iskandar and Colijn 2000, Stuart et al. 2006, Inger et al. 2009), despite the recent increase of am-

phibian species described from the island (e.g. Teynie et al. 2010, Matsui et al. 2012, Hamidy and Kurniati 2015, Smart et al. 2017, Wostl et al. 2017). This also holds true for other herpetofauna, such as reptiles (Orlov and Ryabov 2002, David and Das 2003, Das 2005, Harvey et al. 2015, Wostl et al. 2016). Large scale and strategic sampling efforts are of the utmost priority in order to reveal the true faunal diversity and distribution patterns on this incredibly biodiverse island.

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References

- Aguayo R, Lavilla EO, Candiotti VMF, Camacho T (2009) Living in fast-flowing water: morphology of the gastromyzophorous tadpole of the bufonid *Rhinella quechua* (*R. veraguensis* Group). *Journal of Morphology* 270: 1431–1442. <https://doi.org/10.1002/jmor.10768>
- Altig R (2007) A primer for the morphology of anuran tadpoles. *Herpetological Conservation and Biology* 2(1): 71–74.
- Altig R (2006) Discussions of the origin and evolution of the oral apparatus of anuran tadpoles. *Acta Herpetologica* 1(2): 95–105.
- Altig R, Johnston GF (1989) Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetological Monographs* 3(1989): 81–109. <https://doi.org/10.2307/1466987>
- Biju SD, Garg S, Mahony S, Wijayathilaka N, Senevirathne G, Meegaskumbura M (2014) DNA barcoding, phylogeny and systematics of Golden-backed frogs (*Hylarana*, Ranidae) of the Western Ghats-Sri Lanka biodiversity hotspot, with the description of seven new species. *Contributions to Zoology* 83(4): 269–335.
- Blyth E (1855) Report of the Curator, Zoological Department, for March meeting. *Journal of the Asiatic Society of Bengal* 24: 187–188.
- Blyth E (1856 “1855”) Report for October Meeting, 1855. *Journal of the Asiatic Society of Bengal* 24: 711–723.
- Boistel R, Grosjean S, Lötters S (2005) Tadpole of *Ateolopus franciscus* from French Guyana, with comments on other larvae of the genus (Anura: Bufonidae). *Journal of Herpetology* 39(1): 148–153. [https://doi.org/10.1670/0022-1511\(2005\)039\[0147:TOAFFF\]2.0.CO;2](https://doi.org/10.1670/0022-1511(2005)039[0147:TOAFFF]2.0.CO;2)
- Bossuyt F, Milinkovitch M (2002) Convergent adaptive radiations in Madagascan and Asian ranid frogs reveal covariation between larval and adult traits. *PNAS* 97: 6585–6590. <https://doi.org/10.1073/pnas.97.12.6585>
- Boulenger GA (1882) Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum. Second Edition. London: Taylor and Francis.
- Boulenger GA (1884) Descriptions of new species of reptiles and batrachians in the British Museum.—Part. II. *Annals and Magazine of Natural History, Series 5*, 13: 396–398. <https://doi.org/10.1080/00222938409459259>
- Boulenger GA (1891) On new or little-known Indian and Malayan reptiles and batrachians. *Annals and Magazine of Natural History, Series 6*, 8: 288–292. <https://doi.org/10.1080/00222939109460437>

- Boulenger GA (1893) Descriptions of new reptiles and batrachians obtained in Borneo by Mr. A. Everett and Mr. C. Hose. Proceedings of the Zoological Society of London 1893: 522–528.
- Boulenger GA (1909) Descriptions of four new frogs and a new snake discovered by Mr. H. Sauter in Formosa. Annals and Magazine of Natural History Series 8, 4: 492–495. <https://doi.org/10.1080/00222930908692704>
- Boulenger GA (1920) Reptiles and batrachians collected in Korinchi, West Sumatra, by Messrs. H.C. Robinson and C. Boden Kloss. Journal of the Federated Malay States Museums 8: 285–306.
- Castresana J (2000). Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Molecular Biology and Evolution 17: 540–552. <https://doi.org/10.1093/oxfordjournals.molbev.a026334>
- Chan KO, Brown RM (2017) Did true frogs 'dispersify'? Biology Letters 13(8): 20170299. <https://doi.org/10.1098/rsbl.2017.0299>
- Che J, Pang J, Zhao H, Wu GF, Zhao EM, Zhang YP (2007) Phylogeny of Raninae (Anura: Ranidae) inferred from mitochondrial and nuclear sequences. Molecular Phylogenetics and Evolution 43(1): 1–13. <https://doi.org/10.1016/j.ympev.2006.11.032>
- Cope ED (1865) Sketch of the primary groups of Batrachia s. Salientia. Natural History Review. New Series 5: 97–120.
- Cope ED (1868) An examination of the Reptilia and Batrachia obtained by the Orton Expedition to Ecuador and the Upper Amazon, with notes on other species. Proceedings of the Academy of Natural Sciences of Philadelphia 20: 96–140.
- Dayrat B (2005) Towards integrative taxonomy. Biological Journal of the Linnean Society 85(3): 407–415. <https://doi.org/10.1111/j.1095-8312.2005.00503.x>
- David P, Das I (2003) A new species of the snake genus *Amphiesma* (Serpentes: Colubridae: Natricinae) from western Sumatra, Indonesia. Raffles Bulletin of Zoology 51(2): 413–420.
- Das I (2005) Revision of the genus *Cnemaspis* Strauch, 1887 (Sauria: Gekkonidae), from the Mentawai and adjacent archipelagos off western Sumatra, Indonesia, with the description of four new species. Journal of Herpetology 39(2): 233–247. <https://doi.org/10.1670/61-02A>
- Dereeper A, Guignon V, Blanc G, Audic S, Buffet S, Chevenet F, Dufayard JF, Guindon S, Lefort V, Lescoq M, Claverie JM (2008) Phylogeny.fr: robust phylogenetic analysis for the non-specialist. Nucleic Acids Research 36: 465–469. <https://doi.org/10.1093/nar/gkn180>
- de Queiroz K (2005) A unified concept of species and its consequences for the future of taxonomy. Proceedings-California Academy of Sciences 56: 196–215.
- Dever JA, Fuiten AM, Konu Ö, Wilkinson JA (2012) Cryptic Torrent Frogs of Myanmar: An examination of the *Amolops marmoratus* species complex with the resurrection of *Amolops afghanus* and the identification of a new species. Copeia 2012: 57–76. <https://doi.org/10.1643/CH-10-180>
- Duellman WE (2001) Hylid frogs of Middle America. Society for the Study of Amphibians and Reptiles, USA.
- Dubois A (1892) Notes sur la classification des Ranidae (Amphibiens anoures). Bulletin Mensuel de la Société Linnéenne de Lyon 61: 305–352.
- Fei L, Ye Cy, Jiang Jp (2010) Phylogenetic systematics of Ranidae. Herpetologica Sinica/Liang qi pa xing dong wu xue yan jiu 12: 1–43.
- Frost DR, Grant T, Faivovich J, Bain RH, Haas A, Haddad CF, De Sá RO, Channing A, Wilkinson M, Donnellan SC, Raxworthy CJ (2006) The amphibian tree of life. Bulletin of the American Museum of Natural History 297: 1–370. [https://doi.org/10.1206/0003-0090\(2006\)297\[0001:TATOL\]2.0.CO;2](https://doi.org/10.1206/0003-0090(2006)297[0001:TATOL]2.0.CO;2)
- Frost DR (2017) Amphibian Species of the World: an Online Reference. Version 6.0 (accessed 23. April 2017). Electronic Database accessible at <http://research.amnh.org/herpetology/amphibia/index.html>. American Museum of Natural History, New York, USA.
- Gan L, Hertwig ST, Das I, Haas A (2015) The anatomy and structural connectivity of the abdominal sucker in the tadpoles of *Huia cavitimpanum*, with comparisons to *Meristogenys jerboa* (Lissamphibia: Anura: Ranidae). Journal of Zoological Systematics and Evolutionary Research 54(1): 1–14.
- Günther ACLG (1858) Neue Batrachier in der Sammlung des britischen Museums. Archiv für Naturgeschichte. Berlin 24: 319–328. <https://doi.org/10.5962/bhl.part.5288>
- Günther ACLG (1872) On the reptiles and amphibians of Borneo. Proceedings of the Zoological Society of London 1872: 586–600.
- Goebel AM, Donnelly JM, Atz ME (1999) PCR primers and amplification methods for 12S ribosomal DNA, the control region, cytochrome oxidase I, and cytochrome b in bufonids and other frogs, and an overview of PCR primers which have amplified DNA in amphibians successfully. Molecular Phylogenetics and Evolution 11(1): 163–199. <https://doi.org/10.1006/mpev.1998.0538>
- Gosner KL (1960) A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16: 183–190.
- Grosjean S, Ohler A, Chuaynkern Y, Cruaud C, Hassanin A (2015) Improving biodiversity assessment of anuran amphibians using DNA barcoding of tadpoles. Case studies from Southeast Asia. Comptes Rendus Biologies 338(5): 351–361. <https://doi.org/10.1016/j.crvi.2015.03.015>
- Grossmann W, Manthey U (1997) Amphibien & Reptilien Südostasiens. Natur und Tier Verlag, Münster.
- Guayasamin JM, Bustamante MR, Almeida-Reinoso DIEGO, Funk WC (2006) Glass frogs (Centrolenidae) of Yanayacu Biological Station, Ecuador, with the description of a new species and comments on centrolenid systematics. Zoological Journal of the Linnean Society 147(4): 489–513. <https://doi.org/10.1111/j.1096-3642.2006.00223.x>
- Haas A, Das I (2011) Describing east Malaysian tadpole diversity: status and recommendations for standards and procedures associated with larval amphibian description and documentation. Bonner Zoologische Monographien 57: 29–46.
- Hamidi H, Kumiati H (2015) A new species of tree frog genus *Rhacophorus* from Sumatra, Indonesia (Amphibia, Anura). Zootaxa 3947(1): 049–066. <https://doi.org/10.11646/zootaxa.3947.1.3>
- Harvey MB, o'Connell KA, Barraza G, Riyanto A, Kurniawan N, Smith NE (2015) Two new species of *Cyrtodactylus* (Squamata: Gekkonidae) from the Southern Bukit Barisan Range of Sumatra and an estimation of their phylogeny. Zootaxa 4020(3): 495–516. <https://doi.org/10.11646/zootaxa.4020.3.5>
- Hillis DM, Bull JJ (1993) An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Systematic Biology 42: 182–192. <https://doi.org/10.1093/sysbio/42.2.182>
- Huelsenbeck JP, Ronquist F (2001) MrBayes: Bayesian inference of phylogenetic trees. Bioinformatics Applications Note 17(8): 754–755. <https://doi.org/10.1093/bioinformatics/17.8.754>
- Huelsenbeck JP, Rannala B (2004) Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. Systematic Biology 53: 904–913. <https://doi.org/10.1080/10635150490522629>
- Inger RF (1985) Tadpoles of the forested regions of Borneo. Fieldiana 26: 1–89.

- Inger RF (1966) The systematics and zoogeography of the Amphibia of Borneo. *Fieldiana Zoology* 52: 1–402.
- Inger RF (1986). Diets of tadpoles living in a Bornean rain forest. *Alytes* 5(4): 153–164.
- Inger RF, Gritis PA (1983) Variation in Bornean frogs of the *Amolops jerboa* species group, with description of two new species. *Field Museum of Natural History*. <https://doi.org/10.5962/bhl.title.5644>
- Inger RF, Kottelat M (1998) A new species of ranid frog from Laos. *Raffles Bulletin of Zoology* 46: 29–34.
- Inger RF, Voris HK (2001) The biogeographical relations of the frogs and snakes of Sundaland. *Journal of Biogeography* 28(7): 863–891. <https://doi.org/10.1046/j.1365-2699.2001.00580.x>
- Inger RF, Iskandar DT (2005) A collection of amphibians from West Sumatra, with description of a new species of *Megophrys* (Amphibia: Anura). *The Raffles Bulletin of Zoology* 53(1): 133–142.
- Inger RF, Stuart BL, Iskandar DT (2009) Systematics of a widespread Southeast Asian frog, *Rana chalconota* (Amphibia: Anura: Ranidae). *Zoological Journal of Linnean Society* 155(1): 123–147. <https://doi.org/10.1111/j.1096-3642.2008.00440.x>
- Inger RF, Stuebing RB (2009) New species and new records of Bornean frogs (Amphibia: Anura). *The Raffles Bulletin of Zoology* 57(2): 527–535.
- Iskandar DT, Mumpuni (2004) *Chalcorana crassiovis*. (errata version published in 2016) The IUCN Red List of Threatened Species 2004: e.T58580.A89367065. Downloaded on 16 April 2017.
- Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. *Molecular Biology and Evolution* 33(7): 1870–1874. <https://doi.org/10.1093/molbev/msw054>.
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30(4): 772–780. <https://doi.org/10.1093/molbev/mst010>
- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Mentjies P, Drummond A (2012) Geneious basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28(12): 1647–1649. <https://doi.org/10.1093/bioinformatics/bts199>
- Kluge AG (1989) A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). *Systematics Zoology* 38: 7–25. <https://doi.org/10.2307/2992432>
- Kluge AG (2004) On total evidence: for the record. *Cladistics* 20: 205–207. <https://doi.org/10.1111/j.1096-0031.2004.00020.x>
- Kok PJ, Kalamandean M (2008) Introduction to the taxonomy of the Amphibians of Kaieteur National Park, Guyana. *Abc Taxa*, Belgium.
- Kuramoto M, Wang CS, Yü HT (1984) Breeding, larval morphology and experimental hybridization of Taiwanese Brown Frogs, *Rana longicrus* and *R. sauteri*. *Journal of Herpetology* 18(4): 387–395. <https://doi.org/10.2307/1564101>
- Lanfear R, Calcott B, Ho SY, Guindon S (2012) PartitionFinder: Combined Selection of Partitioning Schemes and Substitution Models for Phylogenetic Analyses. *Molecular Biology and Evolution* 29(6): 1695–1701. <https://doi.org/10.1093/molbev/mss020>
- Liu W, Yang D, Ferraris C, Matsui M (2000) *Amolops beilulus*: A new species of stream-breeding frog from western Yunnan, China (Anura: Ranidae). *Copeia* 2000(2): 536–541. [https://doi.org/10.1643/0045-8511\(2000\)000\[0536:ABANSO\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2000)000[0536:ABANSO]2.0.CO;2)
- Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In *Proceedings of the Gateway Computing Environments Workshop (GCE)*, pp 1–8. New Orleans, LA. <https://doi.org/10.1109/GCE.2010.5676129>
- Manthey U, Denzer W (2014) Südostasiatische Anuren im Fokus Spezies der Gattung *Huia* (sensu lato) Yang, 1991 (amphibia: Anura: Ranidae). *Sauria* 36(4): 31–48.
- Malkmus R, Manthey U, Vogel G, Hoffmann P, Kosuch J (2002) Amphibians and Reptiles of Mount Kinabalu (North Borneo). A. R. G. Gantner K G, Koeltz Scientific Books, Koenigstein.
- Matsui M, Nabhitabhata J (2006) A new species of *Amolops* from Thailand (Amphibia, Anura, Ranidae). *Zoological Science* 23(8): 727–732. <https://doi.org/10.2108/zsj.23.727>
- Matsui M, Shimada T, Liu WZ, Maryati M, Khonsue W, Orlov N (2006) Phylogenetic relationships of Oriental torrent frogs in the genus *Amolops* and its allies (Amphibia, Anura, Ranidae). *Molecular Phylogenetic and Evolution* 38(3): 659–666. <https://doi.org/10.1016/j.ympev.2005.11.019>
- Matsui M, Yambun P, Sudin A (2007) Taxonomic relationships of *Ansonia avotis* (Inger, Tan and Yambun 2001) and *Pedostibes maculatus* (Mocquard 1890), with a description of a new genus (Amphibia, Bufonidae). *Zoological Science* 24: 1159–1166. <https://doi.org/10.2108/zsj.24.1159>
- Matsui M, Shimada T, Sudin A (2010) A New Species of *Meristogenys* (Amphibia, Anura, Ranidae) from Sabah, Borneo. *Zoological Science* 27: 61–66. <https://doi.org/10.2108/zsj.27.61>
- Matsui M, Mumpuni, Hamidy A (2012) Description of a new species of *Hylarana* from Sumatra (Amphibia, Anura). *Current Herpetology* 31(1): 38–46. <https://doi.org/10.5358/hj.31.38>
- McDiarmid, Altig A (1999) *Tadpole: The Biology of Anuran Larvae* (pp. 453). The University of Chicago Press.
- Mulcahy DG, Beckstead TH, Sites Jr JW (2011) Molecular systematics of the *Leptodeirini* (Colubroidea: Dipsadidae) revisited: Species-tree analyses and multi-locus data. *Copeia* 2011: 407–417. <https://doi.org/10.1643/CH-10-058>
- Noble GK (1929) The adaptive modifications of the arboreal tadpoles of *Hoplophryne* and the torrent tadpoles of *Staurois*. *Bulletin American Museum of Natural History* 58: 291–334.
- Nodzinski E, Inger RF (1990) Uncoupling of related structural changes in metamorphosing torrent-dwelling tadpoles. *Copeia* 1990(4): 1047–1054. <https://doi.org/10.2307/1446488>
- Ngo A, Murphy RW, Liu W, Lathrop A, Orlov NL (2006) The phylogenetic relationships of the Chinese and Vietnamese waterfall frogs of the genus *Amolops*. *Amphibian-Reptiles* 27: 81–92. <https://doi.org/10.1163/156853806776052010>
- Oberhammer E, Barten C, Schweizer M, Das I, Haas A, Hertwig ST (2014) Description of the tadpoles of three rare species of *Megophryid* frogs (Amphibia: Anura: Megophryidae) from Gunung Mulu, Sarawak, Malaysia. *Zootaxa* 3835(1): 059–079. <https://doi.org/10.11646/zootaxa.3835.1.3>
- Oliver LA, Prendini E, Kraus F, Raxworthy CJ (2015) Systematics and biogeography of the *Hylarana* frog (Anura: Ranidae) radiation across tropical Australasia, Southeast Asia, and Africa. *Molecular Phylogenetic and Evolution* 90: 176–192. <https://doi.org/10.1016/j.ympev.2015.05.001>
- Orlov NL, Ryabov SA (2002) A new species of the genus *Boiga* (Serpentes, Colubridae, Colubrinae) from Tanahjampea island and description of (Black Form) of *Boiga cynodon* complex from Sumatra (Indonesia). *Russian Journal of Herpetology* 9(1): 33–56.

- Padial JM, Castroviejo-Fisher S, Köhler J, Vilà C, Chaparro JC, De la Riva I (2009) Deciphering the products of evolution at the species level: the need for an integrative taxonomy. *Zoologica Scripta* 38(4): 431–447. <https://doi.org/10.1111/j.1463-6409.2008.00381.x>
- Padial JM, Miralles A, De la Riva I, Vences M (2010) The integrative future of taxonomy. *Frontiers in Zoology* 7(16): 1–14. <https://doi.org/10.1186/1742-9994-7-16>
- Pauly GB, Hillis DM, Cannatella DC (2004) The history of a nearctic colonization: molecular phylogenetics and biogeography of the Neartic toads (*Bufo*). *Evolution* 58: 2517–2535. <https://doi.org/10.1111/j.0014-3820.2004.tb00881.x>
- Pyron A, Wiens JJ (2011) A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution* 61(2): 543–583. <https://doi.org/10.1016/j.ympev.2011.06.012>
- Rambaut A, Suchard M, Xie W, Drummond A (2014) Tracer v. 1.6. Institute of Evolutionary Biology, University of Edinburgh.
- Rao D, Yang D (1994) The study of early development and evolution of *Torrentophryne aspiniia*. *Zoological Research* 15: 142–157.
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19(12): 1572–1574. <https://doi.org/10.1093/bioinformatics/btg180>
- Ribeiro-Júnior MA, Gardner TA, Ávila-Pires TC (2008) Evaluating the effectiveness of herpetofaunal sampling techniques across a gradient of habitat change in a tropical forest landscape. *Journal of Herpetology* 42(4): 733–749. <https://doi.org/10.1670/07-097R3.1>
- Ryan WBF, Carbotte SM, Coplan JO, O'Hara S, Melkonian A, Arko R, Weissel RA, Ferrini V, Goodwillie A, Nitsche F, Bonczkowski J, Zemsky R (2009) Global Multi-Resolution Topography synthesis. *Geochemistry Geophysics Geosystems* 10(3): Q03014. <https://doi.org/10.1029/2008GC002332>
- Rueda-Solano LA, Vargas-Salinas F, Rivera-Correa M (2015) The highland tadpole of the harlequin frog *Ateolopus carrikeri* (Anura: Bufonidae) with an analysis of its microhabitat preferences. *Salamandra* 51: 25–32.
- Schlegel H (1837) *Abbildungen neuer oder unvollständig bekannter Amphibien, nach der Natur oder dem Leben entworfen, herausgegeben und mit einem erläuternden Texte begleitet. Part 1.* Düsseldorf: Amz & Co..
- Shimada T, Matsui M, Nishikawa K, Eto K (2015) A New Species of *Meristogenys* (Anura: Ranidae) from Sarawak, Borneo. *Zoological Science* 32(5): 474–484. <https://doi.org/10.2108/zs140289>
- Shimada T, Matsui M, Sudin A, Mohamed M (2007) Identity of larval *Meristogenys* from a single stream in Sabah, Malaysia (Amphibia: Ranidae). *Zoological Journal of Linnean Society* 151: 173–189. <https://doi.org/10.1111/j.1096-3642.2007.00319.x>
- Shimada T, Matsui M, Yambun P, Lakim M, Mohamed M (2008) Detection of two cryptic taxa in *Meristogenys amoropalamus* (Amphibia, Ranidae) through nuclear and mitochondrial DNA analyses. *Zootaxa* 1843: 24–34.
- Shimada T, Matsui M, Yambun P, Sudin A (2011) A taxonomic study of Whitehead's torrent frog, *Meristogenys whiteheadi*, with descriptions of two new species (Amphibia: Ranidae). *Zoological Journal of Linnean Society* 161: 157–183. <https://doi.org/10.1111/j.1096-3642.2010.00641.x>
- Smart U, Sarker GC, Arifin U, Harvey MB, Sidik I, Hamidy A, Kumiawan N, Smith EN (2017) A new genus and two new species of arboreal toads from the highlands of Sumatra with a phylogeny of Sundaland toad genera. *Herpetologica* 73: 63–75. <https://doi.org/10.1655/Herpetologica-D-16-00041>
- Stamatakis A (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Stuart BL (2008) The phylogenetic problem of *Huia* (Amphibia: Ranidae). *Molecular Phylogenetic and Evolution* 46(1): 49–60. <https://doi.org/10.1016/j.ympev.2007.09.016>
- Stuart BL, Chan-ard T (2005) Two new *Huia* (Amphibia: Ranidae) from Laos and Thailand. *Copeia* 2005(2): 279–289. <https://doi.org/10.1643/CH-04-137R3>
- Stuart BL, Inger RF, Voris HK (2006) High level of cryptic species diversity revealed by sympatric lineages of Southeast Asian forest frogs. *Biology Letters* 2: 470–474. <https://doi.org/10.1098/rsbl.2006.0505>
- Talavera G, Castresana J (2007) Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic Biology* 56: 564–577. <https://doi.org/10.1080/10635150701472164>
- Teynie A, David P, Ohler A (2010) Note on a collection of Amphibians and Reptiles from Western Sumatra (Indonesia), with the description of a new species of the genus *Bufo*. *Zootaxa* 2416: 1–43.
- Tschudi Jv (1838) *Classification der Batrachier mit Berücksichtigung der fossilen Thiere dieser Abtheilung der Reptilien.* Neuchâtel: Petitpierre.
- Van Kampen PN (1910) *Beitrag zur Kenntnis der Amphibienlarven des indischen Archipels.* *Natuurkundig Tijdschrift voor Nederlandsch-Indië* 69: 25–48.
- Van Kampen PN (1923) *The amphibia of the Indo-Australian archipelago.* EJ Brill, Ltd.
- Van Tuijl L (1995) Revised catalogue of the type specimens of recent amphibians and reptiles in the "Zoologisch Museum", University of Amsterdam, The Netherlands. *Bulletin. Zoologisch Museum, Universiteit van Amsterdam* 14: 125–144.
- Waser LE, Schweizer M, Haas A, Das I, Jankowski A, Min PY, Hertwig ST (2016) From a lost world: an integrative phylogenetic analysis of *Ansonia stoliczka*, 1870 (Lissamphibia: Anura: Bufonidae), with the description of a new species. *Organisms Diversity & Evolution* 1–17. <https://doi.org/10.1007/s13127-016-0294-2>
- Watters JL, Cummings ST, Flanagan RL, Siler CD (2016) Review of morphometric measurements used in anuran species descriptions and recommendations for a standardized approach. *Zootaxa* 4072(4): 477–495. <https://doi.org/10.11646/zootaxa.4072.4.6>
- Wostl E, Sidik I, Trilaksono W, Shaney KJ, Kumiawan N, Smith EN (2016) Taxonomic status of the Sumatran Pitviper *Trimeresurus (Popeia) toba* David, Petri, Vogel & Doria, 2009 (Squamata: Viperidae) and other Sunda Shelf species of the subgenus *Popeia*. *Journal of Herpetology* 50(4): 633–641. <https://doi.org/10.1670/15-045>
- Wostl E, Riyanto A, Hamidy A, Kumiawan N, Smith EN, Harvey MB (2017) A taxonomic revision of the *Philautus* (Anura: Rhacophoridae) of Sumatra with the description of four new species. *Herpetological Monographs* 31(1): 70–113. <https://doi.org/10.1655/HERP-MONOGRAPHS-D-16-00007>
- Yang DT (1991) Phylogenetic systematics of the *Amolops* group of ranid frogs of southeastern Asia and the Greater Sunda Islands. *Fieldiana: Zoology New Series* 63: 1–42. <https://doi.org/10.5962/bhl.title.2854>

Appendix 1

Specimens examined

(* bold = measured, star (*) = sequenced)

Sumaterana crassiovis comb. n. (adults, n = 262)

Provinsi Aceh – Kabupaten Pidie, Mountain above Geumpang, Transmigrasi community, old road to mining camp, 4.85824°N, 96.21348°E, 1090 m a.s.l., UTA.A64868; Kabupaten Bener Meriah, road between Bireun-Takengon, 4.82623°N, 96.74841°E, 924 m a.s.l., UTA.A64856-60; Kabupaten Bener Meriah, foot of Berni Terlong, near Desa Rambune, pantan Pediangah, Tihmang gagah, 4.76379°N, 96.78131°E, 1184 m a.s.l., UTA.A64853; Kabupaten Aceh Tengah, Taman Buru Linge-Isaq, 4.37958°N, 97.29158°E, 1000 m a.s.l., **MZB.AMPH.29196**, **MZB.AMPH.29198**, **ZMH.A14168–69**; Kabupaten Gayo Lues, Kampung Ise-Ise, 4.25511°N, 97.18366°E, 1129 m a.s.l., UTA.A64855; Kabupaten Gayo Lues, Kedah, Blangkajeren, Rain Forest lodge, 3.97806°N, 97.25314°E, 1376 m a.s.l., UTA.A64851, UTA.A64852; Kabupaten Gayo Lues, Marpunge, Taman Nasional Gunung Leuser, 3.79289°N, 97.64417°E, 1190 m a.s.l., **MZB.AMPH.29188**, **MZB.AMPH.29190**, **MZB.AMPH.29192**, **MZB.AMPH.29194**, **ZMH.A14216–17**, **ZMH.A14219**; Kabupaten Nagan Raya, Road from Nagan Raya to Terangun, 3.95839°N, 96.85218°E, 795 m a.s.l., UTA.A64864–66; Kabupaten Aceh Selatan, Gunung Putri Tidur near Tapak Tuan, 3.2921°N, 97.19642°E, 481 m a.s.l., UTA.A64867; Kabupaten Gayo Lues, Marpunge, Taman Nasional Gunung Leuser, 3.77103°N, 97.63801°E, 1065 m a.s.l., **MZB.AMPH.29186***, **ZMH.A14218**.

Provinsi Sumatera Utara – Kabupaten Dili Serdang, Sungai DAM Bumi Perkemahan Sibolangit, 3.27347°N, 98.53586°E, 881–965 m a.s.l., **MZB.AMPH.29326***, **MZB.AMPH.29327–29**, **MZB.AMPH.29330–37**; Kabupaten Dili Serdang, Sungai Batu Belah Bumi Perkemahan Sibolangit, 3.27522°N, 98.53613°E, 880–965 m a.s.l., **MZB.AMPH.29338–39**, **MZB.AMPH.29340–41**, **MZB.AMPH.29342–44**; Kabupaten Dili Serdang, Sungai Derek Bumi Perkemahan Sibolangit, 3.27688°N, 98.53472°E, 877–908 m a.s.l., **MZB.AMPH.29345–47**; Kabupaten Karo, sungai Taman Wisata Alam Deleng Lancuk, 3.19668°N, 98.39298°E, 1416–1427 m a.s.l., **MZB.AMPH.29348–49**, **MZB.AMPH.29350**, **MZB.AMPH.29351**, **MZB.AMPH.29352**, **MZB.AMPH.29353–54**; Kabupaten Karo, Kecamatan Berastagi, Air Terjun Sikulikap, 3.24047°N, 98.53878°E, 1156 m a.s.l., **MZB.AMPH.23492–93**, UTA.A64879–81; Kabupaten Toba Samosir, Gunung Panglulubao, 2.60514°N, 99.04629°E, 1397 m a.s.l., **MZB.AMPH.23496–97**, **MZB.AMPH.23506**, UTA.A64833*, UTA.A64882–86; Kabupaten Humbung Hasundutan, Gunung Pinaipan, 2.18325°N, 98.60513°E, 1309 m a.s.l., **MZB.AMPH.23498**; Kabupaten Tapanuli Selatan, slope of Gunung T. Anjing, 1.68449°N, 99.34737°E, 1253 m a.s.l., **MZB.AMPH.23505**; Kabupaten Mandailing Natal, Huta Baringin Julu, Taman Nasional Batang Gadis, 0.66636°N, 99.57191°E, 1271 m a.s.l., UTA.A64894–902, **MZB.AMPH.23507–11**, UTA.A64835*, **MZB.AMPH.23513–14**; Kabupaten Mandailing Natal, slope of Dolok Malea above Kampung Mompang, 0.97500°N, 99.57959°E, 991

m a.s.l., **MZB.AMPH.23499–501**, **MZB.AMPH.23503–04**, UTA.A64887–93; Kabupaten Mandailing Natal, road between Panyabungan and Natal, 0.72544°N, 99.54497°E, 804 m a.s.l., **MZB.AMPH.23490–91**.

Provinsi Sumatera Barat – Kabupaten Pasaman, Kecamatan Panti, Stream 3 Cagar Alam Rimbo Panti, 0.35220°N, 100.04933°E, 425 m a.s.l., **MZB.AMPH.29200***, **MZB.AMPH.29202**, **MZB.AMPH.29204**, **ZMH.A14170–73**; Kabupaten Pasaman, Kecamatan Panti, Stream 1 Batu Ampar, Cagar Alam Rimbo Panti, 0.35056°N, 100.04490°E, 450–500 m a.s.l., **MZB.AMPH.29206**, **MZB.AMPH.29208**, **MZB.AMPH.29210**, **ZMH.A14191–92**; Kabupaten Pasaman, Kecamatan Panti, Stream 1 Batu Ampar, Cagar Alam Rimbo Panti, 0.34789°N, 100.03748°E, 1000 m a.s.l., MVZ271526*; Kabupaten Payakumbuh, Kecamatan Pangkalan Koto Baru, Road from Payakumbuh to Pangkalan, 0.01905°N, 100.72205°E, 621 m a.s.l., UTA.A64847; Kabupaten Payakumbuh, small creek next to main road connecting Payakumbuh-Riau, 0.01916°S, 100.72226°E, 606–624 m a.s.l., **MZB.AMPH.29320***, **MZB.AMPH.29322**, **MZB.AMPH.29324**, **ZMH.A14223–25**; Kabupaten Solok, Kecamatan Gunung Talang, Stream 1 Lubuak Sulasiah, 0.95782°S, 100.57112°E, 1040–1084 m a.s.l., **MZB.AMPH.29212**, **MZB.AMPH.29214**, **MZB.AMPH.29216**, **MZB.AMPH.29218**, **MZB.AMPH.29220**, **MZB.AMPH.29222**, **MZB.AMPH.29224**, **ZMH.A14206–13**; Kabupaten Solok, Kecamatan Gunung Talang, Stream 2 Lubuak Sulasiah, 0.94529°S, 100.54630°E, 1104 m a.s.l., **MZB.AMPH.29226**; Kabupaten Solok, Kecamatan Gunung Talang, Desa Kayu Jao, 0.99717°S, 100.63952°E, 1270 m a.s.l., **ZMH.A14195**; Kabupaten Solok, Kecamatan Gunung Talang, Stream 1 Desa Kayu Jao, 0.99557°S, 100.64334°E, 1315–1350 m a.s.l., **MZB.AMPH.29228**, **MZB.AMPH.29230**, **ZMH.A14198**; Kabupaten Solok, Kecamatan Gunung Talang, Stream 2 Kayu Jao, 0.99980°S, 100.63550°E, 1195 m a.s.l., **MZB.AMPH.29232**, **MZB.AMPH.29234**, **ZMH.A14221–22**; Kabupaten Solok, Road from Kayu Aro-Padang near Surian, 1.13573°S, 100.80255°E, 1417 m a.s.l., **MZB.AMPH.22341**, UTA.A62438; Kabupaten Solok Selatan, Muara Labuh, Taman Nasional Kerinci Seblat, 1.45534°S, 101.00020°E, 640–643 m a.s.l., **MZB.AMPH.29253**, **MZB.AMPH.29255**, **ZMH.A14136–37**; Kabupaten Solok Selatan, Padang Aro, Taman Nasional Kerinci Seblat, 1.559317°S, 101.31072°E, 605 m a.s.l., **ZMH.A14197***; Kabupaten Solok Selatan, Batang Blangir, Padang Aro, Taman Nasional Kerinci Seblat, 1.61750°S, 101.24780°E, 975 m a.s.l., **MZB.AMPH.29237**, **MZB.AMPH.29241**, **MZB.AMPH.29243**, **MZB.AMPH.29245**, **MZB.AMPH.29247**, **MZB.AMPH.29239**, **ZMH.A14179–84**; Kabupaten Solok Selatan, stream at the foot hill of Lake Bontak, Taman Nasional Kerinci Seblat, 1.60325°S, 101.26391°E, 850 m a.s.l., **MZB.AMPH.29249**, **MZB.AMPH.29251**, **ZMH.A14226–28**.

Provinsi Jambi – Kabupaten Kerinci, trail to Danau Tujuh, 1.71076°S, 101.36986°E, 1506 m a.s.l., **MZB.AMPH.22221**, **MZB.AMPH.22222**, **MZB.AMPH.22223**, **MZB.AMPH.22334**, UTA.A64904, UTA.A64905, UTA.A64906; Kabupaten Kerinci, road between Sungai Penuh and Tapan, west of crest, 2.04139°S, 101.31462°E 1250 m a.s.l., **MZB.AMPH.22345**; Kabupaten Kerinci, Gunung Kuyit, Taman Nasional Kerinci-Seblat, 2.26013°S, 101.49512°E, 1355 m a.s.l., **MZB.AMPH.22336**, **MZB.AMPH.22338**, **MZB.AMPH.22339***, **MZB.AMPH.22340**,

UTA.A64907–13; Kabupaten Kerinci, Bukit Tapan, Taman Nasional Kerinci Seblat, 2.06988°S, 101.26235°E, 726 m a.s.l., **MZB.AMPH.29257**, 2.06543°S, 101.26771°E, 787 m a.s.l., **ZMH.A14193**; Kabupaten Kerinci, Sungai Kuyit, Bukit Tapan, Taman Nasional Kerinci Seblat, 2.06925°S, 101.28656°E, 909–916 m a.s.l., **MZB.AMPH.29259**, **MZB.AMPH.29261**, **MZB.AMPH.29263**, **MZB.AMPH.29265**, **MZB.AMPH.29267**, **MZB.AMPH.29269**, **ZMH.A14201–05**.

Provinsi Bengkulu. – Kabupaten Lebong, Stream at Camp 2 Desa Seblat Ulu, Taman Nasional Kerinci Seblat, 2.95330°S, 102.13955°E, 758–774 m a.s.l., **ZMH.A14166–67**, **MZB.AMPH.29271**; Kabupaten Lebong, Stream at Camp 3 Desa Seblat Ulu, Taman Nasional Kerinci Seblat, 2.95100°S, 102.16345°E, 716–723 m a.s.l., **MZB.AMPH.29273**, **MZB.AMPH.29275***, **MZB.AMPH.29277**; Kabupaten Lebong, Stream at Camp 1 Desa Seblat Ulu, Taman Nasional Kerinci Seblat, 2.95330°S, 102.13955°E, 723 m a.s.l., **MZB.AMPH.29276**, **ZMH.A14165**.

Provinsi Sumatera Selatan. – Kabupaten Pagar Alam Selatan, road from Manna to Pagar Alam, 4.11296°S, 103.10007°E, 772 m a.s.l., **UTA.A64870**, **UTA.A64873–75**, **UTA.A64877**; Kabupaten Muara Enim, Gunung Patah near Desa Segamit, 4.21742°S, 103.46823°E, 1545 m a.s.l., **UTA.A64849**; Kabupaten Muara Enim, Sungai Lematan Desa Batu Surau, 4.13725°S, 103.58640°E, 1048–1069 m a.s.l., **MZB.AMPH.29312**, **MZB.AMPH.29314**, **MZB.AMPH.29316**, **MZB.AMPH.29318**, **ZMH.A14149***, **ZMH.A14150–53**; Kabupaten Ogan Komering Ulu Selatan, Kecamatan Kisam Tinggi, Gunung Nanti, Desa Gunung Megang, 4.24586°S, 103.83415°E, 1048–1062 m a.s.l., **MZB.AMPH.29302**, **MZB.AMPH.29304**, **MZB.AMPH.29306**, **MZB.AMPH.29308**, **ZMH.A14140–43**, **MZB.AMPH.29310**, 4.24543°S, 103.8352°E, 874 m a.s.l., **ZMH.A14139***.

Provinsi Lampung. – Kabupaten Lampung Barat, Curug Berdua, Gunung Abung, Desa Purajaya, 5.03730°S, 104.54828°E, 956–979 m a.s.l., **MZB.AMPH.29282**, **MZB.AMPH.29284**, **MZB.AMPH.29286**, **MZB.AMPH.29288***, **MZB.AMPH.29290**, **ZMH.A14144–48**; Kabupaten Lampung Barat, Sumber Jaya, 5.04456°S, 104.44930°E, 1022 m a.s.l., **MZB.AMPH.29292**, **MZB.AMPH.29294**, **ZMH.A14214–15**; Kabupaten Lampung Barat, Road Liwa to Krui, 5.06458°S, 104.05465°E, 673 m a.s.l., **MZB.AMPH.22344**, **MZB.AMPH.22343**, **UTA.A62440**; Kabupaten Lampung Barat, Sungai Pauh, Gedong Surian, 5.06651°S, 104.46261°E, 935–961 m a.s.l., **ZMH.A14200**, **MZB.AMPH.29279**, **ZMH.A14199**; Kabupaten Tanggamus, Air Terjun Talang Ogan, 5.37933°S, 104.66043°E, 754–717 m a.s.l., **MZB.AMPH.29296**, **MZB.AMPH.29298**, **MZB.AMPH.29300**, **ZMH.A14185*–86**, **ZMH.A14188**, **ZMH.A14186**.

Sumaterana crassiovis comb. n. (tadpoles, n = 21)

Provinsi Sumatera Barat. – Kabupaten Lima Puluh Koto, Desa Tanjung Bungo, 0.15188°N, 100.47468°E, 388 m a.s.l., **MZB.AMPH.29363**; Kabupaten Payakumbuh, Stream next to the road between Payakumbuh-Riau 0.01917°S, 100.72226°E, 600–627 m a.s.l., **MZB.AMPH.29355***, **MZB.AMPH.29356**, **ZMH.A12649** (n = 6); Kabupaten Solok Selatan, Muara Labuh, Taman Nasional Kerinci-Seblat, 1.45534°S, 101.00020°E, 640–643 m a.s.l., **MZB.AMPH.29359**, **ZMH.A12650***; Kabupaten

Solok Selatan, Kecamatan Sangir, Desa Padang Aro, Taman Nasional Kerinci-Seblat, 1.61750°S, 101.24780°E, 975 m a.s.l., **MZB.AMPH.29361**, **ZMH.A12651**, **ZMH.A12652** (n = 5).

Provinsi Sumatera Selatan. – Kabupaten Muara Enim, Desa Batu Surau, 4.13725°S, 103.58640°E, 1048–1069 m a.s.l., **MZB.AMPH.29364**, **MZB.AMPH.29365***.

Sumaterana montana sp. n. (adults, n = 28)

Provinsi Aceh. – Kabupaten Bener Meriah, foot of Berni Terlong, near Desa Rambune, pantan Pediangah, Tihmang gagah, 4.77054°N, 96.79341°E, 1377 m a.s.l., **UTA.A64930**; Kabupaten Gayo Lues, Stream Along Road S. (up) from Ise-Ise, 4.22357°N, 97.18655°E, 1827 m a.s.l., **UTA.A64931**, **UTA.A64932**, **UTA.A64933**, **UTA.A64934**; Kabupaten Gayo Lues, Stream in Lemon Grass Plantation, 3.97234°N, 97.23405°E, 1638 m a.s.l., **UTA.A64935**; Kabupaten Gayo Lues, Kedah, Blangkajeren, Rain forest lodge, 3.9771°N, 97.25256°E, 1355 m a.s.l., **UTA.A64929**; Kabupaten Gayo Lues, Marpunge, Taman Nasional Gunung Leuser, 3.79289°N, 97.64417°E, 1190 m a.s.l., **MZB.AMPH.29375**, **ZMH.A14164***.

Provinsi Sumatera Utara. – Kabupaten Karo, Gunung Sibuat, Above Kampung Naga Linga, 2.91076°N, 98.46313°E, 1625 m a.s.l., **MZB.AMPH.23522–24**, **UTA.A64834***, **UTA.A64929**; Kabupaten Toba Samosir, Gunung Pangulubao, 2.60441°N, 99.04599°E, 1392 m a.s.l., **UTA.A64927**, **UTA.A64926**; Kabupaten Samosir, vicinity of Tele, 2.55397°N, 98.59806°E, 1774 m a.s.l., **MZB.AMPH.23516*** (paratype), **MZB.AMPH.23517** (paratype), **UTA.A64829** (paratype); 2.54691°N, 98.61414°E, 1780 m a.s.l., **MZB.AMPH.23518–20** (paratype), **UTA.A64830–32** (paratype); Kabupaten Simalungun, Simpang Tele, 2.52733°N, 98.63364°E, 1800 m a.s.l., Kabupaten Humbung Hasundutan, 2.18325°N, 98.60513°E, 1309 m a.s.l., **UTA.A64928**.

Provinsi Bengkulu. – Kabupaten Lebong, Desa Seblat Ulu, Taman Nasional Kerinci Seblat, 2.88525°S, 102.12993°E, 2000 m a.s.l., **ZMH.A14194** (paratype); 2.88413°S, 102.13073°E, 2033 m a.s.l., **MZB.AMPH.29377*** (holotype).

Sumaterana dabulescens sp. n. (adults, n = 38)

Provinsi Aceh. – Kabupaten Pidie, Krueng Meriam, Tangse, 4.938417°N, 95.98375°E, 314 m a.s.l., **UTA.A64921** (paratype); 4.93852°N, 95.98294°E, 323 m a.s.l., **UTA.A64922** (paratype), **UTA.A64923** (paratype); Kabupaten Pidie, Kecamatan Tangse, Stream along Tangse-Geumpang road, 4.93869°N, 95.9825°E, 333 m a.s.l., **UTA.A64924** (paratype); Kabupaten Pidie, Desa Mane, 4.92091°N, 96.12275°E, 761 m a.s.l., **MZB.AMPH.29381** (paratype), **MZB.AMPH.29383** (paratype), **MZB.AMPH.29385** (paratype), **MZB.AMPH.29387** (paratype), **MZB.AMPH.29389** (paratype), **ZMH.A14154–58** (paratype), **UA.2014.0397** (paratype); 4.91926°N, 96.12300°E, 747 m a.s.l., **MZB.AMPH.29392**, **MZB.AMPH.29384**, **ZMH.A14187**, **ZMH.A14190**; 4.89949°N, 96.13168°E, 700 m a.s.l., **ZMH.A14188**; Kabupaten Aceh Tengah, Road Takengon-Bierut, Enang-Enang Resort, 4.88649°N, 96.72689°E, 604 m a.s.l., **UTA.A64917** (paratype), **UTA.A64918**; Kabupaten Bener Meriah, 4.82623°N, 96.74841°E, 924 m a.s.l., **UTA.A64919** (paratype); Kabupaten Pidie, Road Tutut

to Geumpang, 4.65267°N, 96.09203°E, 593 m a.s.l., UTA. A64920; Kabupaten Aceh Tengah, Sungai Air Jambu, Taman Buru Linge Isaq, 4.36482°N, 97.24783°E, 440 m a.s.l., **MZB.AMPH.29396*** (holotype), **MZB.AMPH.29398** (paratype), **MZB.AMPH.29400** (paratype), **MZB.AMPH.29402** (paratype), **ZMH.A14159** (paratype), **ZMH.A14161–62** (paratype), **UA.2014.0214** (paratype); Kabupaten Aceh Tengah, red water stream, Taman Buru Linge Isaq, 4.37958°N, 97.29158°E, 1000 m a.s.l., **ZMH.A14163**; Kabupaten Aceh Tengah, Taman Buru Linge-Isaq, 4.338036°N, 97.28096°E, 600 m a.s.l., **MZB.AMPH.29405**, **MZB.AMPH.29407–09**, **ZMH.A14174**.

Sumaterana dabulescens sp. n. (juvenile, n = 1)

Provinsi Aceh. – Kabupaten Pidie, Kecamatan Mane, Desa Mane, 4.92334°N, 96.12215°E, 792 m a.s.l., **MZB.AMPH.29378***.

Sumaterana dabulescens sp. n. (tadpoles, n = 8)

Provinsi Aceh. – Kabupaten Pidie, Kecamatan Mane, Stream 3 Mane, 4.91926°N, 96.12300°E, 747 m a.s.l., **MZB.AMPH.29410** (n = 5), **MZB.AMPH.29411***, **ZMH.A12655**, **MZB.AMPH.29413**.

Supplementary material 1

List of sequences and GenBank accession number

Authors: Umilaela Arifin, Utpal Smart, Stefan T. Hertwig, Eric N. Smith, Djoko T. Iskandar, Alexander Haas

Data type: molecular data

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Link: <https://doi.org/10.3897/zse.94.22120.suppl1>

Supplementary material 2

Illustration of morphological characters

Authors: Umilaela Arifin, Utpal Smart, Stefan T. Hertwig, Eric N. Smith, Djoko T. Iskandar, Alexander Haas

Data type: species data

Explanation note: Illustration of morphological characters measured in this study: A) for adults, B) for tadpoles.

Explanation for each acronym available in Tables 2 and 3. Illustration by L. Waser.

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Link: <https://doi.org/10.3897/zse.94.22120.suppl2>

Supplementary material 3

Pairwise genetic distance

Authors: Umilaela Arifin, Utpal Smart, Stefan T. Hertwig, Eric N. Smith, Djoko T. Iskandar, Alexander Haas

Data type: molecular data

Explanation note: Pairwise genetic distance (uncorrected p) within crassiovis-group and all taxa used in this study based on 16S sequence, calculated using MEGA 7.1.025. Values are in percentage (%).

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Link: <https://doi.org/10.3897/zse.94.22120.suppl3>

Supplementary material 1

Species	Voucher no	GenBank Accession no and Genseq Nomenclature				Locality	Study
		12S	16S	RAG1	TYR		
<i>Staurois guttatus</i>	NHMBE1056532	MG909682-genseq-4	MG909607-genseq-4	MG909642-genseq-4	MG909718-genseq-4	Malaysia, Sarawak, Gunung Mulu NP	This study
<i>Amolops afghanus</i>	CAS221313	MG909643-genseq-4	MG909570-genseq-4	MG909608-genseq-4	MG909683-genseq-4	Myanmar, Kachin State, Putao District, Machanbaw Township, Ahtonga Village	This study
<i>Amolops indoburmanensis</i>	CAS234720	MG909644-genseq-4	MG909571-genseq-4	MG909610-genseq-4	MG909686-genseq-4	Myanmar, Chin State, Saw Stream, Kanpetlet Township, Mindat Division	This study
<i>Amolops marmoratus</i>	CAS221675	MG909645-genseq-4	MG909572-genseq-4	MG909611-genseq-4	MG909684-genseq-4	Myanmar, Shan State, Kalaw Township, What Phu Ye Camp	This study
<i>Amolops panhai</i>	CAS229816	MG909646-genseq-4	MG909606-genseq-4	MG909609-genseq-4	MG909685-genseq-4	Myanmar, Tanintharyi Division, Da Wei District, Thayet Chaung Township, East of Mal Ke Village, border of Nwa La Bo Reserve Forest along Ngwe Taung Stream	This study
<i>Chalcorana megalonesa</i>	FMNH 268981	NA	NA	KR264404-genseq-4	KR264478-genseq-4	Malaysia, Sarawak	Oliver et al. 2015
<i>Chalcorana chalconota</i>	MZB.AMPH. 30399	MG909679-genseq-4	NA	MG909638-genseq-4	MG909688-genseq-4	Indonesia, Provinsi Jawa Tengah, Kabupaten Banyumas, Curug Cipendok	This study
<i>Hydrophylax malabarica</i>	BNHS 5880	NA	KM068968-genseq-4	KM069242-genseq-4	NA	India, Amboli	Biju et al. 2014
<i>Hydrophylax leptoglossa</i>	CAS 239886	NA	KR264065-genseq-4	KR264388-genseq-4	KR264456-genseq-4	Myanmar, Kyaukpyu District	Oliver et al. 2015
<i>Hylarana erythraea</i>	MZB.AMPH. 29423	MG909680-genseq-4	MG909597-genseq-4	MG909639-genseq-4	MG909689-genseq-4	Indonesia, Provinsi Aceh, Taman Nasional Gunung Leuser	This study
<i>Hylarana macrodactyla</i>	FMNH 255186	NA	KR264071-genseq-4	KR264392-genseq-4	KR264463-genseq-4	Laos, Champasak Province	Oliver et al. 2015

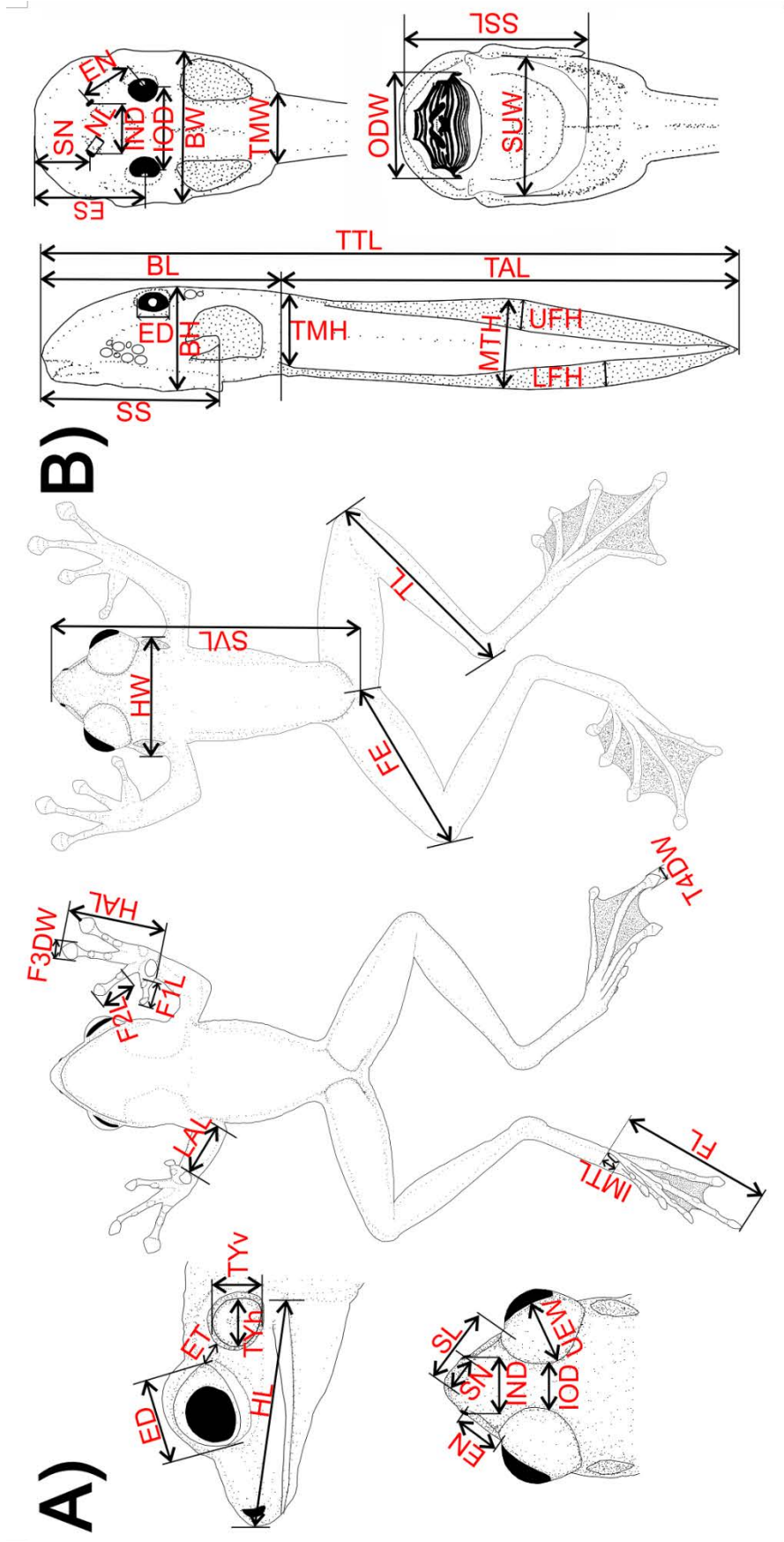
<i>Odorrana hosii</i>	NHMBE1061612	MG909647-genseq-4	MG909605-genseq-4	MG909612-genseq-4	MG909687-genseq-4	Malaysia, Sarawak, Palungan, Gunung Murud	This study
<i>Odorrana livida</i>	FMNH 263415	NA	NA	EF088260-genseq-4	EU076784-genseq-4	Thailand, Prachuap Kirikhan Province	Stuart 2008
<i>Meristogenys jerboa</i>	KUHE 12028	AB211470-genseq-4	AB211493-genseq-4	AB526662-genseq-4	NA	Malaysia, Sarawak	Matsui et al. 2006; Shimada et al. 2008
<i>Meristogenys kinabaluensis</i>	NHMBE1064112	MG909678-genseq-4	MG909598-genseq-4	MG909633-genseq-4	MG909711-genseq-4	Malaysia, Sabah, Gunung Kinabalu National Park, Sayap Substation, Sungai Kemantis trail	This study
<i>Huia cavitympanum</i>	RMBR 2283	MG909681-genseq-4	MG909602-genseq-4	MG909632-genseq-4	MG909710-genseq-4	Indonesia, Kalimantan, Bukit Baka Bukit Raya NP	This study
<i>Huia masonii</i>	MZB.AMPH. 29424	MG909676-genseq-4	MG909599-genseq-4	MG909634-genseq-4	MG909712-genseq-4	Indonesia, Provinsi Jawa Barat, Kabupaten Sumedang, Curug Cijambu	This study
<i>Huia sumatrana</i>	UTA.A64939	MG909677-genseq-4	MG909600-genseq-4	MG909635-genseq-4	MG909713-genseq-4	Indonesia, Provinsi Sumatera Utara, Kabupaten Langkat, Outskirts of Bukit Lawang Town	This study
<i>Huia melasma</i>	FMNH 271377	MG909675-genseq-4	MG909601-genseq-4	MG909637-genseq-4	MG909715-genseq-4	Laos, Luang Namtha Prov, Vieng Phou Kha Dist.	This study
<i>Huia melasma</i>	FMNH 270711	MG909674-genseq-4	NA	NA	MG909714-genseq-4	Thailand, Nan, Amphoe Pua, Tambol Auan	This study
<i>Clinotarsus penelope</i>	FMNH 268338	MG909672-genseq-4	MG909603-genseq-4	MG909640-genseq-4	MG909716-genseq-4	Thailand, Ranong Prov.	This study
<i>Clinotarsus alticola</i>	FMNH 263424	MG909673-genseq-4	MG909604-genseq-4	MG909641-genseq-4	MG909717-genseq-4	Thailand, Prachuap Kirikhan, Hua Hin	This study
Specimen 1	MZB.AMPH. 29186	MG909657-genseq-3	MG909582-genseq-3	MG909619-genseq-3	MG909703-genseq-3	Indonesia, Provinsi Aceh, Kabupaten Gayo Lues, Marpunge, Taman Nasional Gunung Leuser	This study

Specimen 2	MZB.AMPH. 29326	MG909658- genseq-3	MG909583- genseq-3	MG909614- genseq-3	MG909709- genseq-3	Indonesia, Provinsi Sumatera Utara, Kabupaten Dili Serdang, Sungai DAM Bumi Perkemahan Sibolangit	This study
Specimen 3	MZB.AMPH. 29355	MG909661- genseq-3	MG909585- genseq-3	NA	NA	Indonesia, Provinsi Sumatera Barat, Kabupaten Payakumbuh, Stream next to the road betw een Payakumbuh-Riau	This study
Specimen 4	MZB.AMPH. 29320	MG909660- genseq-3	MG909584- genseq-3	MG909623- genseq-3	MG909704- genseq-3	Indonesia, Provinsi Sumatera Barat, Kabupaten Payakumbuh, small creek next to main road connecting Payakumbuh-Riau	This study
Specimen 5	UTA.A6483 3	MG909659- genseq-3	MG909586- genseq-3	MG909615- genseq-3	MG909705- genseq-3	Indonesia, Provinsi Sumatera Utara, Kabupaten Toba Samosir, Gunung Pangulubao	This study
Specimen 6	UTA.A6483 5	MG909662- genseq-3	MG909587- genseq-3	MG909618- genseq-3	MG909706- genseq-3	Indonesia, Provinsi Sumatera Barat, Kabupaten Mandiling Natal, Huta Baringin Julu, Taman Nasional Batang Gadis	This study
Specimen 7	ZMH.A1419 7	MG909655- genseq-3	MG909581- genseq-3	MG909617- genseq-3	MG909695- genseq-3	Indonesia, Provinsi Sumatera Barat, Kabupaten Solok Selatan, Padang Aro, Taman Nasional Kerinci Seblat	This study
Specimen 8	ZMH.A1265 0	MG909654- genseq-3	MG909580 genseq-3	NA	NA	Indonesia, Provinsi Sumatera Barat, Kabupaten Solok Selatan, Muara Labuh, Taman Nasional Kerinci-Seblat	This study

Specimen 9	MZB.AMPH. 22339	MG909656- genseq-3	MG909579- genseq-3	MG909621- genseq-3	MG909694- genseq-3	Indonesia, Provinsi Jambi, Kabupaten Kerinci, Gunung Kunyit, Taman Nasional Kerinci- Seblat	This study
Specimen 10	MZB.AMPH. 29275	MG909653- genseq-3	MG909578- genseq-3	MG909620- genseq-3	MG909693- genseq-3	Indonesia, Provinsi Bengkulu, Kabupaten Lebong, Desa Seblat Ulu, Taman Nasional Kerinci Seblat,	This study
Specimen 11	ZMHA.1413 9	MG909652- genseq-3	MG909577- genseq-3	MG909616- genseq-3	MG909692- genseq-3	Indonesia, Provinsi Sumatera Selatan, Kabupaten Ogan Komerling Ulu Selatan, Kecamatan. Kisam Tinggi, Gunung Nanti, Desa Gunung Megang	This study
Specimen 12	MZB.AMPH. 29365	MG909651- genseq-3	MG909575- genseq-3	NA	NA	Indonesia, Provinsi Sumatera Selatan, Kabupaten Muara Enim, Desa Batu Surau	This study
Specimen 13	ZMHA.1414 9	MG909650- genseq-3	MG909574- genseq-3	MG909622- genseq-3	MG909691- genseq-3	Indonesia, Provinsi Sumatera Selatan, Kab. Muara Enim, Desa Batu Surau	This study
Specimen 14	ZMHA.1418 5	MG909649- genseq-3	MG909576- genseq-3	MG909624- genseq-3	MG909700- genseq-3	Indonesia, Provinsi Lampung, Kabupaten Tanggamus, Air Terjun Talang Ogan	This study
Specimen 15	MZB.AMPH. 29288	MG909648- genseq-3	MG909573- genseq-3	MG909613- genseq-3	MG909690- genseq-3	Indonesia, Provinsi Lampung, Kabupaten Lampung Barat, Gunung Abung	This study
Specimen 16	MVZ271526	MG909664- genseq-4	MG909589- genseq-4	MG909626- genseq-4	MG909702- genseq-4	Indonesia, Provinsi Sumatera Barat, Kabupaten Pasaman, Cagar Alam Rimbo Panti	This study

Specimen 17	MZB.AMPH. 29200	MG909663- genseq-3	MG909588- genseq-3	MG909625- genseq-3	MG909701- genseq-3	Indonesia, Provinsi Sumatera Barat, Kabupaten Pasaman, Cagar Alam Rimbo Panti	This study
Specimen 18	MZB.AMPH. 23516	MG909668- genseq-2	MG909590- genseq-2	MG909627- genseq-2	MG909696- genseq-2	Indonesia, Provinsi Sumatera Utara, Kabupaten Samosir, vicinity of Tele	This study
Specimen 19	UTA.A6483 4	MG909669- genseq-3	MG909591- genseq-3	MG909636- genseq-3	MG909699- genseq-3	Indonesia, Provinsi Sumatera Utara, Kabupaten Karo, Gunung Sibuatan	This study
Specimen 20	MZB.AMPH. 29377	MG909671- genseq-1	MG909593- genseq-1	MG909629- genseq-1	MG909698- genseq-1	Indonesia, Provinsi Bengkulu, Kabupaten Lebong, Desa Seblat Ulu, Taman Nasional Kerinci- Seblat,	This study
Specimen 21	ZMHA.1416 4	MG909670- genseq-3	MG909592- genseq-3	MG909628- genseq-3	MG909697- genseq-3	Indonesia, Provinsi Aceh, Kabupaten Gayo Lues, Marpunge, Taman Nasional Gunung Leuser	This study
Specimen 22	MZB.AMPH. 29411	MG909667- genseq-3	MG909596- genseq-3	NA	NA	Indonesia, Provinsi Aceh, Kabupaten Pidie, Mane	This study
Specimen 23	MZB.AMPH. 29378	MG909666- genseq-3	MG909595- genseq-3	MG909631- genseq-3	MG909708- genseq-3	Indonesia, Provinsi Aceh, Kabupaten Pidie, Mane	This study
Specimen 24	MZB.AMPH. 29396	MG909665- genseq-1	MG909594- genseq-1	MG909630- genseq-1	MG909707- genseq-1	Indonesia, Provinsi Aceh, Kabupaten Aceh Tengah, Taman Buru Linge-Isaq	This study

Supplementary material 2



Supplementary material 3

	1	2	3	4	5	6	7
1 <i>Aafghanus</i> _CAS221313							
2 <i>Aindoburmanensis</i> _CAS234720	8.74%						
3 <i>Amarmoratus</i> _CAS221675	10.45%	11.51%					
4 <i>Apanhai</i> _CAS229816	14.07%	11.09%	10.66%				
5 Clade A_MZB.AMPH.29186_Aceh	14.71%	13.86%	14.50%	14.93%			
6 Clade A_MZB.AMPH.29336_Sumatera Utara*	14.29%	13.86%	14.07%	14.93%	0.43%		
7 Clade A_UTA.A64833_Sumatera Utara	14.07%	13.86%	13.86%	14.93%	0.64%	0.21%	
8 Clade A_UTA.A64835_Sumatera Utara	14.29%	13.65%	13.43%	14.50%	1.07%	1.07%	0.85%
9 Clade A_ZMHA.14197_Sumatera Barat*	14.71%	14.29%	14.50%	15.14%	2.56%	2.56%	2.35%
10 Clade A_ZMHA.12650_Tad_Sumatera Barat	14.50%	14.07%	14.29%	14.93%	2.35%	2.35%	2.13%
11 Clade A_MZB.AMPH.22339_Jambi	13.86%	14.50%	13.65%	14.50%	2.99%	2.99%	2.77%
12 Clade A_MZB.AMPH.29320_Sumatera Barat	14.29%	13.65%	14.07%	14.71%	1.07%	1.07%	0.85%
13 Clade A_MZB.AMPH.29355_Tad_Sumatera Barat	14.29%	13.65%	14.07%	14.71%	1.07%	1.07%	0.85%
14 Clade A_MZB.AMPH.29275_Bengkulu	13.65%	14.93%	13.22%	14.93%	2.99%	2.99%	2.77%
15 Clade A_ZMHA.14149_Sumatera Selatan	13.65%	14.93%	13.22%	14.93%	2.99%	2.99%	2.77%
16 Clade A_MZB.AMPH.29365_Tad_Sumatera Selatan	13.65%	14.93%	13.22%	14.93%	2.99%	2.99%	2.77%
17 Clade A_ZMHA.14139_Sumatera Selatan	13.65%	14.93%	13.22%	14.93%	2.99%	2.99%	2.77%
18 Clade A_MZB.AMPH.29288_Lampung	13.65%	14.93%	13.22%	14.93%	2.99%	2.99%	2.77%
19 Clade A_ZMHA.14185_Lampung	13.65%	14.93%	13.22%	14.93%	2.99%	2.99%	2.77%
20 Clade A_MZB.AMPH.29200_Sumatera Barat	14.50%	15.78%	13.22%	14.71%	4.90%	4.48%	4.26%
21 Clade A_MVZ271526_Sumatera Barat	14.50%	15.78%	13.22%	14.71%	4.90%	4.48%	4.26%
22 Clade B_MZB.Amph.23516_Sumatera Utara	13.01%	14.71%	13.65%	14.50%	8.10%	7.68%	7.89%
23 Clade B_UTA.A64834_Sumatera Utara	13.22%	14.71%	13.01%	14.29%	7.25%	6.82%	7.04%
24 Clade B_ZMHA.14164_Aceh	13.01%	14.50%	12.79%	14.29%	7.46%	7.04%	7.25%
25 Clade B_MZB.AMPH.29377_Bengkulu	13.43%	14.71%	13.01%	14.71%	7.68%	7.25%	7.46%
26 Clade C_MZB.AMPH.29396_Aceh	14.93%	13.86%	14.50%	15.99%	8.10%	7.68%	7.89%
27 Clade C_MZB.AMPH.29378_Aceh	13.86%	13.22%	13.86%	14.93%	7.68%	7.68%	7.89%
28 Clade C_MZB.AMPH.29411_Tad_Aceh	13.86%	13.22%	13.86%	14.93%	7.68%	7.68%	7.89%
29 <i>Hylarana erytraea</i> _MZB.AMPH.29423	13.65%	15.99%	15.35%	15.99%	15.57%	15.57%	15.35%
30 <i>Hylarana macrodactyla</i> _FMNH255186	15.57%	16.42%	16.63%	18.12%	15.57%	15.57%	15.78%
31 <i>Hydrophylax leptoglossa</i> _CAS239886	15.78%	14.07%	13.01%	13.22%	11.51%	11.51%	11.51%
32 <i>Hydrophylax malabarica</i> _BNHS5880	14.71%	14.07%	13.01%	12.58%	11.51%	11.09%	11.30%
33 <i>Huia masonii</i> _MZB.AMPH.29424	17.48%	17.06%	12.79%	15.14%	16.20%	15.99%	15.78%
34 <i>Huia sumatrana</i> _ENS17018	18.98%	15.78%	14.50%	15.14%	14.93%	14.93%	14.93%
35 <i>Huia melasma</i> _FMNH271377	17.91%	16.63%	14.71%	14.07%	13.86%	14.07%	14.07%
36 <i>Huia cavitypanum</i> _RMBR2283	17.91%	16.63%	14.71%	16.42%	12.37%	12.37%	12.58%
37 <i>Meristogenys jerboa</i> _KUHE12028	11.94%	11.51%	11.51%	11.73%	10.23%	10.23%	10.45%
38 <i>Meristogenys kinabaluensis</i> _NHMBE1064112	12.15%	11.73%	11.73%	11.94%	11.94%	11.94%	11.94%
39 <i>Clinotarsus alticola</i> _FMNH263424	15.35%	14.71%	13.65%	15.35%	13.22%	13.22%	13.43%
40 <i>Clinotarsus penelope</i> _FMNH268338	15.14%	14.50%	13.43%	15.14%	13.01%	13.01%	13.22%
41 <i>Odorrana hosii</i> _NHMBE1061612	15.35%	13.86%	13.86%	13.43%	14.50%	14.07%	14.07%
42 <i>Stauroids guttatus</i> _NHMBE1056532	19.62%	18.55%	18.12%	18.55%	17.91%	18.12%	18.12%

		8	9	10	11	12	13	14
1	<i>Aafghanus</i> _CAS221313							
2	<i>Aindoburmanensis</i> _CAS234720							
3	<i>Amarmoratus</i> _CAS221675							
4	<i>Apanhai</i> _CAS229816							
5	Clade A_MZB.AMPH.29186_Aceh							
6	Clade A_MZB.AMPH.29336_Sumatera Utara*							
7	Clade A_UTA.A64833_Sumatera Utara							
8	Clade A_UTA.A64835_Sumatera Utara							
9	Clade A_ZMHA.14197_Sumatera Barat*	2.35%						
10	Clade A_ZMHA.12650_Tad_Sumatera Barat	2.13%	0.21%					
11	Clade A_MZB.AMPH.22339_Jambi	2.77%	1.28%	1.07%				
12	Clade A_MZB.AMPH.29320_Sumatera Barat	1.28%	1.92%	1.71%	2.35%			
13	Clade A_MZB.AMPH.29355_Tad_Sumatera Barat	1.28%	1.92%	1.71%	2.35%	0.00%		
14	Clade A_MZB.AMPH.29275_Bengkulu	2.77%	2.35%	2.13%	1.07%	2.35%	2.35%	
15	Clade A_ZMHA.14149_Sumatera Selatan	2.77%	2.35%	2.13%	1.07%	2.35%	2.35%	0.00%
16	Clade A_MZB.AMPH.29365_Tad_Sumatera Selatan	2.77%	2.35%	2.13%	1.07%	2.35%	2.35%	0.00%
17	Clade A_ZMHA.14139_Sumatera Selatan	2.77%	2.35%	2.13%	1.07%	2.35%	2.35%	0.00%
18	Clade A_MZB.AMPH.29288_Lampung	2.77%	2.35%	2.13%	1.07%	2.35%	2.35%	0.00%
19	Clade A_ZMHA.14185_Lampung	2.77%	2.35%	2.13%	1.07%	2.35%	2.35%	0.00%
20	Clade A_MZB.AMPH.29200_Sumatera Barat	4.69%	4.48%	4.26%	4.05%	4.26%	4.26%	4.48%
21	Clade A_MVZ271526_Sumatera Barat	4.69%	4.48%	4.26%	4.05%	4.26%	4.26%	4.48%
22	Clade B_MZB.Amph.23516_Sumatera Utara	8.32%	7.68%	7.46%	7.68%	7.68%	7.68%	8.53%
23	Clade B_UTA.A64834_Sumatera Utara	7.46%	6.82%	6.61%	6.82%	7.04%	7.04%	7.68%
24	Clade B_ZMHA.14164_Aceh	7.68%	7.04%	6.82%	7.04%	7.25%	7.25%	7.89%
25	Clade B_MZB.AMPH.29377_Bengkulu	7.89%	7.68%	7.46%	7.68%	7.46%	7.46%	8.32%
26	Clade C_MZB.AMPH.29396_Aceh	8.74%	8.53%	8.32%	9.38%	7.89%	7.89%	9.59%
27	Clade C_MZB.AMPH.29378_Aceh	8.32%	7.68%	7.46%	8.53%	7.46%	7.46%	8.74%
28	Clade C_MZB.AMPH.29411_Tad_Aceh	8.32%	7.68%	7.46%	8.53%	7.46%	7.46%	8.74%
29	<i>Hylarana erytraea</i> _MZB.AMPH.29423	15.35%	15.78%	15.57%	15.35%	15.57%	15.57%	14.71%
30	<i>Hylarana macrodactyla</i> _FMNH255186	16.20%	16.42%	16.20%	16.42%	16.20%	16.20%	16.42%
31	<i>Hydrophylax leptoglossa</i> _CAS239886	11.51%	11.94%	11.73%	11.51%	11.94%	11.94%	11.73%
32	<i>Hydrophylax malabarica</i> _BNHS5880	11.73%	12.15%	11.94%	12.37%	11.51%	11.51%	12.37%
33	<i>Huia masonii</i> _MZB.AMPH.29424	15.57%	16.20%	15.99%	15.78%	16.20%	16.20%	15.35%
34	<i>Huia sumatrana</i> _ENS17018	14.93%	15.57%	15.35%	15.57%	15.14%	15.14%	15.35%
35	<i>Huia melasma</i> _FMNH271377	13.65%	14.07%	13.86%	13.86%	14.07%	14.07%	13.86%
36	<i>Huia cavitympanum</i> _RMBR2283	12.37%	13.43%	13.22%	13.01%	12.79%	12.79%	13.01%
37	<i>Meristogenys jerboa</i> _KUHE12028	10.45%	10.23%	10.02%	10.23%	10.87%	10.87%	11.09%
38	<i>Meristogenys kinabaluensis</i> _NHMBE1064112	11.94%	12.58%	12.37%	11.73%	12.15%	12.15%	11.73%
39	<i>Clinotarsus alticola</i> _FMNH263424	13.01%	13.65%	13.43%	13.01%	13.43%	13.43%	13.01%
40	<i>Clinotarsus penelope</i> _FMNH268338	12.79%	13.43%	13.22%	12.79%	13.22%	13.22%	12.79%
41	<i>Odorrana hosii</i> _NHMBE1061612	14.50%	14.07%	13.86%	13.65%	13.86%	13.86%	13.65%
42	<i>Staurois guttatus</i> _NHMBE1056532	17.48%	18.76%	18.55%	18.34%	18.34%	18.34%	18.55%

		15	16	17	18	19	20	21
1	<i>Aafghanus</i> _CAS221313							
2	<i>Aindoburmanensis</i> _CAS234720							
3	<i>Amarmoratus</i> _CAS221675							
4	<i>Apanhai</i> _CAS229816							
5	Clade A_MZB.AMPH.29186_Aceh							
6	Clade A_MZB.AMPH.29336_Sumatera Utara*							
7	Clade A_UTA.A64833_Sumatera Utara							
8	Clade A_UTA.A64835_Sumatera Utara							
9	Clade A_ZMH.A14197_Sumatera Barat*							
10	Clade A_ZMH.A12650_Tad_Sumatera Barat							
11	Clade A_MZB.AMPH.22339_Jambi							
12	Clade A_MZB.AMPH.29320_Sumatera Barat							
13	Clade A_MZB.AMPH.29355_Tad_Sumatera Barat							
14	Clade A_MZB.AMPH.29275_Bengkulu							
15	Clade A_ZMH.A14149_Sumatera Selatan							
16	Clade A_MZB.AMPH.29365_Tad_Sumatera Selatan	0.00%						
17	Clade A_ZMH.A14139_Sumatera Selatan	0.00%	0.00%					
18	Clade A_MZB.AMPH.29288_Lampung	0.00%	0.00%	0.00%				
19	Clade A_ZMH.A14185_Lampung	0.00%	0.00%	0.00%	0.00%			
20	Clade A_MZB.AMPH.29200_Sumatera Barat	4.48%	4.48%	4.48%	4.48%	4.48%		
21	Clade A_MVZ271526_Sumatera Barat	4.48%	4.48%	4.48%	4.48%	4.48%	0.00%	
22	Clade B_MZB.Amph.23516_Sumatera Utara	8.53%	8.53%	8.53%	8.53%	8.53%	7.04%	7.04%
23	Clade B_UTA.A64834_Sumatera Utara	7.68%	7.68%	7.68%	7.68%	7.68%	6.61%	6.61%
24	Clade B_ZMH.A14164_Aceh	7.89%	7.89%	7.89%	7.89%	7.89%	6.82%	6.82%
25	Clade B_MZB.AMPH.29377_Bengkulu	8.32%	8.32%	8.32%	8.32%	8.32%	6.82%	6.82%
26	Clade C_MZB.AMPH.29396_Aceh	9.59%	9.59%	9.59%	9.59%	9.59%	8.74%	8.74%
27	Clade C_MZB.AMPH.29378_Aceh	8.74%	8.74%	8.74%	8.74%	8.74%	7.89%	7.89%
28	Clade C_MZB.AMPH.29411_Tad_Aceh	8.74%	8.74%	8.74%	8.74%	8.74%	7.89%	7.89%
29	<i>Hylarana erytraea</i> _MZB.AMPH.29423	14.71%	14.71%	14.71%	14.71%	14.71%	16.20%	16.20%
30	<i>Hylarana macrodactyla</i> _FMNH255186	16.42%	16.42%	16.42%	16.42%	16.42%	17.06%	17.06%
31	<i>Hydrophylax leptoglossa</i> _CAS239886	11.73%	11.73%	11.73%	11.73%	11.73%	12.37%	12.37%
32	<i>Hydrophylax malabarica</i> _BNHS5880	12.37%	12.37%	12.37%	12.37%	12.37%	11.30%	11.30%
33	<i>Huia masonii</i> _MZB.AMPH.29424	15.35%	15.35%	15.35%	15.35%	15.35%	15.35%	15.35%
34	<i>Huia sumatrana</i> _ENS17018	15.35%	15.35%	15.35%	15.35%	15.35%	14.71%	14.71%
35	<i>Huia melasma</i> _FMNH271377	13.86%	13.86%	13.86%	13.86%	13.86%	14.07%	14.07%
36	<i>Huia cavitympanum</i> _RMBR2283	13.01%	13.01%	13.01%	13.01%	13.01%	11.94%	11.94%
37	<i>Meristogenys jerboa</i> _KUHE12028	11.09%	11.09%	11.09%	11.09%	11.09%	10.87%	10.87%
38	<i>Meristogenys kinabaluensis</i> _NHMBE1064112	11.73%	11.73%	11.73%	11.73%	11.73%	12.15%	12.15%
39	<i>Clinotarsus alticola</i> _FMNH263424	13.01%	13.01%	13.01%	13.01%	13.01%	14.29%	14.29%
40	<i>Clinotarsus penelope</i> _FMNH268338	12.79%	12.79%	12.79%	12.79%	12.79%	14.07%	14.07%
41	<i>Odorrana hosii</i> _NHMBE1061612	13.65%	13.65%	13.65%	13.65%	13.65%	14.50%	14.50%
42	<i>Staurois guttatus</i> _NHMBE1056532	18.55%	18.55%	18.55%	18.55%	18.55%	19.40%	19.40%

		22	23	24	25	26	27	28
1	<i>Aafghanus</i> _CAS221313							
2	<i>Aindoburmanensis</i> _CAS234720							
3	<i>Amarmoratus</i> _CAS221675							
4	<i>Apanhai</i> _CAS229816							
5	Clade A_MZB.AMPH.29186_Aceh							
6	Clade A_MZB.AMPH.29336_Sumatera Utara*							
7	Clade A_UTA.A64833_Sumatera Utara							
8	Clade A_UTA.A64835_Sumatera Utara							
9	Clade A_ZMH.A14197_Sumatera Barat*							
10	Clade A_ZMH.A12650_Tad_Sumatera Barat							
11	Clade A_MZB.AMPH.22339_Jambi							
12	Clade A_MZB.AMPH.29320_Sumatera Barat							
13	Clade A_MZB.AMPH.29355_Tad_Sumatera Barat							
14	Clade A_MZB.AMPH.29275_Bengkulu							
15	Clade A_ZMH.A14149_Sumatera Selatan							
16	Clade A_MZB.AMPH.29365_Tad_Sumatera Selatan							
17	Clade A_ZMH.A14139_Sumatera Selatan							
18	Clade A_MZB.AMPH.29288_Lampung							
19	Clade A_ZMH.A14185_Lampung							
20	Clade A_MZB.AMPH.29200_Sumatera Barat							
21	Clade A_MVZ271526_Sumatera Barat							
22	Clade B_MZB.Amph.23516_Sumatera Utara							
23	Clade B_UTA.A64834_Sumatera Utara	0.85%						
24	Clade B_ZMH.A14164_Aceh	1.07%	0.21%					
25	Clade B_MZB.AMPH.29377_Bengkulu	1.71%	1.28%	1.49%				
26	Clade C_MZB.AMPH.29396_Aceh	8.10%	7.68%	7.89%	8.10%			
27	Clade C_MZB.AMPH.29378_Aceh	8.74%	8.32%	8.53%	8.74%	1.92%		
28	Clade C_MZB.AMPH.29411_Tad_Aceh	8.74%	8.32%	8.53%	8.74%	1.92%	0.00%	
29	<i>Hylarana erytraea</i> _MZB.AMPH.29423	15.57%	15.78%	15.57%	15.78%	15.78%	14.93%	14.93%
30	<i>Hylarana macrodactyla</i> _FMNH255186	16.42%	16.20%	15.99%	16.42%	17.06%	16.42%	16.42%
31	<i>Hydrophylax leptoglossa</i> _CAS239886	14.07%	13.43%	13.22%	13.43%	13.86%	13.65%	13.65%
32	<i>Hydrophylax malabarica</i> _BNHS5880	11.73%	11.51%	11.30%	11.30%	12.37%	12.15%	12.15%
33	<i>Huia masonii</i> _MZB.AMPH.29424	15.78%	14.93%	15.14%	14.93%	15.78%	16.20%	16.20%
34	<i>Huia sumatrana</i> _ENS17018	15.57%	15.14%	15.35%	14.71%	14.29%	14.93%	14.93%
35	<i>Huia melasma</i> _FMNH271377	16.42%	15.57%	15.78%	15.78%	15.78%	15.14%	15.14%
36	<i>Huia cavitympanum</i> _RMBR2283	12.79%	12.37%	12.58%	12.15%	12.37%	12.79%	12.79%
37	<i>Meristogenys jerboa</i> _KUHE12028	10.66%	9.81%	9.59%	10.23%	11.51%	11.09%	11.09%
38	<i>Meristogenys kinabaluensis</i> _NHMBE1064112	10.87%	10.87%	11.09%	10.87%	11.73%	11.73%	11.73%
39	<i>Clinotarsus alticola</i> _FMNH263424	14.07%	13.65%	13.65%	14.07%	13.65%	13.01%	13.01%
40	<i>Clinotarsus penelope</i> _FMNH268338	13.86%	13.43%	13.43%	13.86%	13.43%	12.79%	12.79%
41	<i>Odorrana hosii</i> _NHMBE1061612	14.71%	14.93%	14.93%	14.93%	14.93%	14.50%	14.50%
42	<i>Staurois guttatus</i> _NHMBE1056532	19.62%	18.98%	18.76%	19.40%	18.76%	19.19%	19.19%

		29	30	31	32	33	34	35
1	<i>Aafghanus</i> _CAS221313							
2	<i>Aindoburmanensis</i> _CAS234720							
3	<i>Amarmoratus</i> _CAS221675							
4	<i>Apanhai</i> _CAS229816							
5	Clade A_MZB.AMPH.29186_Aceh							
6	Clade A_MZB.AMPH.29336_Sumatera Utara*							
7	Clade A_UTA.A64833_Sumatera Utara							
8	Clade A_UTA.A64835_Sumatera Utara							
9	Clade A_ZMH.A14197_Sumatera Barat*							
10	Clade A_ZMH.A12650_Tad_Sumatera Barat							
11	Clade A_MZB.AMPH.22339_Jambi							
12	Clade A_MZB.AMPH.29320_Sumatera Barat							
13	Clade A_MZB.AMPH.29355_Tad_Sumatera Barat							
14	Clade A_MZB.AMPH.29275_Bengkulu							
15	Clade A_ZMH.A14149_Sumatera Selatan							
16	Clade A_MZB.AMPH.29365_Tad_Sumatera Selatan							
17	Clade A_ZMH.A14139_Sumatera Selatan							
18	Clade A_MZB.AMPH.29288_Lampung							
19	Clade A_ZMH.A14185_Lampung							
20	Clade A_MZB.AMPH.29200_Sumatera Barat							
21	Clade A_MVZ271526_Sumatera Barat							
22	Clade B_MZB.Amph.23516_Sumatera Utara							
23	Clade B_UTA.A64834_Sumatera Utara							
24	Clade B_ZMH.A14164_Aceh							
25	Clade B_MZB.AMPH.29377_Bengkulu							
26	Clade C_MZB.AMPH.29396_Aceh							
27	Clade C_MZB.AMPH.29378_Aceh							
28	Clade C_MZB.AMPH.29411_Tad_Aceh							
29	<i>Hylarana erytraea</i> _MZB.AMPH.29423							
30	<i>Hylarana macrodactyla</i> _FMNH255186	9.59%						
31	<i>Hydrophylax leptoglossa</i> _CAS239886	11.09%	12.15%					
32	<i>Hydrophylax malabarica</i> _BNHS5880	10.87%	11.94%	8.32%				
33	<i>Huia masonii</i> _MZB.AMPH.29424	18.34%	18.76%	14.50%	14.29%			
34	<i>Huia sumatrana</i> _ENS17018	16.20%	15.99%	13.22%	13.65%	10.87%		
35	<i>Huia melasma</i> _FMNH271377	15.57%	16.20%	11.30%	13.01%	15.35%	13.43%	
36	<i>Huia cavitympanum</i> _RMBR2283	17.06%	15.57%	11.94%	13.22%	14.29%	14.07%	13.65%
37	<i>Meristogenys jerboa</i> _KUHE12028	11.94%	12.58%	10.45%	9.81%	13.86%	13.86%	12.79%
38	<i>Meristogenys kinabaluensis</i> _NHMBE1064112	11.94%	14.50%	10.66%	10.87%	13.01%	13.86%	13.22%
39	<i>Clinotarsus alticola</i> _FMNH263424	17.48%	17.91%	13.86%	13.86%	16.63%	16.42%	15.57%
40	<i>Clinotarsus penelope</i> _FMNH268338	17.27%	17.70%	13.65%	13.65%	16.42%	16.63%	15.35%
41	<i>Odorrana hosii</i> _NHMBE1061612	17.27%	18.55%	11.51%	14.29%	17.06%	17.91%	15.57%
42	<i>Staurois guttatus</i> _NHMBE1056532	18.76%	19.19%	15.78%	19.62%	19.40%	19.19%	18.34%

		36	37	38	39	40	41
1	<i>Aafghanus</i> _CAS221313						
2	<i>Aindoburmanensis</i> _CAS234720						
3	<i>Amarmoratus</i> _CAS221675						
4	<i>Apanhai</i> _CAS229816						
5	Clade A_MZB.AMPH.29186_Aceh						
6	Clade A_MZB.AMPH.29336_Sumatera Utara*						
7	Clade A_UTA.A64833_Sumatera Utara						
8	Clade A_UTA.A64835_Sumatera Utara						
9	Clade A_ZMH.A14197_Sumatera Barat*						
10	Clade A_ZMH.A12650_Tad_Sumatera Barat						
11	Clade A_MZB.AMPH.22339_Jambi						
12	Clade A_MZB.AMPH.29320_Sumatera Barat						
13	Clade A_MZB.AMPH.29355_Tad_Sumatera Barat						
14	Clade A_MZB.AMPH.29275_Bengkulu						
15	Clade A_ZMH.A14149_Sumatera Selatan						
16	Clade A_MZB.AMPH.29365_Tad_Sumatera Selatan						
17	Clade A_ZMH.A14139_Sumatera Selatan						
18	Clade A_MZB.AMPH.29288_Lampung						
19	Clade A_ZMH.A14185_Lampung						
20	Clade A_MZB.AMPH.29200_Sumatera Barat						
21	Clade A_MVZ271526_Sumatera Barat						
22	Clade B_MZB.Amph.23516_Sumatera Utara						
23	Clade B_UTA.A64834_Sumatera Utara						
24	Clade B_ZMH.A14164_Aceh						
25	Clade B_MZB.AMPH.29377_Bengkulu						
26	Clade C_MZB.AMPH.29396_Aceh						
27	Clade C_MZB.AMPH.29378_Aceh						
28	Clade C_MZB.AMPH.29411_Tad_Aceh						
29	<i>Hyalarana erytraea</i> _MZB.AMPH.29423						
30	<i>Hyalarana macrodactyla</i> _FMNH255186						
31	<i>Hydrophylax leptoglossa</i> _CAS239886						
32	<i>Hydrophylax malabarica</i> _BNHS5880						
33	<i>Huia masonii</i> _MZB.AMPH.29424						
34	<i>Huia sumatrana</i> _ENS17018						
35	<i>Huia melasma</i> _FMNH271377						
36	<i>Huia cavitympanum</i> _RMBR2283						
37	<i>Meristogenys jerboa</i> _KUHE12028	11.09%					
38	<i>Meristogenys kinabaluensis</i> _NHMBE1064112	11.94%	6.18%				
39	<i>Clinotarsus alticola</i> _FMNH263424	15.99%	12.58%	11.51%			
40	<i>Clinotarsus penelope</i> _FMNH268338	15.78%	12.37%	11.30%	0.21%		
41	<i>Odorrana hosii</i> _NHMBE1061612	15.99%	12.58%	12.58%	15.57%	15.35%	
42	<i>Staurois guttatus</i> _NHMBE1056532	19.19%	15.78%	16.42%	17.91%	18.12%	18.55%

CHAPTER 3
**A new species of the genus *Pulchrana* Dubois,
1992 (Amphibia, Ranidae) from Sumatra,
Indonesia**

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Author contribution

I hereby confirm that Umilaela Arifin conceived and designed the study, analyzed the data, and wrote the paper.

Hamburg, 04.12.2018

A handwritten signature in black ink, appearing to read 'Alexander Haas', written in a cursive style.

Prof. Dr. Alexander Haas

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

Umilaela Arifin^{1*}, Ganjar Cahyadi², Utpal Smart³, André Jankowski¹, Alexander Haas¹

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

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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

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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 H₂O, 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'-TCCRGTA YRCTTACCDTGT TACGA-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 (Netherlands). 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 CoreDRAW 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

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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
<i>Pulchrana baramica</i>	FMNH 248218	Brunei, Borneo Island, Belait District	KF477628	Brown & Siler, 2013 and Chan et al., 2014
<i>Pulchrana baramica</i>	KUHE 53640	Malaysia, Borneo Island, Sarawak, Mulu	AB719217, AB719234	Matsui et al., 2012
<i>Pulchrana banjarana</i>	LSUHC 5128	Malaysia, Malay Peninsula, Pahang, Cameron Highlands	KF477644	Brown & Siler, 2013 and Chan et al., 2014
<i>Pulchrana banjarana</i>	ZRC 8326	Malaysia, Malay Peninsula, Pahang, Cameron Highlands	KF477645	Brown & Siler, 2013 and Chan et al., 2014
<i>Pulchrana centropeninsularis</i>	DWNP 0489	Malaysia, Malay Peninsula, Pahang, Kuala Gandah	KF477745	Brown & Siler, 2013 and Chan et al., 2014
<i>Pulchrana centropeninsularis</i>	MZB. Amph.28765	Indonesia, Sumatra Island, Jambi Province, Harapan Rain Forest	MG783353, MG783362	This study
<i>Pulchrana centropeninsularis</i>	MZB. Amph.28766	Indonesia, Sumatra Island, Jambi Province, Harapan Rain Forest	MG783352, MG783361	This study
<i>Pulchrana fantastica</i> , new species	MZB. Amph.28946	Indonesia, Sumatra Island, Aceh Province, Gunung Leuseur National Park	MG783359, MG783367	This study
<i>Pulchrana fantastica</i> , new species	MZB. Amph.28891	Indonesia, Sumatra Island, Aceh Province, Taman Buru Linge Isaq	MG783360, MG783368	This study
<i>Pulchrana fantastica</i> , new species	MK 334	Indonesia, Sumatra Island, Sumatera Utara Province, Langkat, Bandar Baru, Batak Mountains	KF477646	Brown & Siler, 2013 and Chan et al., 2014
<i>Pulchrana fantastica</i> , 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
<i>Pulchrana glandulosa</i>	KUHE 53618	Malaysia, Borneo Island, Sarawak, Mulu	AB719206, AB719223	Matsui et al., 2012
<i>Pulchrana grandocula</i>	KU 306492	Philippines, Samar Island, Samar Province, Municipality of San Jose de Baun, Barangay Poblacion	KF477660	Brown & Siler, 2013 and Chan et al., 2014
<i>Pulchrana grandocula</i>	PNM 8848	Philippines, Mindanao Island, Davao City Province, Municipality of Calinan, Barangay Malagos	KF477676	Brown & Siler, 2013 and Chan et al., 2014
<i>Pulchrana mangyanum</i>	KU 303566	Philippines, Mindoro Island, Municipality of Paypayama, Barangay Carmundo	KF477687	Brown & Siler, 2013 and Chan et al., 2014
<i>Pulchrana mangyanum</i>	KU 303578	Philippines, Mindoro Island, Municipality of Bongabong, Barangay Formon	KF477686	Brown & Siler, 2013 and Chan et al., 2014
<i>Pulchrana moellendorffi</i>	KU 309009	Philippines, Palawan Island, Palawan Province, Municipality of Puerto Princesa City, Barangay Irawan	KF477696	Brown & Siler, 2013 and Chan et al., 2014

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

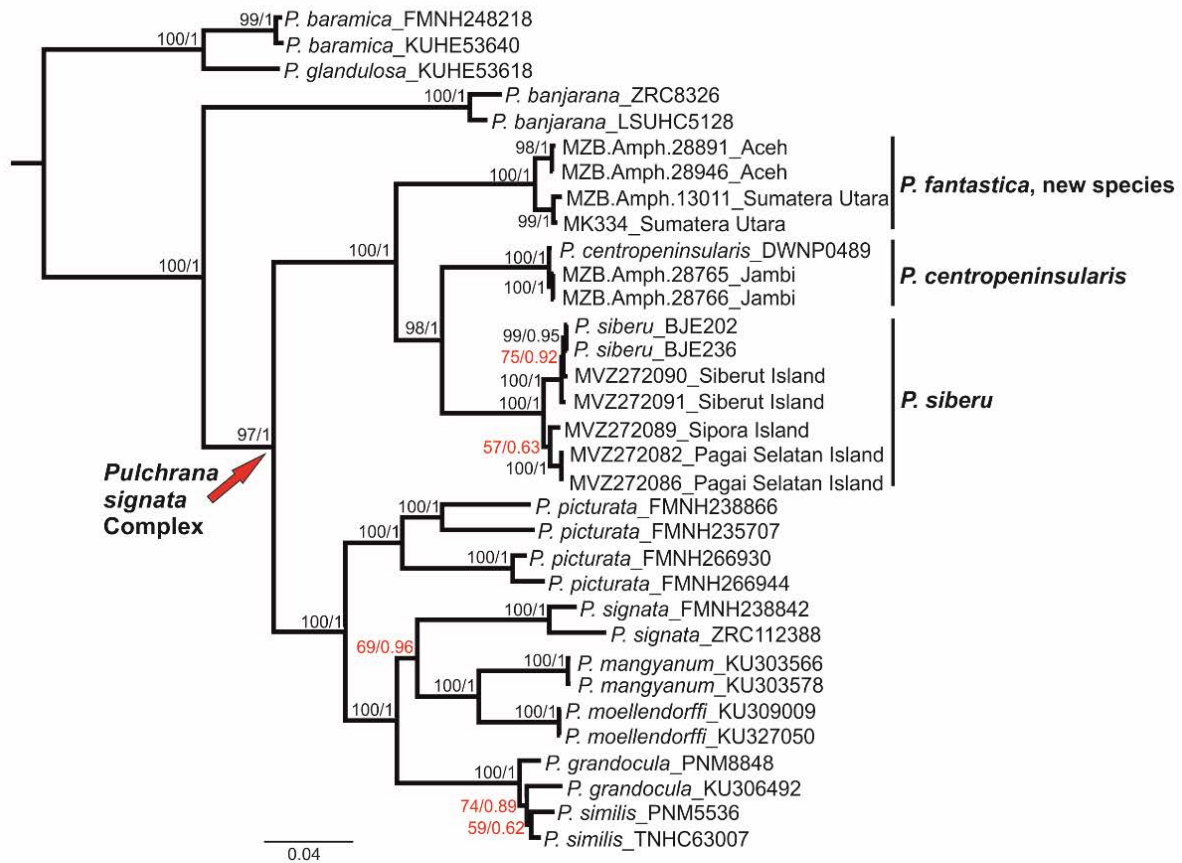


Fig. 1. Phylogenetic tree depicting the relationship between *Pulchrana fantastica*, new species and congeners based on BI. ML tree shows similar topology as BI. Node support representing bootstraps value and posterior probabilities (BS/PP).

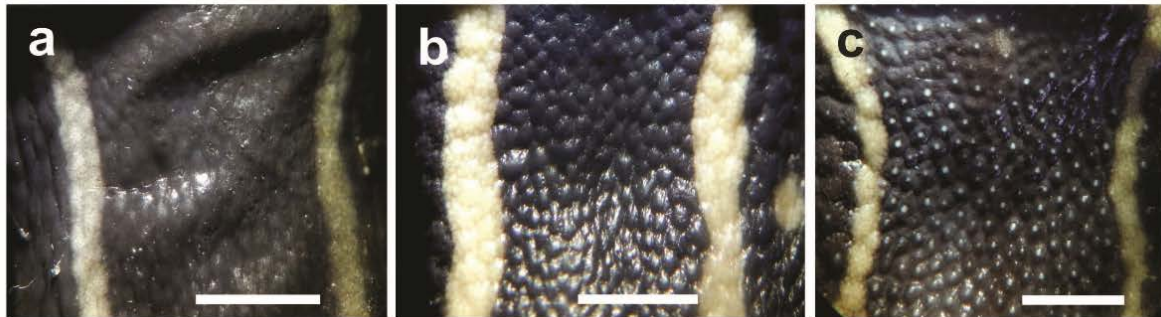


Fig. 2. Left to right; examples of dorsal skin textures in members of the *Pulchrana siberu*, *P. centropeninsularis*, and *P. fantastica*, new species: (a) finely granulated (MZB.Amph.28896); (b) granular (MZB.Amph.28765); (c) or with white tipped keratinised asperities (MZB.Amph.13011). Scale bar =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

MZB.Amph.28765: I(1⁻ — 1⁺)II(1⁰ — 2⁻)III(1⁻ — 2⁰)IV(2⁻ — 1/2)V; for MZB.Amph.28766: I(1/2 — 1⁻)II(1/2 — 11/2)III(1⁻ — 2⁰)IV(2⁻ — 1/2)V; for MZB.Amph.28767: I(1/2 — 1⁺)II(1/2 — 11/2)III(1⁻ — 2⁰)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

Arifin et al.: New *Pulchrana* from SumatraTable 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 <i>P. glandulosa</i> KUHE 53618											
2 <i>P. baramica</i> KUHE 53640	0.064										
3 <i>P. baramica</i> FMNH 248218	0.064	0.005									
4 <i>P. banjarana</i> ZRC 8326	0.163	0.172	0.170								
5 <i>P. banjarana</i> LSUHC 5128	0.160	0.168	0.167	0.012							
6 <i>P. picturata</i> FMNH 235707	0.169	0.155	0.154	0.161	0.163						
7 <i>P. picturata</i> FMNH 238866	0.169	0.166	0.166	0.170	0.172	0.066					
8 <i>P. picturata</i> FMNH 266944	0.151	0.150	0.152	0.151	0.152	0.087	0.090				
9 <i>P. picturata</i> FMNH 266930	0.157	0.150	0.151	0.150	0.149	0.088	0.090	0.021			
10 <i>P. signata</i> ZRC 112388	0.155	0.152	0.152	0.167	0.169	0.115	0.104	0.109	0.108		
11 <i>P. signata</i> FMNH 238842	0.154	0.152	0.152	0.166	0.166	0.110	0.103	0.108	0.109	0.022	
12 <i>P. siberu</i> 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 <i>P. siberu</i> 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 <i>P. siberu</i> 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 <i>P. siberu</i> 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 <i>P. siberu</i> 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 <i>P. siberu</i> 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 <i>P. centropeninsularis</i> 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 <i>P. centropeninsularis</i> 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 <i>P. centropeninsularis</i> 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 <i>P. fantastica</i> , 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 <i>P. fantastica</i> , 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 <i>P. fantatisca</i> , 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 <i>P. fantastica</i> , 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 <i>P. moellendorffi</i> 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 <i>P. moellendorffi</i> 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 <i>P. mangyanum</i> 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 <i>P. mangyanum</i> 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 <i>P. grandocula</i> 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 <i>P. grandocula</i> 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 <i>P. similis</i> 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 <i>P. similis</i> PNM 5536	0.171	0.171	0.173	0.172	0.171	0.110	0.110	0.109	0.113	0.107	0.102

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

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

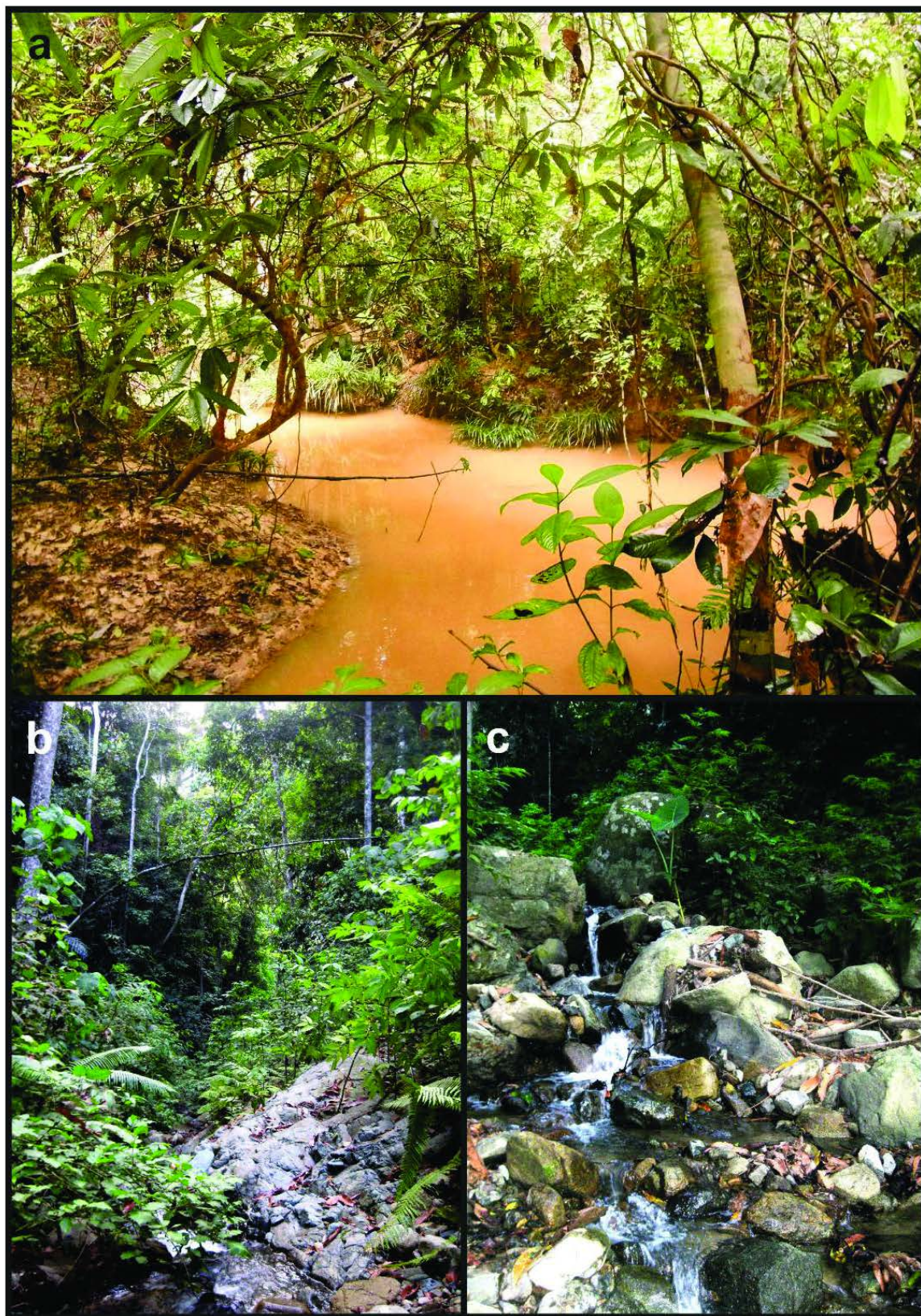


Fig. 3. Habitat of *Fulchrana centropeninsularis*, Hutan Harapan, Jambi (a) and *P. fantastica*, new species, Taman Buru Linge Isaq, Aceh (b, c). Photo by A. Jankowski (a); G. Cahyadi (b, c).

Arifin et al.: New *Pulchrana* from SumatraTable 4. Morphometric variation (in mm) between specimens of *Pulchrana centropeninsularis* from the Malay Peninsula and Jambi.

	<i>P. centropeninsularis</i> (Malay Peninsula; Chan et al., 2014)		<i>P. centropeninsularis</i> (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 (\pm SD), followed by range, in mm.

	<i>P. centropeninsularis</i>	<i>P. centropeninsularis</i>	<i>P. siberu</i>	<i>P. fantastica</i> , 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 \pm 0.1 (37.4–37.6)	38.7 \pm 2.7 (35.5–40.4)	37.0 \pm 2.2 (35.4–39.5)	42.4 \pm 1.3 (40.3–45.2)
HL	14.6 \pm 0.8 (14.0–15.2)	14.8 \pm 0.4 (14.5–15.2)	15.7 \pm 0.1 (15.6–15.9)	15.0 \pm 0.7 (14.1–16.0)
HW	12.3 \pm 0.4 (12.0–12.5)	10.6 \pm 0.6 (10.3–11.3)	13.0 \pm 0.3 (12.6–13.2)	11.5 \pm 0.9 (9.5–12.4)
SL	6.2 \pm 0.4 (5.9–6.4)	6.0 \pm 0.2 (5.8–6.2)	7.0 \pm 0.5 (6.5–7.4)	6.7 \pm 0.2 (6.4–7.0)
IOD	3.4 \pm 0.2 (3.2–3.5)	3.8 \pm 0.1 (3.7–3.9)	4.2 \pm 0.3 (3.8–4.5)	4.0 \pm 0.3 (3.4–4.4)
IND	3.7 \pm 0.1 (3.6–3.7)	3.3 \pm 0.2 (3.1–3.5)	4.1 \pm 0.2 (4.0–4.3)	4.0 \pm 0.2 (3.5–4.3)
ED	5.6 \pm 0.6 (5.1–6.0)	5.4 \pm 0.1 (5.3–5.4)	5.3 \pm 0.3 (5.1–5.3)	6.0 \pm 0.3 (5.5–6.5)
TD	3.5 \pm 1.8 (2.2–4.8)	3.2 \pm 0.2 (3.1–3.4)	3.6 \pm 0.3 (3.3–3.9)	3.5 \pm 0.2 (3.2–3.8)
BL	7.7 \pm 0.5 (7.3–8.0)	8.9 \pm 0.1 (8.8–9.1)	8.0 \pm 0.6 (7.3–8.4)	10.1 \pm 0.5 (9.1–10.6)
FAL	8.2 \pm 0.1 (8.1–8.2)	9.8 \pm 0.6 (9.2–10.5)	9.7 \pm 0.5 (9.2–10.1)	9.5 \pm 0.6 (8.5–10.5)
FL	17.7 \pm 0.1 (17.6–17.7)	18.4 \pm 1.3 (17.5–19.9)	18.7 \pm 1.6 (17.0–20.2)	21.5 \pm 0.9 (20.0–23.5)
TBL	19.6 \pm 0.5 (19.2–19.9)	20.6 \pm 0.5 (20.3–21.3)	20.9 \pm 0.8 (20.0–21.6)	23.2 \pm 0.9 (22.1–25.0)
TL	11.8 \pm 1.6 (10.6–12.9)	11.2 \pm 0.3 (11.0–11.6)	12.1 \pm 0.4 (11.7–12.5)	12.3 \pm 0.8 (11.2–13.9)
HG	4.2 \pm 0.0 (4.2–4.2)	3.4 \pm 0.6 (2.9–4.1)	4.5 \pm 0.3 (4.3–4.8)	3.9 \pm 0.3 (3.2–4.3)

or leaves of small bushes or saplings at 0.2–0.5 m above ground. Male advertisement 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).

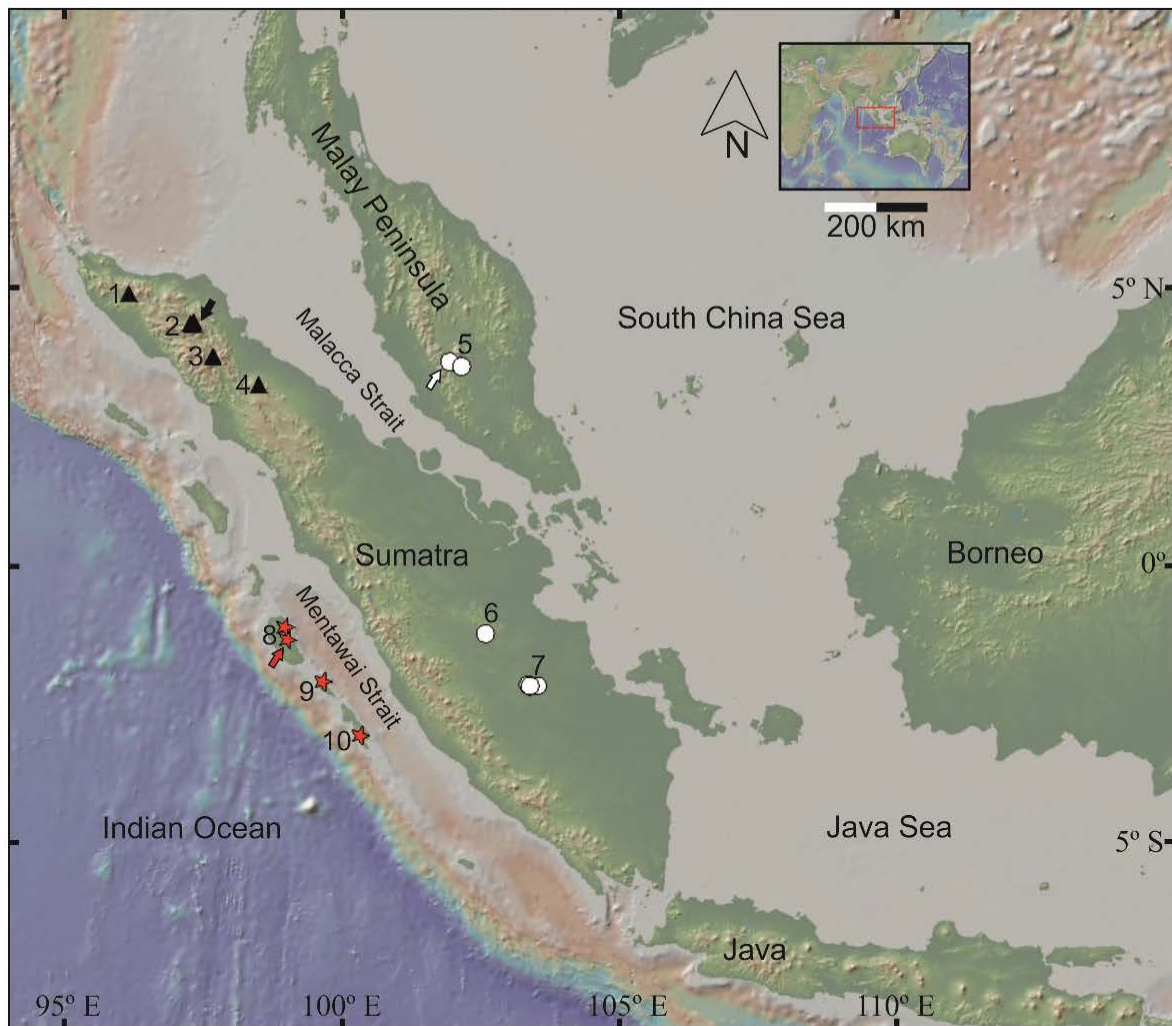


Fig. 4. Geographical distribution of *Pulchrana centropeninsularis* (white circles), *P. fantastica*, new species (black triangles), and *P. siberu* (red stars). Locality information: Manc (1); Taman Buru Linge Isaq (2); Taman Nasional Gunung Leuser (3); Bandar Baru (4), Lakum Forest Reserve & Kuala 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.

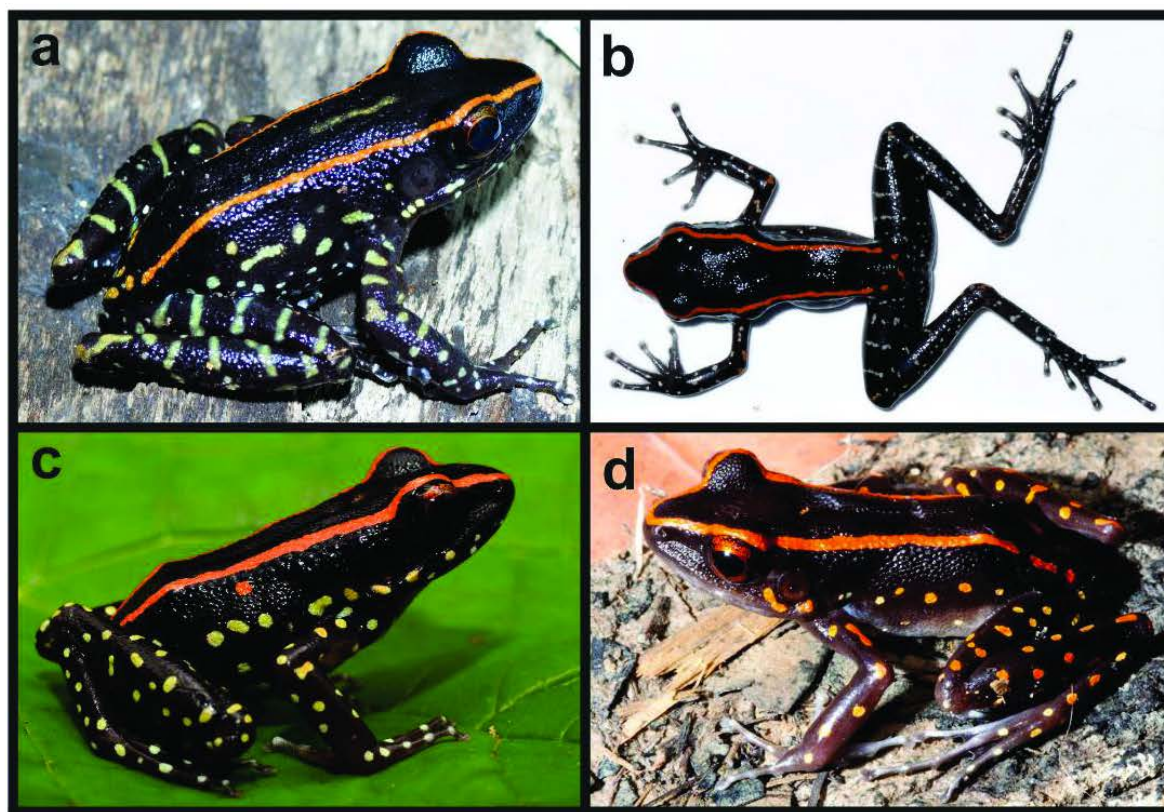
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Fig. 5. Plates comparing the three closely allied Sumatran *Pulchrana* species (a) *P. fantastica*, new species, MZB.Amph.28894, adult male, paratype, Aceh; (b) *P. fantastica*, new species, MZB.Amph.28943, juvenile, Aceh; (c) *P. centropeninsularis*, 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)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

Arifin et al.: New *Pulchrana* from SumatraTable 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
PAL (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

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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)
Tee2TPW (mm)	0.8	0.7	0.7	0.8	0.7	0.6	0.7
Tee3TPW (mm)	0.7	0.8	0.5	0.6	0.6	0.7	0.6
Tee4TPW (mm)	0.7	0.6	0.6	0.8	0.8	0.6	0.6
Tee5TPW (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

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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 ^o)II(1/2 -- 2)III(1- -- 2*) IV(2- -- 1)V	I(1 ^o -- 11/2)II(1/2 -- 2*) III(1- -- 2*) IV(2- -- 1)V	I(1- -- 1 ^o)II(1/2 -- 2*) III(1- -- 2*) IV(2- -- 1)V	I(1 ^o -- 11/2)II(1/2 -- 2*) III(1- -- 2*) IV(2* -- 1)V	I(1- -- 1 ^o)II(1/2 -- 2)III(1- -- 2*) IV(2* -- 1)V	I(1 ^o -- 11/2)II(1/2 -- 2)III(1- -- 21/3) IV(2* -- 1)V	I(1- -- 1 ^o)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 dipterocarp 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 subgenera (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

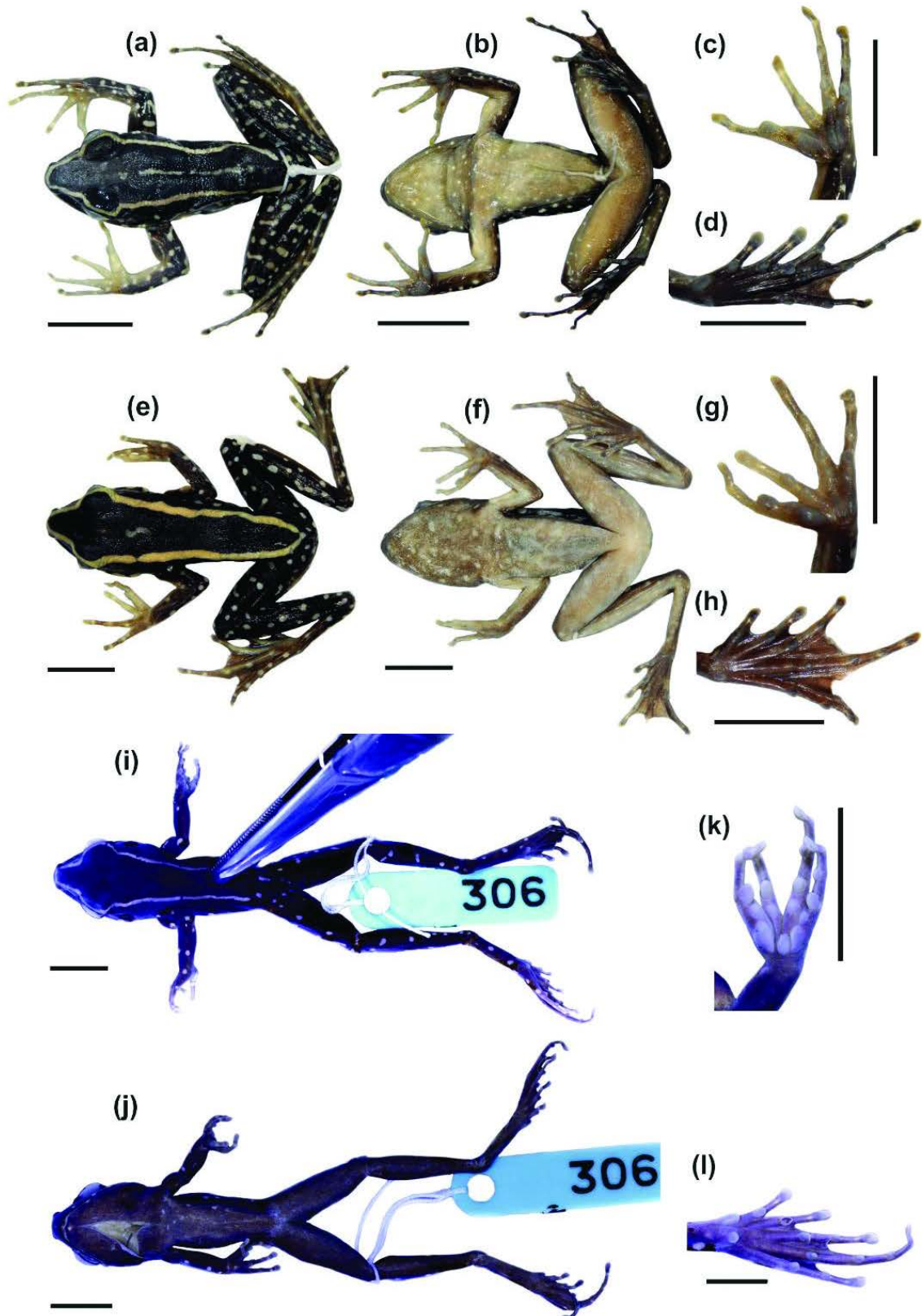
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Fig. 6. Dorsal (a), ventral (b), palmar (c), and plantar (d) views of *Pulchrana fantastica*, new species (MZB.Amph.28891, male, holotype, Aceh); (e–h) *P. centropeninsularis* (MZB.Amph.28767, male, Jambi); (i–l) *P. siberu* (BMNH 1979.306, male, holotype, 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 *Ammirana 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 increase 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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LITERATURE CITED

- Alfaro ME, Zoller S & Lutzoni F (2003) Bayes or bootstrap? A simulation study comparing the performance of Bayesian Markov chain Monte Carlo sampling and bootstrapping in assessing phylogenetic confidence. *Molecular Biology and Evolution*, 20: 255–266.
- Arifin U, Smart U, Hertwig ST, Smith EN, Iskandar DT & Haas A (2018) Molecular phylogenetic analysis of a taxonomically unstable ranid from Sumatra, Indonesia, reveals a new genus with gastromyzophorous tadpoles and two new species. *Zoosystematics and Evolution*, 94: 163–193. <https://doi.org/10.3897/zse.94.22120>.
- Batsch AJGK (1796) Umriss der gesammten Naturgeschichte: ein Auszug aus den frühern Handbüchern des Verfassers für seine Vorlesungen. Jena & Leipzig: Christian Ernst Gabler, i–xvi + 1–287 + 3–160 + [1–32] + [i–vi] + 1–80 pp.
- Brown RM (2015) A new species of stream frog of the genus *Hylarana* from the mountains of southern Mindanao Island, Philippines. *Herpetologica*, 71(3): 223–233.
- Brown RM & Guttman SI (2002) Phylogenetic systematics of the *Rana signata* complex of Philippine and Bornean stream frogs: Reconsideration of Huxley's modification of Wallace's Line at the Oriental–Australian faunal zone interface. *Biological Journal of the Linnean Society*, 76(3): 393–461.

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- Brown RM & Siler CD (2013) Spotted stream frog diversification at the Australasian faunal zone interface, mainland versus island comparisons, and a test of the Philippine ‘dual-umbilicus’ hypothesis. *Journal of Biogeography*, 41: 182–195.
- Chan KO & Noerhayati A (2009) Distribution and natural history notes on some poorly known frogs and snakes from Peninsular Malaysia. *Herpetological Review*, 40: 294–301.
- Chan KO, Brown RM, Lim KK, Ahmad N & Grismer L (2014) A new species of frog (Amphibia: Anura: Ranidae) of the *Hylarana signata* complex from Peninsular Malaysia. *Herpetologica*, 70: 228–240.
- Chan KO & Brown RM (2017) Did true frogs ‘dispersify’?. *Biology Letters*, 13(8): 20170299.
- de Queiroz K (2005) A unified concept of species and its consequences for the future of taxonomy. *Proceedings of the California Academy of Sciences*, 56: 196–215.
- Dring JCM, McCarthy CJ & Whitten AJ (1990) The terrestrial herpetofauna of the Mentawai Islands, Indonesia. *Indo-Malayan Zoology*, 6: 119–132.
- Dubois A (1992) Notes sur la classification des Ranidae (Amphibiens anoures). *Bulletin Mensuel de la Société Limnienne de Lyon*, 61: 305–352.
- Duellman WE & Trueb L (2015) *Marsupial Frogs: Gastrotheca and Allied Genera*. Baltimore: Johns Hopkins University Press, 432 pp.
- Duellman WE & Trueb L (1986) *Biology of Amphibians*. McGraw-Hill, New York, 670 pp.
- Frost DR (2018) *Amphibian Species of the World: An Online Reference*. Version 6.0. American Museum of Natural History, New York, USA. <http://research.amnh.org/herpetology/amphibia/index.html>. (Accessed 1 March 2018).
- Geyh MA, Streif H & Kudrass HR (1979) Sea-level changes during the late Pleistocene and Holocene in the Strait of Malacca. *Nature*, 278: 441–443.
- Goebel AM, Donnelly JM, Atz ME (1999) PCR primers and amplification methods for 12S ribosomal DNA, the control region, cytochrome oxidase I, and cytochrome b in bufonids and other frogs, and an overview of PCR primers which have amplified DNA in amphibians successfully. *Molecular Phylogenetics and Evolution*, 11(1): 163–199. <https://doi.org/10.1006/mpev.1998.0538>.
- Guayasamin JM, Bustamante MR, Almeida-Reinoso D & Funk WC (2006) Glass frogs (Centrolenidae) of Yanayacu Biological Station, Ecuador, with the description of a new species and comments on centrolenid systematics. *Zoological Journal of the Linnean Society*, 147: 489–513.
- Hamidy A & Kurniati H (2015) A new species of tree frog genus *Rhacophorus* from Sumatra, Indonesia (Amphibia, Anura). *Zootaxa*, 3947: 49–66.
- Hillis DM & Bull JJ (1993) An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology*, 42: 182–192.
- Huelsenbeck JP & Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17: 754–755.
- Huelsenbeck JP & Rannala B (2004) Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Systematic Biology*, 53: 904–913.
- Inger RF, Stuart BL & Iskandar DT (2009) Systematics of a widespread Southeast Asian frog, *Rana chalconota* (Amphibia: Anura: Ranidae). *Zoological Journal of the Linnean Society*, 155: 123–147.
- Iskandar DT & Colijn E (2000) Preliminary Checklist of Southeast Asian and New Guinean Herpetofauna: Amphibians. I. Research and Development Centre for Biology, Indonesian Institute of Sciences, 133 pp.
- IUCN (2017) IUCN Red List of Threatened Species, Version 2017.1. www.iucnredlist.org. (Accessed 1 June 2017).
- Katoh K & Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution*, 30: 772–780.
- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Mentjies P & Drummond A (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28(12): 1647–1649.
- Kok PJ & Kalamandeen M (2008) Introduction to the Taxonomy of the Amphibians of Kaieteur National Park, Guyana. Belgian Development Cooperation, 278 pp.
- Lanfear R, Calcott B, Ho SY & Guindon S (2012) PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29: 1695–1701.
- Leong TM & Lim BL (2004) *Rana siberu* Dring, McCarthy & Whitten, 1990-A first record for Peninsular Malaysia (Amphibia: Anura: Ranidae). *Raffles Bulletin of Zoology*, 52: 261–264.
- Margono BA, Potapov PV, Turubanova S, Stolle F & Hansen MC (2014) Primary forest cover loss in Indonesia over 2000–2012. *Nature Climate Change*, 4: 730–735.
- Matsui M, Mumpuni & Hamidy A (2012) Description of a new species of *Hylarana* from Sumatra (Amphibia, Anura). *Current Herpetology*, 31(1): 38–46.
- McLeod DS, Horner SJ, Husted C, Barley A & Iskandar D (2011) Same-same, but different: an unusual new species of the *Limnoneustes kahlii* complex from West Sumatra (Anura: Dicroglossidae). *Zootaxa*, 2883: 52–64.
- Miller MA, Pfeiffer W & Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*. New Orleans, LA, pp. 1–8.
- Mulcahy DG, Beckstead TH & Sites JW Jr (2011) Molecular systematics of the *Leptodeirini* (Colubroidea: Dipsadidae) revisited: Species-tree analyses and multi-locus data. *Copeia*, 20113: 407–417.
- Oliver LA, Prendini E, Kraus F & Raxworthy CJ (2015) Systematics and biogeography of the *Hylarana* frog (Anura: Ranidae) radiation across tropical Australasia, Southeast Asia, and Africa. *Molecular Phylogenetics and Evolution*, 90: 176–192.
- Pauly GB, Hillis DM, Cannatella DC (2004) The history of a nearctic colonization: molecular phylogenetics and biogeography of the Neartic toads (*Bufo*). *Evolution*, 58: 2517–2535. <https://doi.org/10.1111/j.0014-3820.2004.tb00881.x>.
- Rambaut A (2007) FigTree: A Graphical Viewer of Phylogenetic Trees. tree.bio.ed.ac.uk/software/figtree/. (Accessed 1 August 2017).
- Rambaut A & Drummond AJ (2009) Tracer, Version v. 1.45.0. beast.bio.ed.ac.uk/Tracer. (Accessed 1 August 2017).
- Riyanto A & Kurniati H (2014) Three new species of *Chiromantis* Peters 1854 (Anura: Rhacophoridae) from Indonesia. *Russian Journal of Herpetology*, 21: 65–73.
- Ronquist F & Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19: 1572–1574.
- Rowley J, Brown R, Bain R, Kusriani M, Inger R, Stuart B, Wogan G, Thy N, Chan-ard T, Trung CT, Diesmos A, Iskandar DT, Lau M, Ming LZ, Makchai S, Truong NQ & Phimmachak S (2010) Impending conservation crisis for Southeast Asian amphibians. *Biology Letters*, 6: 336–338.
- Ryan WBF, Carbotte SM, Coplan JO, O’Hara S, Melkonian A, Arko R, Weissel RA, Ferrini V, Goodwillie A, Nitsche F, Bonczkowski J & Zemsky R (2009) Global multi-resolution

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- topography synthesis. *Geochemistry Geophysics Geosystems*, 10(3): Q03014. doi:10.1029/2008GC002332.
- Savage JM & Heyer WR (1997) Digital webbing formulae for anurans: a refinement. *Herpetological Review*, 28: 131.
- Smart U, Sarker GC, Arifin U, Harvey MB, Sidik I, Hamidy A, Kurniawan N & Smith EN (2017) A new genus and two new species of arboreal toads from the highlands of Sumatra with a phylogeny of Sundaland toad genera. *Herpetologica*, 73: 63–75.
- Stamatakis A (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22: 2688–2690.
- Stamatakis A (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30: 1312–1313.
- Stuart BL, Inger RF & Voris HK (2006) High level of cryptic species diversity revealed by sympatric lineages of Southeast Asian forest frogs. *Biology Letters*, 2: 470–474.
- Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues AS, Fischman DL & Waller RW (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, 306: 1783–1786.
- Teynie A, David P & Ohler A (2010) Note on a collection of amphibians and reptiles from Western Sumatra (Indonesia), with the description of a new species of the genus *Bufo*. *Zootaxa*, 2416: 1–43.
- Van Kampen PN (1910) Eine neue *Nectophryne*-Art und andere Amphibien von Deli (Sumatra). *Natuurkundig Tijdschrift voor Nederlandsch Indië*, 69: 18–24.
- Voris HK (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography*, 27: 1153–1167.
- Watters JL, Cummings ST, Flanagan RL & Siler CD (2016) Review of morphometric measurements used in anuran species descriptions and recommendations for a standardized approach. *Zootaxa*, 4072(4): 477–495.
- Whittaker K, Koo MS, Wake DB & Vredenburg VT (2013) Global Declines of Amphibians. In: Levin SA (ed.) *Encyclopedia of Biodiversity*. Second Edition, Volume 3. Academic Press, Waltham, MA. Pp. 691–699.
- Wostl E, Riyanto A, Hamidy A, Kurniawan N, Smith EN & Harvey MB (2017) A taxonomic revision of the *Philautus* (Anura: Rhacophoridae) of Sumatra with the description of four new species. *Herpetological Monographs*, 31(1): 98–141.

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.

CHAPTER 4

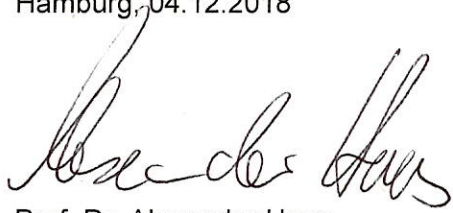
Genetic structure of two genera of Sumatran frogs trace back to ancient volcanic islands origins rather than Paleo-drainage systems

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Author contribution

I hereby confirm that Umilaela Arifin conceived, designed, analyzed the data, and wrote the paper.

Hamburg, 04.12.2018

A handwritten signature in black ink, appearing to read 'Alexander Haas', written in a cursive style.

Prof. Dr. Alexander Haas

Genetic structure of two genera of Sumatran frogs trace back to ancient volcanic islands origins rather than Paleo-drainage systems

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The influence of riverscapes on the distribution and genetic structure of species has been investigated in various taxa and regions. In most cases, the influence of river systems on genetic diversity depends on taxa specific life history traits as well as other geographic factors. Here, we assess the role of the Paleo-drainage systems of the Sunda region (with a focus on the island of Sumatra) in shaping the evolutionary history frogs' genera (*Huia* and *Sumaterana*) that are highly dependent on cascading stream habitats during their larval stage. Our phylogenetic analyses demonstrated that Paleo-drainages had no congruency with the current distribution patterns of *Huia* and *Sumaterana*. Our time divergence analyses estimated these frogs to have colonized Sumatra much earlier than the occurrence of the known drainage systems in the Pleistocene. Interestingly, both genera are genetically structured into northern and southern lineages on the island of Sumatra, which may suggest that the genetic segregation observed today dates back to now connected Sumatran precursor volcanic islands. Our data further corroborate the current underestimation of biodiversity on Sumatra and show that frogs of the genus *Huia* in Sumatra and Java are more diverse than currently known.

Sundaland (the combined landmasses that comprise of the Malay Peninsula, Borneo, Sumatra, and Java, and the shallow sea in between) is one the global hotspot regions with prodigious biodiversity and enormous number of local endemics^{1,2,3}. This diversity and high rate of endemism has primarily been accredited to the dynamic abiotic history of the region especially during the Cenozoic^{4,5}. The geological events during the Cenozoic had caused different configurations of land and sea over time and had impacted the climate, vegetation, and the availability of habitats in time^{6,7,8}. Several studies^{9,10,11,12,,13} have investigated the historical process of the Sundaland to explain unique distribution patterns of the species in the region today.

Despite recurrent sea level fluctuation, most of western parts of Sundaland were terrestrial from the Eocene to the Early Miocene, with some evidence of large freshwater lakes^{14,15}. The volcanic arcs were also formed at the southern margin of the Sunda region during this period^{14,16}. The volcanic activity in Sumatra became more extensive from the Mid Eocene as an impact of the regional subsidence on the island^{14,16,17}. In the Quaternary period of the Last Glaciation Maximum (LGM), the sea level was recorded at its lowest (120 m below present day) and the climate was considerably cooler and drier⁸. However, Morley⁸ suggested that in much of the Quaternary the climate was presumably neither wetter nor drier than during the LGM. The oscillation of sea level during this time has periodically established connections of the landmasses across the Sunda Shelf¹⁸ and has formed four extensive Paleo-river systems in the Sunda and Sahul shelves, i.e., the Malacca Strait river system, the Siam river system, the North Sunda river system, and the East Sunda river system^{19,20}. These Pleistocene drainage systems had impacts on the biodiversity patterns in the region as they served as potential dispersal routes between the Greater Sunda Islands^{19,20}. The freshwater riverine faunas of many of today's rivers that are at present restricted to Indo-China, the Malay Peninsula, or one of the Greater Sunda Islands were connected during the Pleistocene^{11,19,29,21,22}.

While we have a basic understanding of the geology, phylogeographic studies can help elucidate the biological impacts that the biotic changes had. Extant species can be mapped onto the river systems and analyzed with biogeographic and phylogeographic approaches. Genetic structure of population may have strongly influenced by dispersal barriers resulting from fragmentation of the riverscape (define as a mosaic of freshwater river habitat that is spatially structured and hierarchically organized across multiple scales²³). Genetic diversity should be partitioned and regionally distributed according to river drainages if the Paleo-river systems played a major role in the speciation and dispersal of the groups of organisms under study. This appears to be the case, at least for some freshwater organisms and other groups with strong aquatic dependencies, e.g.

the Southeast Asian halfbeak fishes¹² and the Mekong mud snake²⁴. De Bruyn et al.¹² found a strong correlation of phylogenetic partitioning in clades of freshwater fishes with their distributions across river drainages. In this study the Sundaland Paleo-drainages could explain extant patterns of genetic segregations in selected fauna. Further, Lukoschek et al.²⁴ showed that genetic variance of the Mekong mud snake was strongly partitioned geographically, corresponding to the three drainages surveyed. The evidence from these studies suggest that the Quaternary landscapes of Indo-China and the Sunda Shelf shaped the genetic divergence patterns among populations of certain taxa. The influence of rivers on the distribution and genetic structure of fauna has also been tested in various taxa and regions, either as a corridor or barrier (e.g., in the Amazon: frogs²⁵, frogs and small mammals²⁶, mammals²⁷, birds²⁸; on Madagascar: mammals²⁹, frogs³⁰; in the Southern USA: fish³¹; in Eastern Australia: water skinks³²). These studies showed that the influence of rivers systems depends on the taxon's specific life history traits as well as on the particular geographic setting³⁰. The current hydrography of the river systems may not always explain observed species distribution patterns.

Most amphibians undergo a complex life-cycle with sedentary larval forms that strongly depend on aquatic habitats while the terrestrial stages are potentially more prone to disperse. Still, rivers may have barrier effects in amphibian populations and may confine a species dispersal^{33,34,35}. Here we selected two endemic genera of Sumatran ranid frogs (*Huia* and *Sumaterana*) to test whether the Paleo-river systems in Sumatra structured the distribution of genetic diversity in these ranid frogs. Species of *Huia* and *Sumaterana* are the only Sumatran ranids that inhabit torrential streams and possess specialized tadpoles form that is called gastromyzophorous^{36,37,38}. Taxa with gastromyzophorous tadpoles represent an ecomorphological guild that is rare among anurans, and is characterized by the possession of a large-adhesive sucker at the abdomen as an adaptation to torrential stream habitats³⁹. Because of their strong dependency on cascading stream habitats during their larval stage, *Huia* and *Sumaterana* species appear suitable to assess the role of Paleo-drainage systems of the Sunda region, and Sumatra in particular, on the species diversification pattern. Our phylogenetic analyses presents strong evidence that *Huia* encompasses more species-level diversity than acknowledged in current taxonomy. We demonstrate that distribution patterns of *Huia* and *Sumaterana* have no correlation with the Paleo-drainage systems of Sumatra. The diversification process of *Huia* and *Sumaterana* might be more complex, especially because we will argue that they colonized Sumatra much earlier than the Pleistocene river systems existed. Surprisingly, both *Huia* and *Sumaterana* are each genetically structured into a northern and southern lineages. The pattern and its dating

are best explained if we assume that that these clusters go back to isolation on now extinct precursor volcanic islands.

Result

Phylogenetic relationships of Sumatran ranids with gastromyzophorous tadpoles.

We generated new sequence dataset (N=146), comprises of ten concatenated loci of Sumatran frogs of the genere *Huia* and *Sumaterana* along with sequences of closely related taxa within Ranidae (Table S1). We used final concatenated alignment of a total of 7582 bps (28.91% proportion of gaps and completely undetermined characters) to infer phylogenetic relationships of Sumatran ranids that possesses abdominal sucker larvae. Both Maximum Likelihood (ML) and Bayesian Inference (BI) trees revealed the same topology for the relationship of ranid frogs with gastromyzophorous tadpoles (blue color in Fig. 1; original trees from both analyses provided in Fig. S1–S2), with slight differences in arrangement of the terminal nodes (see Fig. S1–S2). *Sumaterana* suggested to be sister taxon of *Clinotarsus* and *Huia sumatrana* was closely related to *H. masonii*. Small differences between ML and BI trees also appeared in the intra-specific relationship of *Meristogenys amoropalamus* from Borneo. In the BI tree (Fig. 1), *M. amoropalamus* was sister to a clade of *M. orphocnemis*+*M. poecilus*, whereas in ML tree this species was sister taxon of unidentified *Meristogenys* species (Fig. S1). Although the mainland Asian genus *Amolops* also possesses gastromyzophorous tadpoles, both trees reconstruct *Amolops* to be closely related to ranid species that do not possess gastromyzophorous tadpoles (e.g., *Odorrana*, *Chalcorana*, *Pulchrana*, *Hylarana*), rather than grouping with *Huia*, *Meristogenys*, *Sumaterana* that have gastromyzophorous tadpoles. In the analyses (Fig. S1), *Clinotarsus*, a ranid taxon with non-gastromyzophorous tadpoles was recovered as nested within the clade of taxa from Sundaland with gastromyzophorous tadpoles (*Huia*, *Meristogenys*, *Sumaterana*), however, with low support values.

Phylogenetic diversity of the genus *Huia*. Before mapping the distribution of *Huia* and *Sumaterana* in relation to the watershed system in Sumatra, we assessed the diversity of the *Huia*. Our phylogenetic trees (Fig. 1) suggested that frogs of the genus *Huia* clearly showed more species-level diversity than currently known. Both ML and BI trees support the recognition of five distinct lineages within *Huia* samples from Sumatra (N=55) and Java (N=6) with strong support values (PP=0.99–1; BS=100); all these lineages show substantial genetic distances to each other (p -distance=6.97%–15.48%, Table S2), qualifying them as candidate species⁴⁰. We further refer to these clades as *H. sumatrana* 1, *H. sumatrana* 2, *H. sumatrana* 3, *H. masonii* 1, and *H. masonii* 2, respectively (Fig. 1).

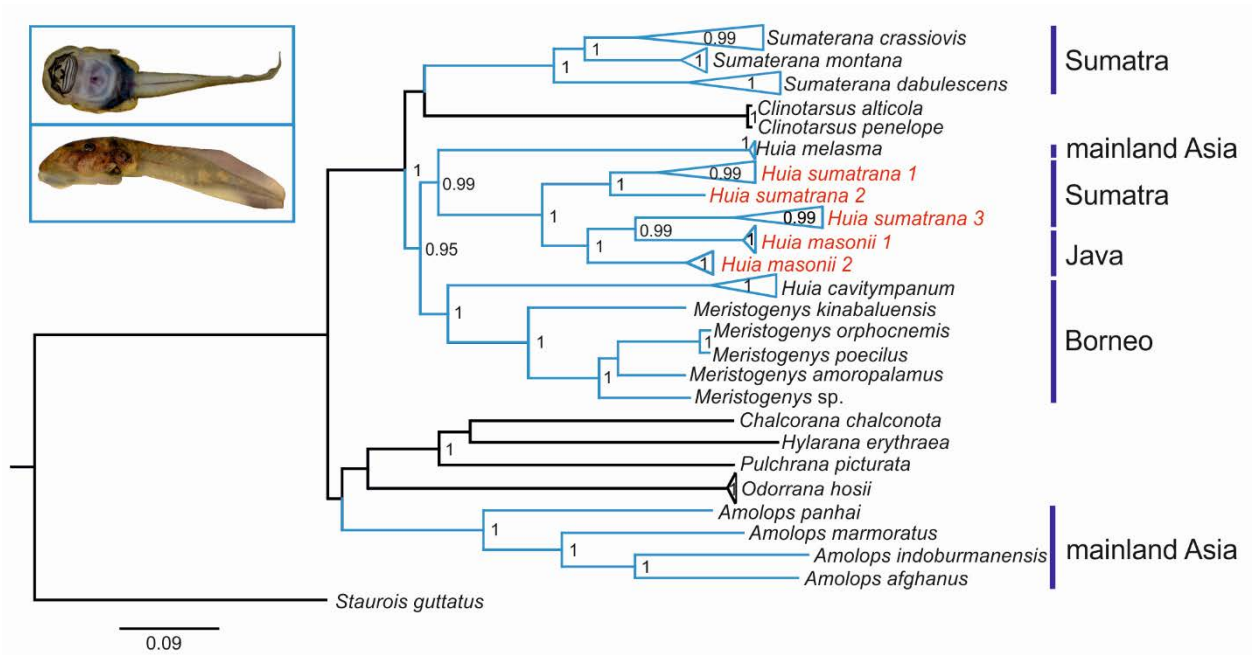


Figure 1 BI tree showing phylogenetic relationships of the Sumatran ranids with gastromyzophorous tadpoles within the family Ranidae. Blue color represent ranid frogs with abdominal sucker tadpoles. Value depicted Posterior Probability (PP) value, nodes without PP value means PP < 0.95. Red color represent the five distinct lineages of *Huia* from Sumatra and Java. Morphology of gastromyzophorous tadpoles (ventral and lateral view) showed on the upper left.

Sumatran Paleo-drainage systems and distribution patterns of Sumatran ranids with abdominal sucker tadpoles. We used the same BI tree in Fig. 1 to map the distribution of genetic variation of *Huia* (*H. sumatrana* 1–3) and *Sumaterana* (*S. crassiovis*, *S. dabulescens*, *S. montana*) onto the respective watershed system in Sumatra (Fig. 2a for *Sumaterana* and Figure 2b for *Huia*). For clarity, we use the terms “watershed/drainage basin” as a region or area bounded peripherally by a divide and draining ultimately to a particular watercourse or body of water; hence our definition a “watershed/drainage system” may comprising several watersheds.

When mapping ancient drainage systems onto the phylogenetic tree (Fig. 2), the geographical distribution of *Sumaterana* and *Huia* did not show any correlation with the Paleo-drainage systems on Sumatra (Fig. 2a-b; see methods for Paleo-drainage systems definition). Frogs of the two genera demonstrated that samples from each Paleo-drainage systems (*sensu* Voris¹⁹) east of the Barisan Mountain range were more closely related to samples from the respective neighboring western watershed that flows into the Indian Ocean than to samples from the neighboring Paleo-drainage system (tree available upon request). Although Clade D shows a monophyletic group of samples from Malacca Strait Paleo-drainage system, all samples were collected from different tributaries but within the same watershed (Sungai Rokan).

Considering its wide distribution across the island, *S. crassiovis* (Fig. 2a Clade A–D), *H. sumatrana* 1 (Fig. 2b Clade I–J), and *H. sumatrana* 2 (Fig. 2b Clade L–N), were chosen to test divergence scenarios. Surprisingly, it seems that the three taxa were genetically structured into the northern (Sumatra-North in Fig. 3) and southern (Sumatra-Central and Sumatra-South in Fig. 3) parts of Sumatra. Clade A, I, and L were distributed in the northern part, whereas clades B2, C, J, and M exhibit southern distributions. Seemingly the Sumatera Barat province (located in the center of the island, comprises part of Sumatra-North and Sumatra-Central in Fig. 3) is the overlapping area between the northern and southern distribution. Samples from Sumatera Barat province occurred in both groups. This is supported by clade B1 that contains samples from Sumatera Barat province, but also samples from Jambi province. Interestingly, clade N encompasses samples from Aceh, Sumatera Barat, and Lampung provinces.

Divergence time estimation and ancestral area reconstruction. We estimated divergence times of the Sumatran frogs with gastromyzophorous tadpoles and their close ranid relatives in order to understand how the diversification history of these frogs may have been linked to geographic or climatic events on Sumatra. The chronogram (Fig. 3) resulting from this analysis slightly differed compared to ML and BI trees in the arrangement of the terminal nodes (particularly in *Huia sumatrana*, *H. masonii*, and *Sumaterana*). Furthermore, in the chronogram, *Clinotarsus* was sister to a clade comprising taxa with gastromyzophorous tadpoles from Sundaland (*Huia+Meristogenys+Sumaterana*) whereas this genus was sister to clade of *Sumaterana* in ML and BI trees.

Our analyses suggest that *Huia+Meristogenys+Sumaterana*, began to diversify in the Early Eocene (approx. 47.75 Ma, Fig. 3) on Sundaland. One group emerged in Sumatra and persisted, while another group dispersed to Java and Borneo. On Sumatra itself, the first *Huia* and *Sumaterana* arose approximately in the Mid–Late Oligocene (27.65 Ma and 25.11 Ma, respectively). While *Sumaterana* shows within island (in situ) diversification at approx. 17.93 Ma and 10.01 Ma, our data suggest *Huia* colonized Sumatra at least two times (Fig. 3). The first split in *Huia* between Sumatra and Java took place approx. 27.65 Ma. The Sumatran lineage later diverged into *H. sumatrana* 1 and *H. sumatrana* 2 in approx. 13.78 Ma. The Javan lineage, however, after the first in situ diversification at approx. 22.11 Ma, re-colonized Sumatra at approx. 16.42 Ma. From the Early Pliocene (~5 Ma), both *Huia* and *Sumaterana* diverged into many intra-specific lineages (Fig. 3).

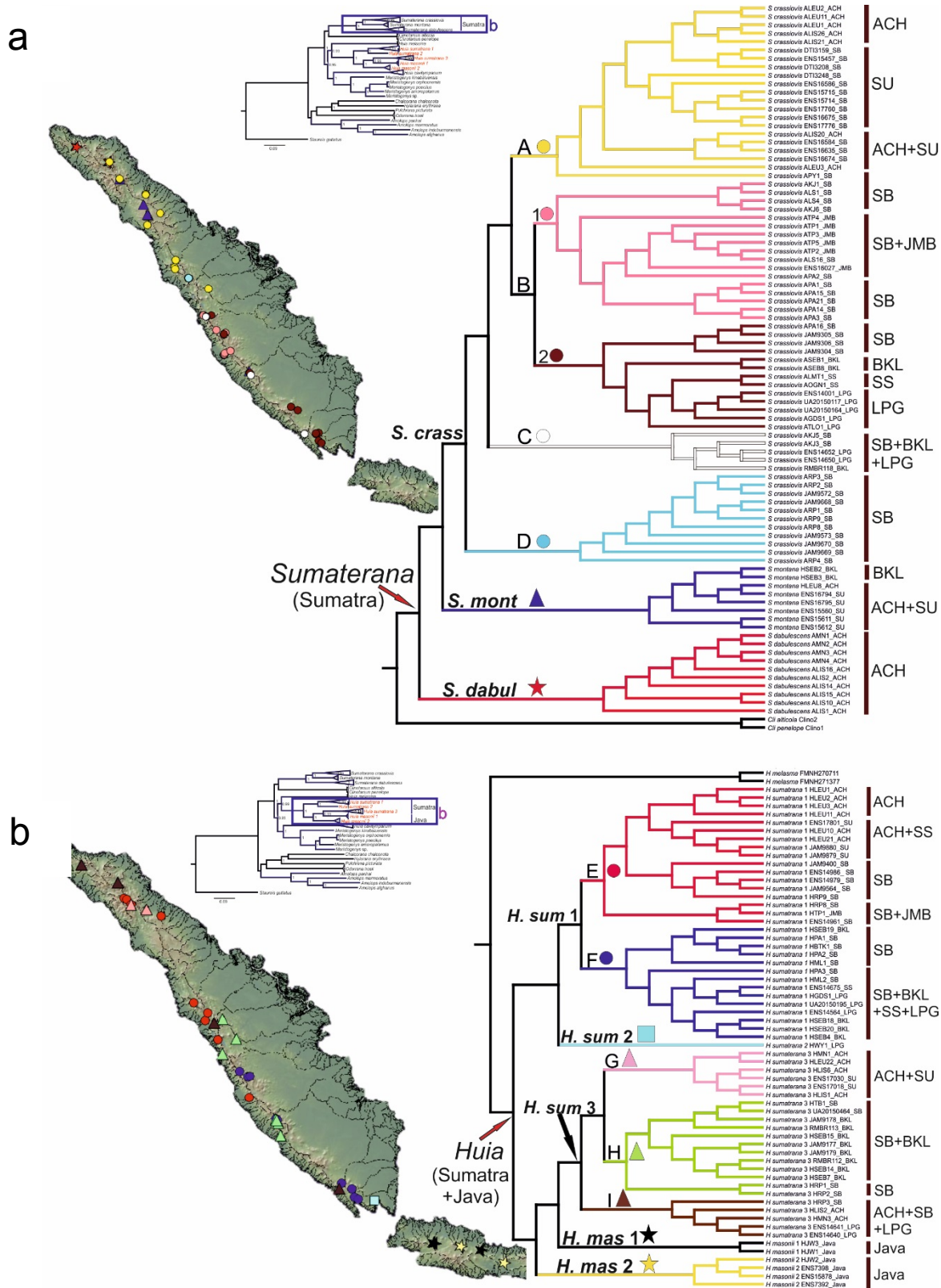


Figure 2 Distribution of *Sumaterana* (a) and *Huia* (b) mapped onto watersheds that flows within the island of Sumatra. Color code on each branches represent the sampling locality of each respective taxa: *Sumaterana crassiovis* (clade A–D, circles), *S. montana* (clade E, triangles), *S. dabulescens* (clade D, stars), *H. sumatrana* 1 (clade I–J, circles), *H. sumatrana* 2 (clade K, square), *H. sumatrana* 3 (clade L–N, triangles), *H. masonii* 1 (clade O, stars), *H. masonii* 2 (clade P, stars). Provinces on Sumatra indicated by ACH (Aceh), SU (Sumatera Utara), SB (Sumatera Barat), JMB (Jambi), BKL (Bengkulu), SS (Sumatera Selatan), LPG (Lampung).

Discussion

Phylogenetic diversity of Sumatran ranids with gastromyzophorous tadpoles. The biodiversity and diversification patterns of amphibians on Sumatra and most of the Sunda region are still poorly understood^{5,41,42}, despite a variety of phylogenetic and taxonomic studies in the last decade have increased current knowledge^{38,43,44,45,46,47}. Geographically dense sampling along with integrative taxonomy approaches^{38,48} are undoubtedly the key to disentangle the true diversity of this region. Establishing phylogenetic hypotheses that transform into stable taxonomy and documenting geographical distribution maps for the fauna of Sumatra are important steps towards an understanding of diversification patterns and processes^{49,50}. Eventually, knowing patterns and processes are a prerequisite for effective conservation measures of particular species because biodiversity hotspots, habitat loss, and escalating threats often coincide^{51,52}.

Sumatran frogs with gastromyzophorous tadpoles is one of many overlooked species in Sumatra due to lack of sampling. In many available studies^{53,54}, this taxon only represented by one samples despite its geographical range throughout the island. Recent study³⁸ has demonstrated that broad and thorough geographic sampling along with the application of integrative taxonomy approaches have successfully recognized *Sumaterana* as a new genus with this unique larvae on the island of Sumatra. Furthermore, through this study we clearly show that *Huia* on this island has more diversity than it has been acknowledged. Three distinct lineages of Sumatran *Huia* along with two distinct lineages of Javan *Huia* were revealed in this study. As a consequence, our study corroborated previous study suggesting underestimated diversity on Sumatra^{38,42,55}. This study also confirmed the hypothesis that species diversity in Sumatra would experience steady increase in the next few years if more sampling efforts are performed^{38,42,56}.

Pleistocene-drainage systems and distribution patterns of Sumatran ranids with abdominal sucker tadpoles. The presence of the Pleistocene Paleo-drainage system in Sundaland, has been proposed as one of the main drivers that strongly influenced the diversification pattern of the Sundaland freshwater fish¹² and Mekong mud snakes²⁴. However, these Paleo-drainages apparently had no effect on the diversification of Sumatran frogs *Huia* and *Sumaterana*, despite the strong dependence on rivers during their larval stages (Fig. 2). These frogs were not genetically structured according to Voris¹⁹ Pleistocene drainage systems. Frogs from the eastern slopes of the Barisan Mountain range apparently were more closely related to individuals from the corresponding western slopes, than to the adjacent Paleo-drainage systems (Fig. 2,

Table S1). This finding suggested different scenario as proposed in previous study¹² because: (1) Voris¹⁹ did not mentioned any ancient watershed that ran towards Indian Ocean (from the western slope of Bukit Barisan Mountain range) in his definition of the Pleistocene drainage systems. In this study we categorized any watershed from the western slope as its own drainage basin. (2) de Bruyn et al.¹² only sampled few localities on Sumatra for their study. This localities located in the eastern slope of Bukit Barisan Mountain range, and fell under Voris¹⁹ Paleo-drainage systems.

Unlike the freshwater fishes and the Mud snakes that fully dependent on water for its dispersal, frogs with gastromyzophorous tadpoles presumably has two dispersal pathways: during their larval form (via rivers) and during adult stage (via terrestrial). Davis et al.²³ proposed that distance or potential barriers to gene flow might shape the genetic variation of particular taxa. We considered the configuration of the Barisan Mountain range (e.g., contour and topology) may influence dispersal route of this group of frogs, assuming west↔east migration need shorter distance compare to north↔south migration route (see Nielson et al.⁵⁷ for similar case). Integrating more methodology, such as landscape ecology, population genetic, and spatial statistics²³, in order to define and quantify dispersal pathways of this group of frogs shall be considered for future studies.

Nonetheless, the frogs examined herein seems largely structured geographically into northern and southern lineages within Sumatra (Fig. 2). The border between the northern and southern group is located in the Sumatera Barat province. The precise location of the border is still vague as some of the samples from the hypothesized border (Sumatera Barat province, comprises part of the Sumatra-North and Sumatra-Central in Fig. 3) were found grouped either in the northern or in the southern lineages. Similar north-south genetic partitioning has also been reported for three species of Sumatran tree frogs of the genus *Rhacophorus* (*R. catamitus*, *R. modestus*, *R. poecilnotus*^{13,58}: northern (Aceh to Sumatera Barat provinces, approximately the region north of Mount Kerinci) and southern (West Sumatra to Lampung provinces, approximately all region below Mount Kerinci).

O'Connell et al.⁵⁸ hypothesized that the divergence between the northern and southern populations was presumably reinforced by the paleoclimate during the Miocene to Pleistocene period. Moreover, the northern populations of the Sumatran *Rhacophorus* were suggested to have occupied the northern region of Sumatra beginning in the Miocene⁵⁸ when suitable habitats were abundant in the region⁷. Yet, this northern route hypothesis might be applied for *Sumaterana*, but not for *Huia*. According to dated

phylogeny and ancestral area reconstruction (Fig. 3), the most recent common ancestor (MRCA) of *Sumaterana* reached Sumatra from mainland Asia (presumably Peninsular Malaysia→Sumatra) at 25.11 Ma (the Late Oligocene). However, the MRCA of the Sumatran *Huia* might have migrated to this island from the mainland Asia with longer route, presumably: (1) mainland Asia→Borneo→Sumatra and/ or (2) mainland Asia→Borneo→Java→Sumatra at approx. 27.65 Ma and 16.42 Ma, respectively (Fig. 3). Both *Huia* and *Sumaterana* have experienced rapid divergence from the Late Miocene or the Early Pliocene onwards (Fig. 3). We considered the Paleo-climatic and geological events during this period^{8,14,16} may have influenced the early divergence within these frogs species.

Several mammals' species have been recorded to exhibit north-south separation on the island of Sumatra, such as Thomas's langur - *Presbytis thomasi* and white-handed gibbon - *Hylobates lar* in the north; and Horsfield's tarsier - *Tarsius bancanus* and Tapir – *Tapirus indicus* in the south⁵⁹. However, Whitten⁵⁹ demonstrated that Toba region is the zoogeographic boundary for this partition and was corroborated by the Sumatran Orangutans⁶⁰. Toba super volcanic eruption^{61,62} might influenced the population structure of these species⁶⁰ and facilitated the recolonization of the species on Sumatra⁶³. More taxa with comprehensive sampling locations should be investigated in order to address genetic segregation within the Sumatran species and understand its geographical history that drives this process.

Diversification of *Sumaterana* and *Huia* on Sumatra. Hall^{14,16} suggested that by the Mid-Late Oligocene major parts of Sundaland were terrestrial, with some freshwater lakes. During this period, northern part of Sumatra has more seasonal climate⁸ and the volcanoes were not existed^{14,16} compared to the southern part of the island (wet climate and several volcanoes were observed). As a consequence, habitat types in the northern and southern parts of Sumatra were different. Our analyses for ancestral area reconstruction suggested that the most recent common ancestor (MRCA) of *Sumaterana* frogs seemingly have only occupied cascading habitats on the Sumatra-North (Fig. 3) when it first migrated at approx. 25.11 Ma. On the other hand, at approx. 27.65 Ma some of the MRCA of *Huia* were migrating from the mainland Asia via Borneo to Sumatra (from the southern part of the island), whereas some others migrated to Java. Between 20–15 Ma, the volcanoes have shifted northwest up to the northern part of Sumatra due to strike-slip faulting, and as response to region-wide Sundaland deformation after Australia's collision with eastern Indonesia^{14,16}. The increase of regional marine transgression led to increased sea levels and therefore, Sumatra gradually submerged^{14,64} resulting in wet climate across the whole island⁸. As a consequence, the

MRCA of *S. montana* and *S. crassiovis* formed local refugia in a top volcanoes of the northern region, and became isolated. On the other hand, the tectonic activity shifted the position of the most western volcano on Java to join the southernmost tip of Sumatra^{14,16}, along with the MRCA of the Javan *Huia* that later gave rise to *H. sumatrana* 3 after long period of isolation due to sea barrier. Within the same time period, the first MRCA of Sumatran *Huia* (Clade I–K, Fig. 2) migrated towards the central region of the island, forming a founding population that was then isolated from the remaining population in the south by sea.

From 10 Ma, sea level gradually decreased, thus resuming gene flow between previously isolated volcanoes. Now, the MRCA of *S. crassiovis* frogs could migrate further south and the MRCA of *Huia* could move northwards occupying all available niches on the island. By 5 Ma (the beginning of Pliocene) onwards, Sumatra gained land cover, and the northern and southern region saw further change in topology, with a rise in the number of volcanoes in the south leading the increase of highland habitat in the southern Sumatra^{14,16}. This mountain building activities became more frequent during the Pleistocene and in many areas also continued into the Holocene⁶⁵. Seasonal climate also suggested during this period⁸. Pyron and Wiens⁶⁶ suggested that mountain regions provide wide variety of life supporting environments that continuously available through climatic alteration. We hypothesized that different environment in the northern and southern parts of Sumatra during Pliocene onwards, has initiated the segregation of the Sumatran fauna (e.g., *Sumaterana* and *Huia*) into the northern and southern groups (see Fig. 2–3). Thus from Pliocene and on, the divergence of both genera became more frequent, compared to the previous period (Fig. 3).

Methods

Taxon sampling and molecular data. We sampled a total of 146 ranid frogs belonging to the genera *Sumaterana* (N = 85) and *Huia* (N = 61) collected along cascading habitats in the island of Sumatra and Java between 2008 2013 and 2016. Samples were obtained from 55 sampling points for *Sumaterana* and 48 sampling points for *Huia* (N=1–4 samples per site) along the Sumatran and Javan transect (Fig. 4, Table S1). Sampling sites represent four Sundaland Paleo-drainage systems east of the Barisan Mountain range (sensu Voris 2000) and also watershed systems that run westward towards the Indian Ocean. Sampling was performed following all general legal guidelines of Germany (Tierschutzgesetz, <https://www.gesetze-im-internet.de/tierschg/BJNR012770972.html>) for handling and euthanizing specimens. Adult frogs were collected by hand and tadpoles were captured using fishnet. Muscle or liver tissues were preserved in either ethanol

(96%), RNA later (Sigma Aldrich, USA) or Lysis buffer (0.5 M Tris / 0.25% EDTA / 2.5% SDS, pH 8.2) for DNA analyses. Specimens were fixed in 4% neutral-buffered formalin and then transferred to 70% ethanol for long term storage. Additionally, we included samples (N=13) from other ranids with gastromyzohorous larvae from Borneo, and mainland Asia: *Amolops afghanus*, n=1; *A. marmoratus*, n=1; *A. indoburmanensis*, n=1; *A. panhai*, n=1; *H. cavitympanum*, n=2; *H. melasma*, n=2; *Meristogenys amoropalamus*, n=1; *M. kinabaluensis*, n=1; *M. orphocnemis*, n=1; *M. poecilus*, n=1; *M. sp.*, n=1; and other closely related ranids (N=8): *Chalcorana chalconota*, n=1; *Clinotarsus penelope*, n=1; *Cli. alticola*, n=1; *Hyl. erythraea*, n=1; *Odorrana hosii*, n=2; *Pulchrana picturata*, n=1; *Staurois guttatus*, n=1); as sister ingroup and outgroup. *Staurois guttatus* was used to root the tree⁵⁴. All specimens are deposited in one of the following museums: Natural History Museum (BMNH), London, United Kingdom; Museum Zoologicum Bogoriense (MZB), Bogor, Indonesia; Zoologisches Museum Hamburg (ZMH), Hamburg, Germany; Museum of the University of Texas Arlington (UTA), Arlington, USA; Museum of Vertebrate Zoology (MVZ), Berkeley, USA; and Field Museum of Natural History (FMNH), Chicago, Illinois USA. Detailed information of the specimens used in this study is available in Table S1.

DNA extraction, PCR, and sequencing followed the protocols³⁸. Sequences of ten loci were generated: five mtDNA (12S, 16S+ tRNA^{val}, COI, Cyt-b, ND2) and five nucDNA (Brain-derived neurotrophic factor, BDNF; Neurotrophin 3, NTF3; Proopiomelanocortin, POMC; recombination-activating gene 1, RAG1; tyrosinase exon 1, TYR). Primer information and PCR annealing temperatures applied for this study are provided in Table S3.

Phylogenetic analysis. The total dataset of the ten concatenated genes consisted of 7582 bps. In order to create a dataset with a minimum amount of missing data, we only used individuals for which at least three loci (or 1,942 bps total length) were successfully sequenced. Our final dataset comprised 146 sequences for *Sumaterana* (N=85) and *Huia* (N=65), and an additional 21 sequences for closely related taxa. We tested a variety of models and partitioning strategies to find the best partitioning scheme and substitution models for the concatenated dataset using Partition Finder v.1.1⁶⁷ and the Bayesian Information Criterion (BIC), which resulted 11 partitions (Table S4).

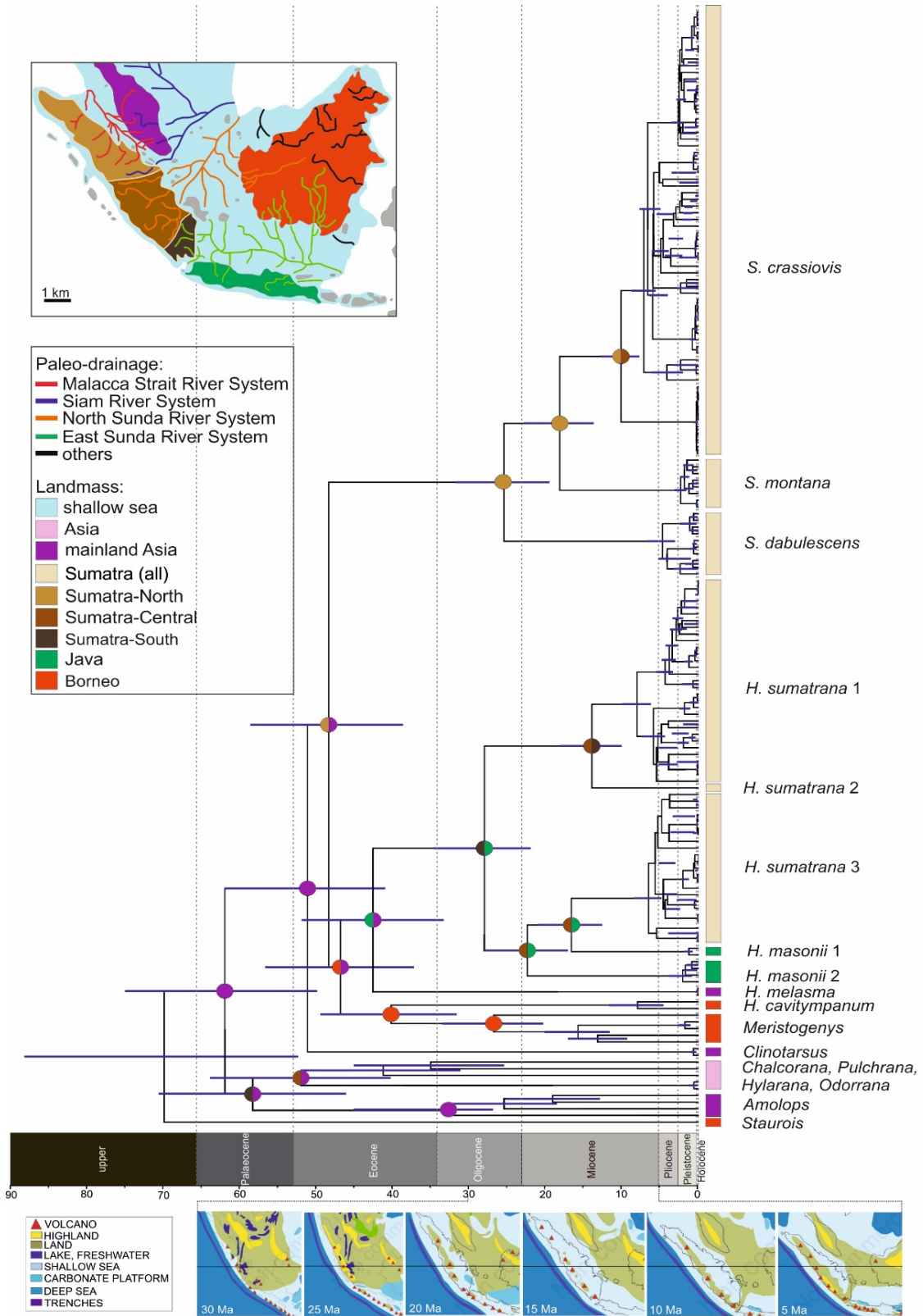


Figure 3 Time divergence estimation of *Huia* and *Sumaterana* on Sumatra and Java. Color and label in the bottom left box is legend for the Cenozoic map of Sundaland (Hall 2013). Color and label in the upper left is legend for the Sundaland map with its respective Pleistocene river systems (redraw from Voris 2000), and indicated the areas of each clade (square) as well as the divergence route of each node (circles).

We used different reconstruction methods to generate phylogenetic trees: Maximum Likelihood (ML) with RAXML v. 8.2.10 (Stamatakis 2014) and Bayesian Inference (BI) with Mr. Bayes v 3.2.6^{68,69} using the CIPRES Science Gateway V 3.3⁷⁰. In RaXML, 11 distinct partitions and associated models were defined and we performed joint branch length optimization. Tree support was obtained using 1000 bootstrap replicates. The final alignment comprises 28.91% of which was proportion of gaps and completely undetermined characters with 3303 distinct alignment patterns and the final Likelihood was -76212.593824.

For Bayesian analysis we performed two independent runs with one cold and three heated chains for 50 million Markov Chain Monte Carlo (MCMC) iterations sampling every 1000 generations. Convergence of runs was assessed using the trace plot of Mr. Bayes, the average split frequencies being < 0.01 and by assessing ESS values (>200) of the log files with Tracer v.1.6⁷¹ after discarding the first 25% of samples as burn in. Fig Tree v.1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>) was used to visualize the 50% majority consensus trees from RaXML and Mr. Bayes. Strong support^{72,73} was defined by nodal support with Bootstrap values (BS) ≥ 70 for the ML tree⁷⁴ and posterior probability value (PP) ≥ 0.95 for Bayesian analyses^{66,75}.

Mapping frogs' distribution pattern. The BI tree was transformed and edited in MESQUITE v3.6⁷⁶ into color coded tree to map the distribution patterns of the Sumatran ranid frogs with gastromyzophorous tadpoles. We followed Voris¹⁹ definition of the four Paleo-drainage systems in Sundaland. Voris did not specify any watersheds that ran into the Indian Ocean (western slope of Bukit Barisan mountain range) in his Paleo-drainage definition. Our samples were collected from both the western and eastern slopes of Bukit Barisan mountain range. Thus, in this study we categorized all watersheds on the western slopes of the mountains as its own drainage system.

Divergence time estimation. We estimated divergence times between lineages of Sumatran ranids with gastromyzophorous tadpoles using BEAST v.2.4.8⁷⁷. We performed analyses with the complete dataset and the partitioning scheme as described above. The molecular clock was calibrated using two evolutionary rates (CYTB and 16S) from published studies of other frogs⁷⁸. However, we set the prior distribution to uniform rather than normal (compare to Tominaga et al.⁷⁸) because the analyses failed to reach convergence under a normal distribution. First, we performed a series of test runs in order to find the optimal settings fitting our data. We varied the clock model, tree prior, and Gamma category and performed runs while retaining the remaining parameters. Each preliminary run was performed for 100 million iterations sampling every 10,000

generations. We then compared the log files and chose the parameter set with the highest likelihood for our final analysis. The best parameter set was as follows: uncorrelated log-normal relaxed clock model, Yule tree prior, and HKY for the substitution model with number of Gamma category set to four. We performed the final analysis in two independent runs of Markov chain for 500 million generations, sampling every 10,000 generations. We used Tracer v.1.6⁷¹ to evaluate stationarity of the Markov chain and potential autocorrelation (effective sample sizes >200). The first 25% of samples were discarded as burn in, and the samples of both runs were combined with LogCombiner v.1.6.1.⁷¹, which identified and annotated the maximum clade credibility tree.

Ancestral Area Reconstruction. We performed statistical analysis for dispersal and vicariance events of the taxa interest using S-DIVA⁷⁹ package on RASP 3.2⁸⁰. We used our calibrated tree from BEAST in this analysis. We labeled each sample with their respective geographical distributions: A (Sumatra-North, comprises all samples from the Malacca Strait and Siam river systems including one from their neighboring watershed in the western slopes of Bukit Barisan), B (Sumatra-Central, comprises all samples from the North Sunda river system including one from their neighboring watershed in the western slopes of Bukit Barisan), C (Sumatra-South, comprises all samples from the East Sunda river system including one from their neighboring watershed in the western slopes of Bukit Barisan), D (Java), E (Borneo), F (Asia). We set two maximum areas at each node leaving other setting to default values.

References

1. Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* 403, 853 (2000).
2. Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M., & Gascon, C. Global biodiversity conservation: the critical role of hotspots. In *Biodiversity hotspots* (pp. 3-22). Springer, Berlin, Heidelberg (2011).
3. De Bruyn, M. *et al.* Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity. *Syst. Biol.* 63, 879–901 (2014).
4. Inger, R. F. Distribution of amphibians in southern Asia and adjacent islands. *Patterns of distribution of amphibians: a global perspective*, 445–482 (1999).
5. Inger, R. F., & Voris, H. K. The biogeographical relations of the frogs and snakes of Sundaland. *J. Biogeogr.* 28, 863–891 (2001).
6. Morley, R. J. *Origin and evolution of tropical rain forests*. John Wiley & Sons (2000).

7. Lohman, D. J. *et al.* Biogeography of the Indo-Australian archipelago. *Ann. Rev. Ecol. Evol. Syst.* 42 (2011).
8. Morley, R. J. A review of the Cenozoic palaeoclimate history of Southeast Asia. *Biotic evolution and environmental change in Southeast Asia* 79–114 (2012).
9. Esselstyn, J. A., Timm, R. M., & Brown, R. M. Do geological or climatic processes drive speciation in dynamic archipelagos? The tempo and mode of diversification in Southeast Asian shrews. *Evolution: Int. J. Org. Evol.* 63, 2595–2610 (2009).
10. Arifin, U., Iskandar, D. T., Bickford, D. P., Brown, R. M., Meier, R., & Kutty, S. N. Phylogenetic relationships within the genus *Staurois* (Anura, Ranidae) based on 16S rRNA sequences. *Zootaxa* 2744, 39–52 (2011).
11. Brown, R. M. *et al.* Evolutionary processes of diversification in a model island archipelago. *Ann. Rev. Eco. Evol. Syst.* 44, 411–435 (2013).
12. De Bruyn, M. *et al.* Paleo-drainage basin connectivity predicts evolutionary relationships across three Southeast Asian biodiversity hotspots. *Syst. Biol.* 62(3), 398–410 (2013).
13. O'Connell, K. A., Smart, U., Smith, E. N., Hamidy, A., Kurniawan, N., & Fujita, M. K. Within-island diversification underlies parachuting frog (*Rhacophorus*) species accumulation on the Sunda Shelf. *J. Biogeogr* 45, 929–940 (2018).
14. Hall, R. The palaeogeography of Sundaland and Wallacea since the Late Jurassic. *J. Limnol.* 72, 1 (2013).
15. Morley, R. J., & Morley, H. P. Mid Cenozoic freshwater wetlands of the Sunda region. *J. Limnol* 72, 2 (2013).
16. Hall, R. Sundaland and Wallacea: geology, plate tectonics and palaeogeography. *Biotic evolution and environmental change in Southeast Asia*, 32–78 (2012).
17. Crow, M.J. Chapter 8: Tertiary volcanicity. In *Sumatra: Geology, Resources and Tectonic Evolution*, ed. A.J. Barber, M.J. Crow and J.S. Milsom. *Geol. Soc. Lond. Mem.* 31, 98–119 (2005).
18. Leonard, J. A., den Tex, R. J., Hawkins, M. T., Muñoz-Fuentes, V., Thorington, R., & Maldonado, J. E. Phylogeography of vertebrates on the Sunda Shelf: a multi-species comparison. *J. Biogeogr.* 42, 871–879 (2015).
19. Voris, H. K. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *J. Biogeogr.* 27, 1153–1167 (2000).
20. Sathiamurthy, E., & Voris, H. K. Maps of Holocene sea level transgression and submerged lakes on the Sunda Shelf. *Trop Nat Hist.* (2), 1–44 (2006).
21. Parenti, L. R. Ocean basins and the biogeography of freshwater fishes. *Aust Syst. Bot.* 4, 137–149 (1991).

22. Zakaria-Ismail, M. Zoogeography and biodiversity of the freshwater fishes of Southeast Asia. In Ecology and conservation of Southeast Asian marine and freshwater environments including wetlands (pp. 41–48). Springer, Dordrecht (1994).
23. Davis, C. D., Epps, C. W., Flitcroft, R. L., & Banks, M. A. Refining and defining riverscape genetics: How rivers influence population genetic structure. *Wiley Interdisciplinary Reviews: Water* 5, e1269 (2018).
24. Lukoschek, V., Osterhage, J. L., Karns, D. R., Murphy, J. C., & Voris, H. K. Phylogeography of the Mekong mud snake (*Enhydryis subtaeniata*): the biogeographic importance of dynamic river drainages and fluctuating sea levels for semiaquatic taxa in Indochina. *Eco Evol* 1, 330–342 (2011).
25. Gascon, C., Loughheed, S. C., & Bogart, J. P. Patterns of Genetic Population Differentiation in Four Species of Amazonian Frogs: A Test of the Riverine Barrier Hypothesis 1. *Biotropica* 30, 104–119 (1998).
26. Gascon, C. *et al.* Riverine barriers and the geographic distribution of Amazonian species. *Proc. Natl. Acad. Sci.* 97, 13672–13677 (2000).
27. Patton, J. L., Da Silva, M. N. F., & Malcolm, J. R. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. *Bull. Ame. Mus. Nat. Hist.* 1–306 (2000).
28. Hayes, F. E., & Sewlal, J. A. N. The Amazon River as a dispersal barrier to passerine birds: effects of river width, habitat and taxonomy. *J. Biogeogr.* 31, 1809–1818 (2004).
29. Goodman, S. M., & Ganzhorn, J. U. Biogeography of lemurs in the humid forests of Madagascar: the role of elevational distribution and rivers. *J. Biogeogr.* 31, 47–55 (2004).
30. Gehring, P. S., Pabijan, M., Randrianirina, J. E., Glaw, F., & Vences, M. The influence of riverine barriers on phylogeographic patterns of Malagasy reed frogs (*Heterixalus*). *Mol. Phylogenet. Evol.* 64, 618–632 (2012).
31. Husemann, M., Ray, J. W., King, R. S., Hooser, E. A., & Danley, P. D. Comparative biogeography reveals differences in population genetic structure of five species of stream fishes. *Biol. J. Linn. Soc.* 107, 867–885 (2012).
32. Pepper, M. *et al.* Speciation in the mountains and dispersal by rivers: Molecular phylogeny of *Eulamprus* water skinks and the biogeography of Eastern Australia. *J. Biogeogr.* 45, 2040–2052 (2018).
33. Li, R., Chen, W., Tu, L., & Fu, J. Rivers as barriers for high elevation amphibians: a phylogeographic analysis of the alpine stream frog of the Hengduan Mountains. *J. Zool.* 277, 309–316 (2009).

34. Zhao, S., Dai, Q., & Fu, J. Do rivers function as genetic barriers for the plateau wood frog at high elevations?. *J. Zool* 279(3), 270–276 (2009).
35. Fouquet, A., Ledoux, J. B., Dubut, V., Noonan, B. P., & Scotti, I. The interplay of dispersal limitation, rivers, and historical events shapes the genetic structure of an Amazonian frog. *Biol. J. Linn. Soc.* 106, 356–373 (2012).
36. Inger, R. F. The systematics and zoogeography of the Amphibia of Borneo. *Field. Zoo.* 52, 1–402 (1966).
37. Altig, R., & Johnston, G. F. Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetol. Monogr.* 81–109 (1989).
38. Arifin, U., Smart, U., Hertwig, S. T., Smith, E. N., Iskandar, D. T., & Haas, A. Molecular phylogenetic analysis of a taxonomically unstable ranid from Sumatra, Indonesia, reveals a new genus with gastromyzophorous tadpoles and two new species. *Zoosyst. Evol.* 94, 163–199 (2018).
39. Gan, L. L., Hertwig, S. T., Das, I., & Haas, A. The anatomy and structural connectivity of the abdominal sucker in the tadpoles of *Hyla cavitympanum*, with comparisons to *Merristogenys jerboa* (Lissamphibia: Anura: Ranidae). *J. Zool. Syst. Evol. Res.* 54, 46–59 (2016).
40. Fouquet, A., Gilles, A., Vences, M., Marty, C., Blanc, M., & Gemmell, N. J. Underestimation of species richness in Neotropical frogs revealed by mtDNA analyses. *PLoS one*, 2(10), e1109 (2007).
41. Iskandar, D. T., & Colijn, E. (2000). Preliminary Checklist of Southeast Asian and New Guinean Herpetofauna: Amphibians. I. Research and Development Centre for Biology, Indonesian Institute of Sciences.
42. Inger, R. F., Stuart, B. L., & Iskandar, D. T. Systematics of a widespread Southeast Asian frog, *Rana chalconota* (Amphibia: Anura: Ranidae). *Zool. J. Linn. Soc.* 155, 123–147 (2009).
43. Teynie, A., David, P., & Ohler, A. Note on a collection of amphibians and reptiles from Western Sumatra (Indonesia), with the description of a new species of the genus *Bufo*. *Zootaxa*, 2416(1), 1–43 (2010).
44. Matsui, M., Mumpuni, Hamidy, A. Description of a new species of *Hylarana* from Sumatra (Amphibia, Anura). *Curr. Herpetol.* 31, 38–46 (2012).
45. Hamidy, A., & Kurniati, H. A new species of tree frog genus *Rhacophorus* from Sumatra, Indonesia (Amphibia, Anura). *Zootaxa*, 3947(1), 049-066 (2015).
46. Smart, U. *et al.* N. A new genus and two new species of arboreal toads from the highlands of Sumatra with a phylogeny of Sundaland toad genera. *Herpetologica* 73, 63–75 (2017).

47. Arifin, U., Cahyadi, G., Smart, U., Jankowski, A., & Haas, A. A new species of the genus *Pulchrana* Dubois, 1992 (Amphibia: Ranidae) from Sumatra, Indonesia. *Raff. Bull. Zool.* 66, 277–299 (2018).
48. Padial, J. M., Miralles, A., De la Riva, I., & Vences, M. The integrative future of taxonomy. *Front. Zool.* 7, 16 (2010).
49. Verdú, M., & Pausas, J. G. Syndrome-driven diversification in a Mediterranean ecosystem. *Evol.* 67, 1756–1766 (2013).
50. Morlon, H. Phylogenetic approaches for studying diversification. *Ecol. Lett.* 17, 508–525 (2014).
51. Cowling, R. M., & Pressey, R. L. Rapid plant diversification: planning for an evolutionary future. *Proc. Nat. Acad. Sci.* 98, 5452–5457 (2001).
52. Joppa, L. N., & Pfaff, A. Global protected area impacts. *Proc. R. Soc. Lond. [Bio.]* 278, 1633–1638 (2011).
53. Stuart, B. L. The phylogenetic problem of *Huia* (Amphibia: Ranidae). *Mol. Phylogenet. Evol.* 46, 49–60 (2008).
54. Pyron, R. A., & Wiens, J. J. A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Mol. Phylogenet. Evol.* 61, 543–583 (2011).
55. Iskandar, D. T., & Erdelen, W. R. Conservation of amphibians and reptiles in Indonesia: issues and problems. *Amph. Rept. Cons.* 4, 60–87 (2006).
56. Stuart, B. L., Inger, R. F., & Voris, H. K. High level of cryptic species diversity revealed by sympatric lineages of Southeast Asian forest frogs. *Biology letters*, 2(3), 470–474 (2006).
57. Nielson, M., Lohman, K., & Sullivan, J. (2001). Phylogeography of the tailed frog (*Ascaphus truei*): implications for the biogeography of the Pacific Northwest. *Evolution*, 55(1), 147–160.
58. O'Connell, K. A., Hamidy, A., Kurniawan, N., Smith, E. N., & Fujita, M. K. Synchronous diversification of parachuting frogs (Genus *Rhacophorus*) on Sumatra and Java. *Mol. Phylogenet. Evol.* 123, 101–112 (2018).
59. Whitten, T. (2000). *The Ecology of Sumatra*, vol. 1. Periplus Edition, Jakarta, Indonesia.
60. Nater, A. *et al.* (2011). Sex-biased dispersal and volcanic activities shaped phylogeographic patterns of extant orangutans (genus: *Pongo*). *Mol. Biol. Evol.* 28, 2275–2288.
61. Rose, W. I., & Chesner, C. A. Dispersal of ash in the great Toba eruption, 75 ka. *Geology*, 15, 913–917 (1987).

62. Rampino, M. R., & Self, S. Volcanic winter and accelerated glaciation following the Toba super-eruption. *Nature*, 359(6390), 50 (1992).
63. Wilting, A., Sollmann, R., Meijaard, E., Helgen, K. M., & Fickel, J. (2012). Mentawai's endemic, relictual fauna: is it evidence for Pleistocene extinctions on Sumatra?. *J. Biogeogr.* 39, 1608–1620.
64. Barber, A. J., Crow, M. J., & Milsom, J. (Eds.). *Sumatra: geology, resources and tectonic evolution*. J. Geol. Soc. London (2005).
65. Katili, J. A. *Sumatra*. J. Geol. Soc. London Special Publ. 4, 317–331 (1974).
66. Pyron, R. A., & Wiens, J. J. Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. *Proc. R. Soc. Lond. [Bio.]* 280, 16–22 (2013).
67. Lanfear, R., Calcott, B., Ho, S. Y., & Guindon, S. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Mol. Biol. Evol.* 29, 1695–1701 (2012).
68. Huelsenbeck, J. P., & Ronquist, F. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17, 754–755 (2001).
69. Ronquist, F., & Huelsenbeck, J. P. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19, 1572–1574 (2003).
70. Miller, M. A., Pfeiffer, W., & Schwartz, T. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In *Gateway Computing Environments Workshop (GCE)*, 1–8 (2010).
71. Rambaut, A., & Drummond, A. J. *Tracer: MCMC trace analysis tool, version 1.5*. University of Oxford: Oxford (2009).
72. Huelsenbeck, J. P., & Rannala, B. Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Syst. Biol.* 53, 904–913 (2004).
73. Mulcahy, D. G., Beckstead, T. H., Sites, & Jr, J. W. Molecular systematics of the Leptodeirini (Colubroidea: Dipsadidae) revisited: Species-tree analyses and multi-locus data. *Copeia* 2011: 407–417 (2011).
74. Hillis, D. M., & Bull, J. J. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Syst. Biol.* 42, 182–192 (1993).
75. Leaché, A. D., & Reeder, T. W. Molecular systematics of the eastern fence lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood, and Bayesian approaches. *Syst. Biol.* 51, 44–68 (2002).
76. Maddison, W. P. & Maddison, D.R. *Mesquite: a modular system for evolutionary analysis*. Version 3.6 <http://www.mesquiteproject.org>. (2018).
77. Bouckaert, R. *et al.* BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. *PLoS Comp. Biol.* 10, e1003537 (2014).

78. Tominaga, A., Matsui, M., Eto, K., & Ota, H. Phylogeny and differentiation of wide-ranging Ryukyu Kajika Frog *Buergeria japonica* (Amphibia: Rhacophoridae): geographic genetic pattern not simply explained by vicariance through strait formation. *Zool. Sci.* 32, 240–247 (2015).
79. Yu Y, Harris AJ, He X. S-DIVA (Statistical Dispersal-Vicariance Analysis): A tool for inferring biogeographic histories. *Mol. Phylogenet. Evol.* 56, 848–50 (2010).
80. Yu Y, Harris AJ, Blair C, He X. RASP (Reconstruct Ancestral State in Phylogenies): A tool for historical biogeography. *Mol. Phylogenet. Evol.* 87, 46–49 (2015).

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Author Contributions

UA conceived the ideas based on discussion with DTI, AH, US, and MH; UA designed sampling; UA, US, and ENS conducted fieldwork and collected the data with additional material from collaborators; UA analyzed and interpreted the data with assistant from AH, MH and US; and UA led the writing with support from all authors.

Additional Information

Supplementary information: Table S1–S4, Fig. S1–S2

Competing Interest. The authors declare that they have no competing interest.

Table S1 List of specimens used in this study, including information concerning Paleo-drainage systems for each samples collected from Sumatra.

	Taxa	Museum no.	Locality	GPS coordinates and elevation (m asl)	Run towards	Watershed (Voris ¹⁹)
1	<i>Amolops afghanus</i>	CAS 221313	Myanmar, Kachin state, Putao Dis.t, Machanbaw Township, Ahtonga Village	27.2616111 097.8019167		
2	<i>Amolops indoburmanensis</i>	CAS 234720	Myanmar, Chin State, Saw Stream, Kanpetlet Township, Mindat Div.	21.1727500 094.0238056; 836		
3	<i>Amolops marmoratus</i>	CAS 221675	Myanmar, Shan State, Kalaw Township, Wat Phu Ye Camp	20.7107500 096.4868056		
4	<i>Amolops panhai</i>	CAS 229816	Myanmar, Taniintharyi Div., Da Wei Dist., Thayet Chaung Township, East of mal Ke Village	13.8416667 098.4547222; 70		
5	<i>Chalcorana chalconota</i>	MZB.Amph.30399	Indonesia, Jawa Barat, Kabupaten Banyumas, Curug Cipendok			
6	<i>Clinotarsus alticola</i>	FMNH 263424	Thailand, Prachuap Kirikhan, Hua Hin			
7	<i>Clinotarsus penelope</i>	FMNH 268338	Thailand, Ranong Prov			
8	<i>Hylarana erythraea</i>	MZB.Amph.29423	Indonesia, Aceh, Taman Nasional Gunung Leuser, Jambur Gele			
9	<i>Huia cavitympanum</i>	NHMBE 1061482	Malaysia, Borneo, Sarawak, Gunung Murud, Sungai Bur, Pa Rabata			
10	<i>Huia cavitympanum</i>	RMBR 2283	Indonesia, Borneo, Taman Nasional Bukit Baka Bukit Raya			
11	<i>Huia sumatrana</i>	UA20140009*	Indonesia, Aceh, Taman Nasional Gunung Leuser	03.87935 097.44811; 900	Indian Ocean	NA
12	<i>Huia sumatrana</i>	UA20140018	Indonesia, Aceh, Taman Nasional Gunung Leuser	03.84398 097.51634; 750	Indian Ocean	NA
13	<i>Huia sumatrana</i>	UA20140022	Indonesia, Aceh, Taman Nasional Gunung Leuser	03.84260 097.52081; 750	Indian Ocean	NA
14	<i>Huia sumatrana</i>	UA20140116*	Indonesia, Aceh, Taman Nasional Gunung Leuser	03.68617 097.65408; 405	Indian Ocean	NA
15	<i>Huia sumatrana</i>	UA20140120*	Indonesia, Aceh, Taman Nasional Gunung Leuser	03.68617 097.65408; 405	Indian Ocean	NA
16	<i>Huia sumatrana</i>	UA20140157*	Indonesia, Aceh, Taman Nasional Gunung Leuser	03.67675 097.65292; 440	Indian Ocean	NA
17	<i>Huia sumatrana</i>	UA20140158*	Indonesia, Aceh, Taman Nasional Gunung Leuser	03.67675 097.65292; 440	Indian Ocean	NA
18	<i>Huia sumatrana</i>	UA20140188*	Indonesia, Aceh, Taman Buru Linge-Isaq	04.36482 097.24957; 440	Malacca Strait	Malacca Strait
19	<i>Huia sumatrana</i>	UA20140205*	Indonesia, Aceh, Taman Buru Linge-Isaq	04.36139 097.24635; 440	Malacca Strait	Malacca Strait

20	<i>Huia sumatrana</i>	UA20140229*	Indonesia, Aceh, Taman Buru Linge-Isaq	04.36018 097.24580; 440	Malacca Strait	Malacca Strait
21	<i>Huia sumatrana</i>	UA20140422*	Indonesia, Aceh, Kabupaten Ulu Masen, Mane	04.90269 096.12771; 700	Indian Ocean	NA
22	<i>Huia sumatrana</i>	UA20140431*	Indonesia, Aceh, Kabupaten Ulu Masen, Mane	04.89949 096.13168; 700	Indian Ocean	NA
23	<i>Huia sumatrana</i>	UA20140981*	Indonesia, Bengkulu, Taman Nasional Kerinci-Seblat	-02.90975 102.11492; 1322	Indian Ocean	NA
24	<i>Huia sumatrana</i>	UA20141019*	Indonesia, Bengkulu, Taman Nasional Kerinci-Seblat	-02.93627 102.10777; 689	Indian Ocean	NA
25	<i>Huia sumatrana</i>	UA20141095*	Indonesia, Bengkulu, Taman Nasional Kerinci-Seblat	-02.95330 102.13956; 726	Indian Ocean	NA
26	<i>Huia sumatrana</i>	UA20141081*	Indonesia, Bengkulu, Taman Nasional Kerinci-Seblat	-02.95250 102.14108; 723	Indian Ocean	NA
27	<i>Huia sumatrana</i>	UA20141061*	Indonesia, Bengkulu, Taman Nasional Kerinci-Seblat	-02.95100 102.16345; 758	Indian Ocean	NA
28	<i>Huia sumatrana</i>	UA20141069*	Indonesia, Bengkulu, Taman Nasional Kerinci-Seblat	-02.95117 102.16345; 761	Indian Ocean	NA
29	<i>Huia sumatrana</i>	UA20141109*	Indonesia, Bengkulu, Taman Nasional Kerinci-Seblat	-02.95117 102.16345; 761	Indian Ocean	NA
30	<i>Huia sumatrana</i>	MVZ271197	Indonesia, Bengkulu, Kabupaten Bengkulu Utara, Kecamatan Agra Makmur, Desa Kemumu	-03.42537 102.26192; 390	Indian Ocean	NA
31	<i>Huia sumatrana</i>	MVZ271198	Indonesia, Bengkulu, Kabupaten Bengkulu Utara, Kecamatan Agra Makmur, Desa Kemumu	-03.42537 102.26192; 390	Indian Ocean	NA
32	<i>Huia sumatrana</i>	MVZ271199	Indonesia, Bengkulu, Kabupaten Bengkulu Utara, Kecamatan Agra Makmur, Desa Kemumu	-03.42537 102.26192; 390	Indian Ocean	NA
33	<i>Huia sumatrana</i>	RMBR112	Indonesia, Bengkulu, Kecamatan Lebong Utara, Desa Air Putih	-03.03712 102.19100	Indian Ocean	NA
34	<i>Huia sumatrana</i>	RMBR113	Indonesia, Bengkulu, Kecamatan Lebong Utara, Desa Air Putih	-03.03712 102.19100	Indian Ocean	NA
35	<i>Huia sumatrana</i>	UA20140828*	Indonesia, Jambi, Taman Nasional Kerinci-Seblat	-02.25833 101.28657; 909	Indian Ocean	NA
36	<i>Huia sumatrana</i>	MZB 22349	Indonesia, Lampung, Kabupaten Tanggamus, Kecamatan Ulubelu, Desa Ngarip	-05.31529 104.54275; 843	Indian Ocean	South Sunda
37	<i>Huia sumatrana</i>	UTA-A 62547	Indonesia, Lampung, Kabupaten Lampung Barat, Way Sindalapai	-05.04678 104.06989; 786	Indian Ocean	NA
38	<i>Huia sumatrana</i>	UTA-A 62548	Indonesia, Lampung, Kabupaten Lampung Barat, Way Sindalapai	-05.04678 104.06989; 786	Indian Ocean	NA
39	<i>Huia sumatrana</i>	UA20150116*	Indonesia, Lampung, Kabupaten Lampung Barat, Gedong Surian, Sungai Pauh	-05.06651 104.46261; 935	South China Sea	East Sunda
40	<i>Huia sumatrana</i>	UA20150202*	Indonesia, Lampung, Kabupaten Pasawaran, Air Terjun Wiyono	-05.42008 104.14370; 632	Indian Ocean	NA

41	<i>Huia sumatrana</i>	UA20150195*	Indonesia, Lampung, Kabupaten Tanggamus, Air Terjun Talang Ogan	-05.37933 104.66043; 717	Indian Ocean	East Sunda
42	<i>Huia sumatrana</i>	ENS17018*	Indonesia, Sumatera Utara, Kabupaten Langkat, outskirts Bukit Lawang	03.53671 098.12759; 192	Malacca Strait	Malacca Strait
43	<i>Huia sumatrana</i>	ENS17030*	Indonesia, Sumatera Utara, Kabupaten Langkat, road to Bukit Lawang	03.53697 098.12658; 163	Malacca Strait	Malacca Strait
44	<i>Huia sumatrana</i>	MZB 23526	Indonesia, Sumatera Utara, Taman Nasional Batang Gadis	00.66669 099.58234; 1137	Indian Ocean	NA
45	<i>Huia sumatrana</i>	MVZ271223	Indonesia, Sumatera Utara, Taman Wisata Alam Sibolangit	03.33245 098.58446; 449	Malacca Strait	Malacca Strait
56	<i>Huia sumatrana</i>	MVZ271224	Indonesia, Sumatera Utara, Taman Wisata Alam Sibolangit	03.33245 098.58446; 449	Malacca Strait	Malacca Strait
47	<i>Huia sumatrana</i>	MZB 22346	Indonesia, Sumatera Selatan, Kabupaten Ogan Komering Ulu, Muara Dua	-04.90009 104.13381; 1464	South China Sea	North Sunda
48	<i>Huia sumatrana</i>	MZB 22348	Indonesia, Sumatera Barat, Kabupaten Pasaman Barat, trail to Mt. Talakmau	00.11365 099.93957; 695	Indian Ocean	NA
49	<i>Huia sumatrana</i>	UTA-A 62437	Indonesia, Sumatera Barat, Kabupaten Pasaman Barat, trail to Mt. Talakmau	00.10499 099.94512; 914	Indian Ocean	NA
50	<i>Huia sumatrana</i>	MZB 22350	Indonesia, Sumatera Barat, Kabupaten Pasaman Barat, trail to Mt. Talakmau	00.10220 099.94822; 974	Indian Ocean	NA
51	<i>Huia sumatrana</i>	UA20140712*	Indonesia, Sumatera Barat, Taman Nasional Kerinci-Seblat, Gunung Bontak	-01.61456 101.25740; 1200	South China Sea	North Sunda
52	<i>Huia sumatrana</i>	UA20140729*	Indonesia, Sumatera Barat, Taman Nasional Kerinci-Seblat, Muara Labuh	-01.45534 101.00020; 640	South China Sea	North Sunda
53	<i>Huia sumatrana</i>	UA20140785*	Indonesia, Sumatera Barat, Taman Nasional Kerinci-Seblat, Muara Labuh	-01.45534 101.00020; 640	South China Sea	North Sunda
54	<i>Huia sumatrana</i>	UA20140663*	Indonesia, Sumatera Barat, Taman Nasional Kerinci-Seblat, Padang Aro	-01.60920 101.32198; 665	South China Sea	North Sunda
55	<i>Huia sumatrana</i>	UA20140673*	Indonesia, Sumatera Barat, Taman Nasional Kerinci-Seblat, Padang Aro	-01.60920 101.32198; 665	South China Sea	North Sunda
56	<i>Huia sumatrana</i>	UA20140674*	Indonesia, Sumatera Barat, Taman Nasional Kerinci-Seblat, Padang Aro	-01.60920 101.32198; 665	South China Sea	North Sunda
57	<i>Huia sumatrana</i>	UA20140455*	Indonesia, Sumatera Barat, Kota Padang, Hutan Penelitian Universitas Andalas	-00.91180 100.46893; 409	Indian Ocean	NA
58	<i>Huia sumatrana</i>	UA20140460*	Indonesia, Sumatera Barat, Cagar Alam Malampah Alahan Panjang	00.04415 100.21522; 360	Indian Ocean	NA
59	<i>Huia sumatrana</i>	UA20140461*	Indonesia, Sumatera Barat, Cagar Alam Malampah Alahan Panjang	00.04415 100.21522; 360	Indian Ocean	NA

60	<i>Huia sumatrana</i>	UA20140498*	Indonesia, Sumatera Barat, Cagar Alam Rimbo Panti	00.35002 100.02207; 615	Malacca Strait	Malacca Strait
61	<i>Huia sumatrana</i>	UA20140504*	Indonesia, Sumatera Barat, Cagar Alam Rimbo Panti	00.35002 100.02207; 615	Malacca Strait	Malacca Strait
62	<i>Huia sumatrana</i>	UA20150431*	Indonesia, Sumatera Barat, Desa Tanjung Bungo	00.15228 100.47551; 334	Indian Ocean	NA
63	<i>Huia sumatrana</i>	JAM9400*	Indonesia, Sumatera Barat, Cagar Alam Lembah Anai	-00.48641 100.33626; 378	Indian Ocean	NA
64	<i>Huia sumatrana</i>	JAM9564*	Indonesia, Sumatera Barat, Cagar Alam Rimbo Panti	00.34982 100.02257; 646	Malacca Strait	Malacca Strait
65	<i>Huia sumatrana</i>	UA20150464*	Indonesia, Sumatera Barat, Kabupaten Sijunjung, Sungai Sumpur Kudus	-00.44910 100.89536; 438	South China Sea	Siam
66	<i>Huia masonii</i>	UA20150011*	Indonesia, Jawa Barat, Kabupaten Sumedang, Sungai Cijambu	-06.82900 107.79900; 1131	Java Sea	East Sunda
67	<i>Huia masonii</i>	UA20150033*	Indonesia, Jawa Tengah, Kabupaten Banyumas, Curug Cipendok	-07.33668 109.13662; 745	Indian Ocean	NA
68	<i>Huia masonii</i>	ENS7392*	Indonesia, Jawa Barat, Kabupaten Bogor, Taman Safari	-06.72600 106.95083	Java Sea	East Sunda
69	<i>Huia masonii</i>	ENS7398*	Indonesia, Jawa Barat, Kabupaten Bogor, Taman Safari	-06.72600 106.95083	Java Sea	East Sunda
70	<i>Huia masonii</i>	MZB.Amph.22371	Indonesia, Jawa Barat, Kabupaten Cianjur, Cibodas Botanical Garden	-06.74181 107.00610; 1405	Java Sea	East Sunda
71	<i>Huia masonii</i>	UA20150051*	Indonesia, Jawa Barat, Palutungan	-06.94403 108.43265; 1174	Java Sea	East Sunda
72	<i>Huia melasma</i>	FMNH 270711	Thailand, Nan, Amphoe Pua, Tambol Auan			
73	<i>Huia melasma</i>	FMNH 271377	Laos, Luang Namtha Prov, Vieng Phou Kha Dist			
74	<i>Meristogenys amoropalamus</i>	NHMBE 1057304	Malaysia, Borneo, Sarawak, Usun Apau National Park			
75	<i>Meristogenys kinabaluensis</i>	NHMBE 1064112	Malaysia, Borneo, Sabah, Sungai Kemantis trail			
76	<i>Meristogenys orphocnemis</i>	NHMBE 1064105	Malaysia, Borneo, Sabah, Sungai Winokok, Bundu Tuhan			
77	<i>Meristogenys poecilus</i>	NHMBE 1064092	Malaysia, Borneo, Sabah, Sungei Tawau, Tawau Hills Park			
78	<i>Meristogenys</i> sp.	NHMBE 1065861	Malaysia, Borneo, Sarawak, Gunung Murud, Palungan			
79	<i>Odorrana hosii</i>	NHMBE 1061612	Malaysia, Borneo, Sarawak, Kubah National Park			
80	<i>Odorrana hosii</i>	NHMBE 1068217	Malaysia, Borneo, Sarawak, Kubah National Park			
81	<i>Staurois guttatus</i>	NHMBE 1056532	Indonesia, Malaysia, Borneo, Sarawak, Gunung Mulu National Park			
82	<i>Pulchrana picturata</i>	UA20140782*	Indonesia, Sumatera Barat, Muara Labuh			

83	<i>Sumaterana crassiovis</i>	MZB.Amph.29288	Indonesia, Lampung, Kabupaten Lampung Barat, Gunung Abung	-05.03730 104.54828; 979	South China Sea	East Sunda
84	<i>Sumaterana crassiovis</i>	ZMH A14195	Indonesia, Sumatera Barat, Kayu Jao	-00.99717 100.63952; 1270	Indian Ocean	NA
85	<i>Sumaterana crassiovis</i>	ZMH A14198	Indonesia, Sumatera Barat, Kayu Jao	-00.99557 100.64334; 1315	Indian Ocean	NA
86	<i>Sumaterana crassiovis</i>	ZMH A14222	Indonesia, Sumatera Barat, Kayu Jao	-00.99980 100.63550; 1195	Indian Ocean	NA
87	<i>Sumaterana crassiovis</i>	MZB.Amph.29232	Indonesia, Sumatera Barat, Kayu Jao	-00.99980 100.63550; 1195	Indian Ocean	NA
88	<i>Sumaterana crassiovis</i>	MZB.Amph.29186	Indonesia, Aceh, Taman Nasional Gunung Leuser, Marpunge	03.77146 097.63773; 1065	Indian Ocean	NA
89	<i>Sumaterana crassiovis</i>	ZMH A14218	Indonesia, Aceh, Taman Nasional Gunung Leuser, Marpunge	03.77146 097.63773; 1065	Indian Ocean	NA
90	<i>Sumaterana crassiovis</i>	ZMH A14220	Indonesia, Aceh, Taman Nasional Gunung Leuser, Marpunge	03.77146 097.63773; 1065	Indian Ocean	NA
91	<i>Sumaterana crassiovis</i>	MZB.Amph.29194	Indonesia, Aceh, Taman Nasional Gunung Leuser, Marpunge	03.79289 097.64417; 1190	Indian Ocean	NA
92	<i>Sumaterana crassiovis</i>	ZMH A14169	Indonesia, Aceh, Taman Buru Linge-Isaq	04.37958 097.29158; 1000	Malacca Strait	Malacca Strait
93	<i>Sumaterana crassiovis</i>	MZB.Amph.29196	Indonesia, Aceh, Taman Buru Linge-Isaq	04.37958 097.29158; 1000	Malacca Strait	Malacca Strait
94	<i>Sumaterana crassiovis</i>	MZB.Amph.29198	Indonesia, Aceh, Taman Buru Linge-Isaq	04.37958 097.29158; 1000	Malacca Stait	Malacca Strait
95	<i>Sumaterana crassiovis</i>	ZMH A14149	Indonesia, Sumatera Selatan, Kabupaten Muara Enim, Desa Batu Surau	-04.13725 103.58640; 1048	Indian Ocean	NA
96	<i>Sumaterana crassiovis</i>	ZMH A14206	Indonesia, Sumatera Barat, Lubuk Selasih	-00.95782 100.57112; 1040	Indian Ocean	NA
97	<i>Sumaterana crassiovis</i>	MZB.Amph.29214	Indonesia, Sumatera Barat, Lubuk Selasih	-00.95782 100.57112; 1040	Indian Ocean	NA
98	<i>Sumaterana crassiovis</i>	MZB.Amph.29226	Indonesia, Sumatera Barat, Lubuk Selasih	-00.94529 100.54630; 1140	Indian Ocean	NA
99	<i>Sumaterana crassiovis</i>	ZMH A14139	Indonesia, Sumatera Barat, Kecamatan Kisam Tinggi, Desa Gunung Megang	-04.24543 103.83520; 874	South China Sea	North Sunda
100	<i>Sumaterana crassiovis</i>	ZMH A14197	Indonesia, Sumatera Barat, Taman Nasional Kerinci-Seblat, Padang Aro	-01.55932 101.31072; 605	South China Sea	North Sunda
101	<i>Sumaterana crassiovis</i>	ZMH A14182	Indonesia, Sumatera Barat, Taman Nasional Kerinci-Seblat, Padang Aro	-01.6175 101.24780; 975	South China Sea	North Sunda
102	<i>Sumaterana crassiovis</i>	MZB.Amph.29237	Indonesia, Sumatera Barat, Taman Nasional Kerinci-Seblat, Padang Aro	-01.6175 101.24780; 975	South China Sea	North Sunda
103	<i>Sumaterana crassiovis</i>	ZMH A14196	Indonesia, Sumatera Barat, Taman Nasional Kerinci-Seblat, Padang Aro	-01.61456 101.25740; 1200	South China Sea	North Sunda
104	<i>Sumaterana crassiovis</i>	ZMH A14228	Indonesia, Sumatera Barat, Taman Nasional Kerinci-Seblat, Padang Aro	-01.60325 101.26391; 825	South China Sea	North Sunda
105	<i>Sumaterana crassiovis</i>	MZB.Amph.29249	Indonesia, Sumatera Barat, Taman	-01.60325 101.26391; 825	South China Sea	North Sunda

			Nasional Kerinci-Seblat, Padang Aro			
106	<i>Sumaterana crassiovis</i>	ZMH A14136	Indonesia, Sumatera Barat, Taman Nasional Kerinci-Seblat, Muara Labuh	-01.45534 101.00020; 640	South China Sea	North Sunda
107	<i>Sumaterana crassiovis</i>	MZB.Amph.29320	Indonesia, Sumatera Barat, Kabupaten Payakumbuh, road Sumbar-Riau	-00.01916 100.72226, 606	South China Sea	Siam
108	<i>Sumaterana crassiovis</i>	ZMH A14171	Indonesia, Sumatera Barat, Cagar Alam Rimbo Panti	00.35220 100.04933; 425	Malacca Strait	Malacca Strait
109	<i>Sumaterana crassiovis</i>	MZB.Amph.29200	Indonesia, Sumatera Barat, Cagar Alam Rimbo Panti	00.35220 100.04933; 425	Malacca Strait	Malacca Strait
110	<i>Sumaterana crassiovis</i>	ZMH A14170	Indonesia, Sumatera Barat, Cagar Alam Rimbo Panti	00.35220 100.04933; 425	Malacca Strait	Malacca Strait
111	<i>Sumaterana crassiovis</i>	MZB.Amph.29202	Indonesia, Sumatera Barat, Cagar Alam Rimbo Panti	00.35220 100.04933; 425	Malacca Strait	Malacca Strait
112	<i>Sumaterana crassiovis</i>	MZB.Amph.29206	Indonesia, Sumatera Barat, Cagar Alam Rimbo Panti	00.35056 100.04490; 450	Malacca Strait	Malacca Strait
113	<i>Sumaterana crassiovis</i>	ZMH A14191	Indonesia, Sumatera Barat, Cagar Alam Rimbo Panti	00.35056 100.04490; 450	Malacca Strait	Malacca Strait
114	<i>Sumaterana crassiovis</i>	ZMH A14165	Indonesia, Bengkulu, Taman Nasional Kerinci-Seblat, Ulu Seblat	-02.95330 102.13955; 726	Indian Ocean	NA
115	<i>Sumaterana crassiovis</i>	MZB.Amph.29275	Indonesia, Bengkulu, Taman Nasional Kerinci-Seblat, Ulu Seblat	-02.95060 102.14988; 716	Indian Ocean	NA
116	<i>Sumaterana crassiovis</i>	ZMH A14185	Indonesia, Lampung, Kabupaten Tanggamus, Air Terjun Talang Ogan	-05.37933 104.66043; 754	Java Sea	East Sunda
117	<i>Sumaterana crassiovis</i>	MZB.Amph.29371	Indonesia, Jambi, Taman Nasional Kerinci-Seblat, Bukit Tapan	-02.32167 101.26235; 726	Indian Ocean	NA
118	<i>Sumaterana crassiovis</i>	ZMH A14193	Indonesia, Jambi, Taman Nasional Kerinci-Seblat, Bukit Tapan	-02.32100 101.26771; 787	Indian Ocean	NA
119	<i>Sumaterana crassiovis</i>	ZMH.A12653	Indonesia, Jambi, Taman Nasional Kerinci-Seblat, Bukit Tapan	-02.30283 101.27170; 812	Indian Ocean	NA
120	<i>Sumaterana crassiovis</i>	ZMH A14205	Indonesia, Jambi, Taman Nasional Kerinci-Seblat, Bukit Tapan	-02.25833 101.28656; 909	Indian Ocean	NA
121	<i>Sumaterana crassiovis</i>	MZB.Amph.29261	Indonesia, Jambi, Taman Nasional Kerinci-Seblat, Bukit Tapan	-02.25833 101.28656; 909	Indian Ocean	NA
122	<i>Sumaterana crassiovis</i>	MZB.Amph.29326	Indonesia, Sumatera Utara, Bumi Perkemahan Sibolangit	03.27347 098.53586; 881	Malacca Strait	Malacca Strait
123	<i>Sumaterana crassiovis</i>	MZB.Amph.29338	Indonesia, Sumatera Utara, Bumi Perkemahan Sibolangit	03.27522 098.53614; 880	Malacca Strait	Malacca Strait
124	<i>Sumaterana crassiovis</i>	MZB.Amph.29345	Indonesia, Sumatera Utara, Bumi Perkemahan Sibolangit	03.27689 098.53472; 877	Malacca Strait	Malacca Strait

125	<i>Sumaterana crassiovis</i>	UTA-A 62439	Indonesia, Lampung, Kabupaten Tanggamus, Ngarip	-05.30638 104.5483; 869	Indian Ocean	South Sunda
126	<i>Sumaterana crassiovis</i>	MZB.Amph.22344	Indonesia, Lampung, Kabupaten Lampung Barat, road Liwa to Krui	-05.06458 104.05465; 673	Indian Ocean	NA
127	<i>Sumaterana crassiovis</i>	MZB.Amph.22343	Indonesia, Lampung, Kabupaten Lampung Barat, road Liwa to Krui	-05.06458 104.05465; 673	Indian Ocean	NA
128	<i>Sumaterana crassiovis</i>	ENS15457*	Indonesia, Sumatera Utara, Kabupaten Karo, Air Terjun Sikulikap	03.24047 098.53878; 1156	Malacca Strait	Malacca Strait
129	<i>Sumaterana crassiovis</i>	MZB.Amph.23490	Indonesia, Sumatera Utara, Kabupaten Mandailing Natal, road Panyabungan-Natal	00.72544 099.54497; 804	Malacca Strait	Malacca Strait
130	<i>Sumaterana crassiovis</i>	MZB.Amph.23491	Indonesia, Sumatera Utara, Kabupaten Mandailing Natal, road Panyabungan-Natal	00.72544 099.54497; 804	Malacca Strait	Malacca Strait
131	<i>Sumaterana crassiovis</i>	MZB.Amph.22339	Indonesia, Jambi, Taman Nasional Kerinci-Seblat, Gunung Kunyit	-02.18926 101.49512; 1355	South China Sea	North Sunda
132	<i>Sumaterana crassiovis</i>	UTA A-64833	Indonesia, Sumatera Utara, Kabupaten Toba-Samosir, Gunung Pangalubao	02.60514 099.04629; 1397	Malacca Strait	Malacca Strait
134	<i>Sumaterana crassiovis</i>	UTA A-64882	Indonesia, Sumatera Utara, Kabupaten Toba-Samosir, Gunung Pangalubao	02.60514 099.04629; 1397	Malacca Strait	Malacca Strait
135	<i>Sumaterana crassiovis</i>	MZB.Amph.23498	Indonesia, Sumatera Utara, Kecamatan Hambung Hasundutan, Gunung Pinapan	02.18325 098.60513; 1309	Indian Ocean	NA
136	<i>Sumaterana crassiovis</i>	UTA A-64887	Indonesia, Sumatera Utara, Kabupaten Mandailing Natal, slope Dolok Malea and Kampung Mompang	00.97500 099.57959; 991	Indian Ocean	NA
137	<i>Sumaterana crassiovis</i>	MZB.Amph.23499	Indonesia, Sumatera Utara, Kabupaten Mandailing Natal, slope Dolok Malea and Kampung Mompang	00.97500 099.57959; 991	Indian Ocean	NA
138	<i>Sumaterana crassiovis</i>	UTA A-64835	Indonesia, Sumatera Utara, Taman Nasional Batang Gadis	00.66636 099.57191; 1271	Indian Ocean	NA
139	<i>Sumaterana crassiovis</i>	UTA A-64894	Indonesia, Sumatera Utara, Taman Nasional Batang Gadis	00.66636 099.57191; 1271	Indian Ocean	NA
140	<i>Sumaterana crassiovis</i>	MVZ271862	Indonesia, Sumatera Barat, Kabupaten Solok, Desa Air Busuk	-00.94203 100.82423; 1150	South China Sea	North Sunda
141	<i>Sumaterana crassiovis</i>	MVZ271863	Indonesia, Sumatera Barat, Kabupaten Solok, Desa Air Busuk	-00.94203 100.82423; 1150	South China Sea	North Sunda
142	<i>Sumaterana crassiovis</i>	MVZ271864	Indonesia, Sumatera Barat, Kabupaten Solok, Desa Air Busuk	-00.94203 100.82423; 1150	South China Sea	North Sunda
143	<i>Sumaterana crassiovis</i>	MVZ271522	Indonesia, Sumatera Barat, Cagar Alam Rimbo Panti	00.34982 100.02257; 646	Malacca Strait	Malacca Strait
144	<i>Sumaterana crassiovis</i>	MVZ271523	Indonesia, Sumatera Barat, Cagar Alam Rimbo Panti	00.34982 100.02257; 646	Malacca Strait	Malacca Strait

145	<i>Sumaterana crassiovis</i>	MVZ271524	Indonesia, Sumatera Barat, Cagar Alam Rimbo Panti	00.34789 100.03748; 1000	Malacca Strait	Malacca Strait
146	<i>Sumaterana crassiovis</i>	MVZ271525	Indonesia, Sumatera Barat, Cagar Alam Rimbo Panti	00.34789 100.03748; 1000	Malacca Strait	Malacca Strait
147	<i>Sumaterana crassiovis</i>	MVZ271526	Indonesia, Sumatera Barat, Cagar Alam Rimbo Panti	00.34789 100.03748; 1000	Malacca Strait	Malacca Strait
148	<i>Sumaterana crassiovis</i>	RMBR118	Indonesia, Bengkulu, Kabupaten Lebong, Desa Air Putih	-03.03712 102.19100	Indian Ocean	NA
149	<i>Sumaterana crassiovis</i>	ZMH.A14200	Indonesia, Lampung, Kabupaten Lampung Barat, Gedong Surian	-05.06651 104.46261; 935	South China Sea	East Sunda
150	<i>Sumaterana crassiovis</i>	MZB.Amph.29292	Indonesia, Lampung, Kabupaten Lampung Barat, Gedong Surian	-05.04456 104.44930; 1022	South China Sea	East Sunda
151	<i>Sumaterana crassiovis</i>	MZB.Amph.29396	Indonesia, Aceh, Taman Buru Linge-Isaq	04.36482 097.24957; 440	Malacca Strait	Malacca Strait
152	<i>Sumaterana crassiovis</i>	MZB.Amph.29415	Indonesia, Aceh, Taman Buru Linge-Isaq	04.36482 097.24957; 440	Malacca Strait	Malacca Strait
153	<i>Sumaterana crassiovis</i>	MZB.Amph.29403	Indonesia, Aceh, Taman Buru Linge-Isaq	04.36482 097.24957; 440	Malacca Strait	Malacca Strait
154	<i>Sumaterana crassiovis</i>	MZB.Amph.29419	Indonesia, Aceh, Taman Buru Linge-Isaq	04.36139 097.24635; 440	Malacca Strait	Malacca Strait
155	<i>Sumaterana crassiovis</i>	MZB.Amph.29405	Indonesia, Aceh, Taman Buru Linge-Isaq	04.37954 097.28175; 600	Malacca Strait	Malacca Strait
156	<i>Sumaterana crassiovis</i>	ZMH A14174	Indonesia, Aceh, Taman Buru Linge-Isaq	04.37954 097.28175; 600	Malacca Strait	Malacca Strait
157	<i>Sumaterana crassiovis</i>	MZB.Amph.29378	Indonesia, Aceh, Kabupaten Ulu Masen, Mane	04.92334 096.12215; 792	Indian Ocean	NA
158	<i>Sumaterana crassiovis</i>	ZMH A14155	Indonesia, Aceh, Kabupaten Ulu Masen, Mane	04.92091 096.12275; 761	Indian Ocean	NA
159	<i>Sumaterana crassiovis</i>	ZMH A14190	Indonesia, Aceh, Kabupaten Ulu Masen, Mane	04.91926 096.12300; 747	Indian Ocean	NA
160	<i>Sumaterana crassiovis</i>	ZMH A14189	Indonesia, Aceh, Kabupaten Ulu Masen, Mane	04.89949 096.13168; 700	Indian Ocean	NA
161	<i>Sumaterana crassiovis</i>	UTA A-64926	Indonesia, Sumatera Utara, Kabupaten Samosir, Simpang Tele	02.52733 098.63364; 1800	Malacca Strait	Malacca Strait
162	<i>Sumaterana crassiovis</i>	MZB.Amph.23516	Indonesia, Sumatera Utara, Kabupaten Samosir, vicinity of Tele	02.55397 098.59806; 1774	Malacca Strait	Malacca Strait
163	<i>Sumaterana crassiovis</i>	UTA A-64829	Indonesia, Sumatera Utara, Kabupaten Samosir, vicinity of Tele	02.55397 098.59806; 1774	Malacca Strait	Malacca Strait
164	<i>Sumaterana crassiovis</i>	UTA A-64834	Indonesia, Sumatera Utara, Kabupaten Ulu Masen, Mane	02.91076 098.46313; 1625	Malacca Strait	Malacca Strait
165	<i>Sumaterana crassiovis</i>	MZB.Amph.23524	Indonesia, Sumatera Utara, Kabupaten Ulu Masen, Mane	02.91076 098.46313; 1625	Malacca Strait	Malacca Strait
166	<i>Sumaterana crassiovis</i>	ZMH A14164	Indonesia, Aceh, Taman Nasional Gunung Leuser, Marpunge	03.79289 97.64417; 1190	Indian Ocean	NA
167	<i>Sumaterana crassiovis</i>	ZMH A14194	Indonesia, Bengkulu, Taman Nasional Kerinci-Seblat, Gunung Baru	-02.88525 102.12993; 2004	Indian Ocean	NA

168	<i>Sumaterana crassiovis</i>	MZB.Amph.29377	Indonesia, Bengkulu, Taman Nasional Kerinci-Seblat, Gunung Baru	-02.88413 102.13073; 2033	Indian Ocean	NA
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*specimen with field number

Table S2 Genetic *p*-distance *Huia sumaterana* and *H. masonii* based on 16S sequences, calculated using MEGA

Taxa	Genetic <i>p</i> -distance (%)
<i>H. sumatrana</i> 1 – <i>H. sumatrana</i> 2	6.97–7.95
<i>H. sumatrana</i> 1 – <i>H. sumatrana</i> 3	13.11–15.20
<i>H. sumatrana</i> 1 – <i>H. masonii</i> 1	14.37–15.48
<i>H. sumatrana</i> 1 – <i>H. masonii</i> 2	11.30–12.69
<i>H. sumatrana</i> 2 – <i>H. sumatrana</i> 3	13.81–15.20
<i>H. sumatrana</i> 2 – <i>H. masonii</i> 1	14.50–15.06
<i>H. sumatrana</i> 2 – <i>H. masonii</i> 2	12.13
<i>H. sumatrana</i> 3 – <i>H. masonii</i> 1	11.58–12.41
<i>H. sumatrana</i> 3 – <i>H. masonii</i> 2	11.72–12.69
<i>H. masonii</i> 1 – <i>H. masonii</i> 2	10.46–11.58

Table S3 Primer information and PCR annealing temperatures applied for this study

Markers	Sequence	Annealing temperature (°C)	Length (bps)	Citation
12S	12SZ-L: AAAGGTTTGGTCCTAGCCTT 12SK-H: TCCRGTAYRCTTACCDTGTACGA	52	825	Goebel et al. (1999)
16S	12sm: GGCAAGTCGTAACATGGTAAG 16sd: CTCCGGTCTGAACTCAGATCACGTAG	51	1406	Pauly et al. (2004), Oliver et al. (2015)
COI	Chmf4: TYTCWACWAAYCAYAAAGAYATCGG Chmr4: AYCTCRGGRTGRCCRAARAATCA	46		Che et al (2012)
CYTB	Cytb-c: CTACTGGTTGTCTCCGATTCATGT CB-J-10933: TATGTTCTACCATGAGGACAAATATC	51		Bossuyt & Millinkovitch (2000), Oliver et al. (2015)
ND2	Met-LND2: CAATGTTGGTTAAAATCCTTCC Trp-HND2: AGGCTTTGAAGGCCTTTGGTC	49		Stuart et al. (2006), Stuart et al. (2010)
BDNF	BDNF-F1: ACCATCCTTTTCCTKACTATGG BDNF-R1: CTATCTCCCCTTTTAATGGTC	57		
NTF3	NTF3-F3: TCTTCCTTATCTTTGTGGCATCCACGCTA NTF3-R3: ACATTGRGAATTCCAGTGTGTCGTC	56		
POMC	POMC DRV F1: ATATGTCATGASCCAYTTYCGCTGCAA POMC DRV R1: GGCRTTYTTGAAWAGAGTCATTAGWGG	56		
RAG1	Rag1 1F: GCMTTGCTSCCRGGGTATCA Rag1 2R: TCAATGGACGGAAGGGTTTCAATAA	50	801	Oliver et al. (2015)
TYR	Tyr1A: AGGTCCTTTRAGCAAGGAATG Tyr1G: TGCTGGGCRCTCTCTCCARTCCCA	57	579	Oliver et al. (2015)

Table S4 Substitution model resulted from Partition Finder

Model	Loci
GTR + I+ G	(1) 12S, 16S, and tRNA ^{val} (2) CYTB codon 3 (3) CYTB codon 1 and ND2 codon 1 (4) NTF3 codon 3, POMC codon 3, and TYR codon 3 (5) NTF3 codon 1, POMC codon 1, RAG1 codon 1, TYR codon 1, and TYR codon 2
GTR+G	COI codon 3 and ND2 codon 3
SYM+I+G	(1) BDNF codon 3 and COI codon 1 (2) NTF3 codon 2, POMC codon 2
K80+I+G	BDNF codon 1, BDNF codon 2, COI codon 2, and RAG1 codon 2
HKY+I+G	CYTB codon 2 and ND2 codon 2
HKY+G	RAG1 codon 3

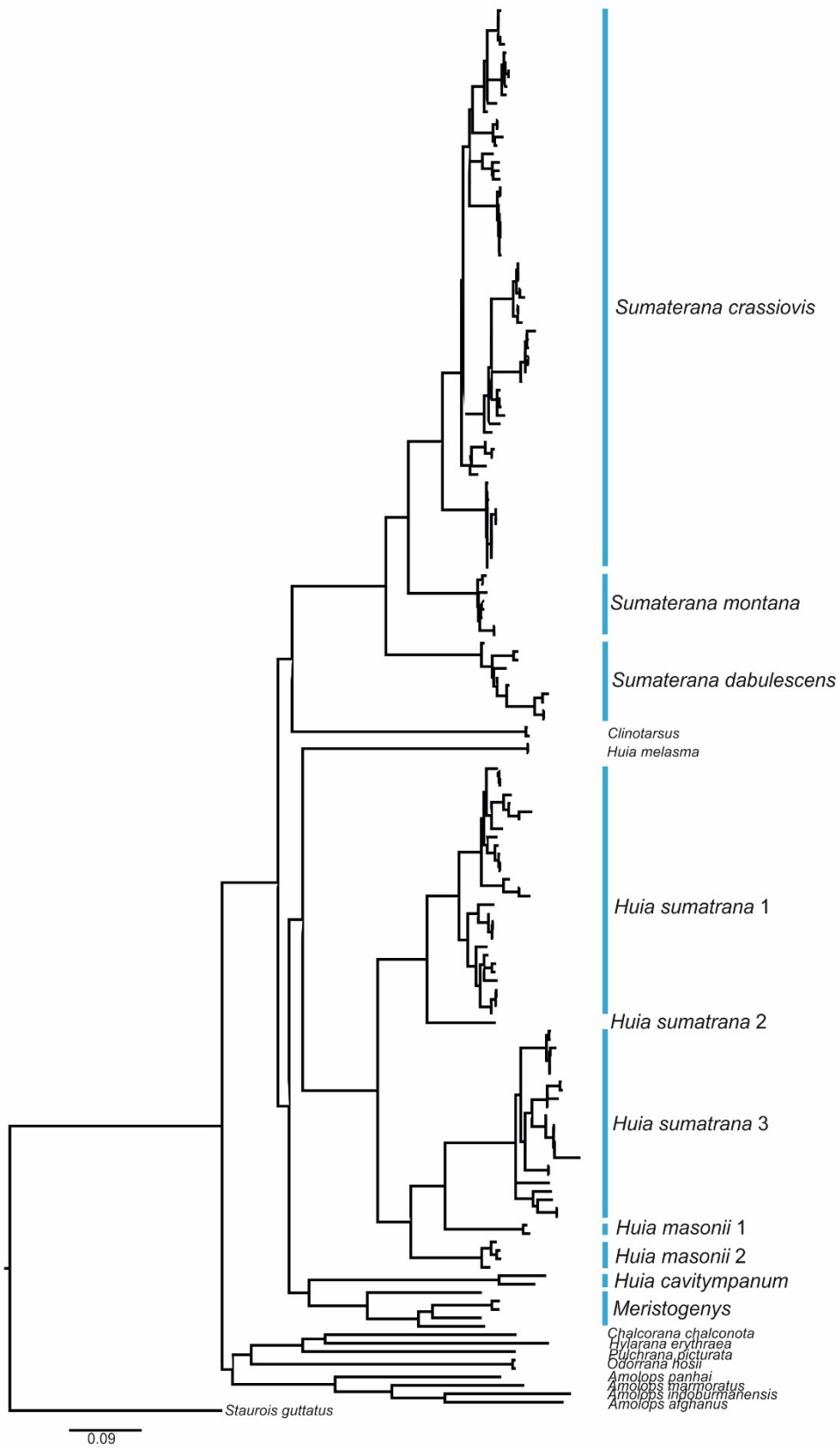


Figure S1 Original tree reconstruction using BI analysis

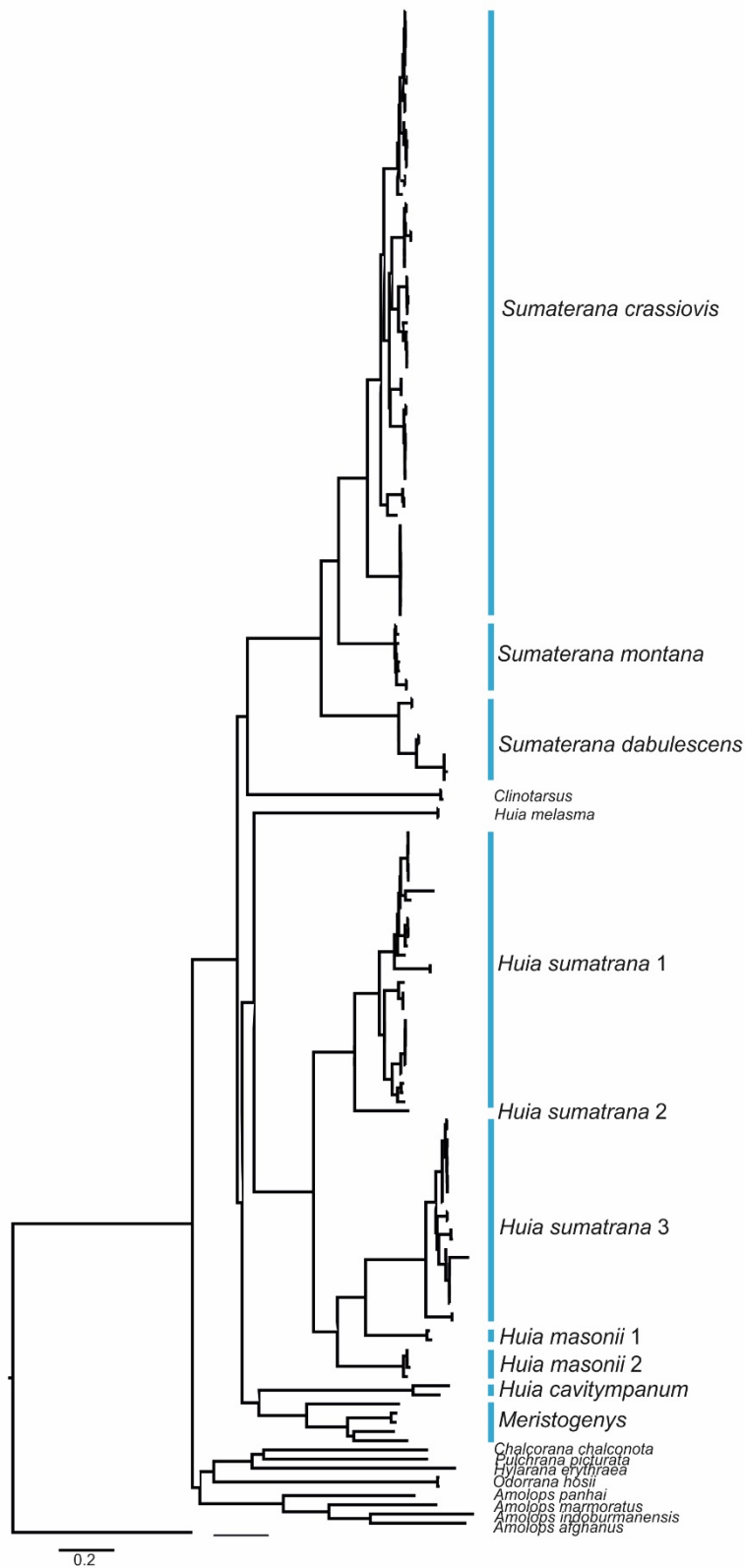


Figure S2 Original tree reconstruction using ML analysis

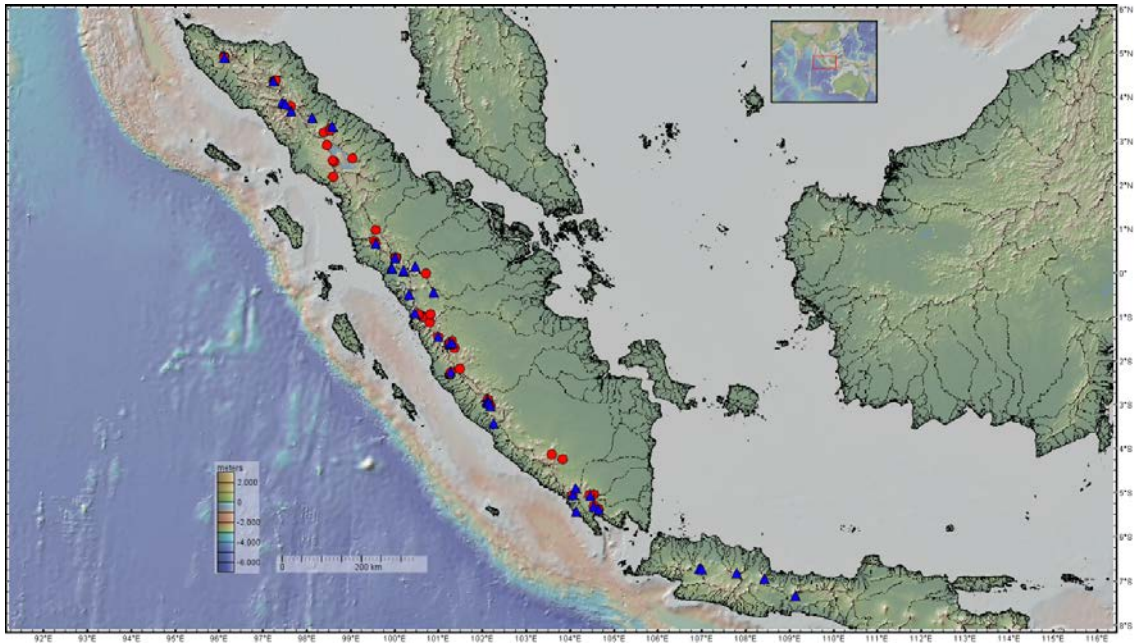


Figure S3 Map of sampling localities of ranid frogs' genus *Huia* and *Sumaterana* used in this study

CHAPTER 5

General discussion

I Phylogenetic systematics and diversity of Cascade Frogs

Cascade Frogs are a very unique group of frogs with specialized larval forms and living in special habitat types. Since the refinement of the definition of what constitutes Cascade Frogs by Inger (1966), the number of species subsumed as Cascade Frogs has increased. Considerable sampling effort and various approaches have been established to delimit species and quantify the diversity and distribution of this group (e.g., Yang 1991, Liu et al. 2000, Bain et al. 2003, Orlov et al. 2003, Matsui and Nabhitabhata 2006, Shimada et al. 2007, Stuart 2008, Stuart et al. 2010, Shimada et al. 2011, Jiang et al. 2016, Arifin et al. 2018a). The application of more than one source of evidence, such as the addition of molecular data to support morphological data, has accelerated species discovery within Cascade Frogs (see Frost 2018 for details). However, certain parts of the geographical range of these frogs have been poorly sampled (e.g., Indonesian part of Borneo [Kalimantan], Java, Sumatra, the Malay Peninsula; see Chapter I section III.3), and Cascade Frog species from these regions have been represented by a relatively low number of samples in previous studies (e.g., Stuart 2008, Wiens et al. 2009, Pyron and Wiens 2011). This has resulted in phylogenetic ambiguity and taxonomic uncertainty for over a decade (e.g., paraphyly of *Huia*; see Chapter I section III.4). These issues form the core of this study.

The position of *Huia* in the phylogeny of the Asian ranid frogs has been very perplexing for quite some time (see taxonomic history in Frost 2018). Prior to my study, this genus was consistently recovered as a paraphyletic group in molecular studies (e.g., Stuart 2008, Wiens et al. 2009, Pyron and Wiens 2011) with the type species (*H. cavitympanum*) is more closely related to the Bornean species of *Meristogenys*, than to other *Huia* species. Assuming insufficient sampling in previous studies, my study investigated the potential of a more comprehensive taxon sampling in the phylogeny of Cascade Frogs. Through this study, I was able to increase the number of Cascade Frogs specimens from a poorly sampled region of Sumatra. Thus, a comprehensive dataset of the Cascade Frogs, particularly for Sumatra, was generated in this study to reconstruct the most up-to-date phylogenetic tree of Cascade Frogs relationship. As expected, the present study, with more adequate taxonomic and regional sampling, revealed hitherto undiscovered cryptic and endemic diversity in Sumatran Cascade Frogs (Chapter 2 and 4).

The molecular analyses indicated at least five distinct lineages within the genus *Huia* from Sumatra and Java, comprising up to three candidate species (Chapter 4). Surprisingly, my study also recognized another species of frogs possessing gastromyzophorous tadpoles on Sumatra, in addition to Sumatran *Huia* (Chapter 2): *Chalcorana crassiovis*, a Sumatran endemic that was taxonomically divisive until recently. DNA sequences of unidentified tadpoles possessing abdominal suckers from Sumatra were matched with adults of this taxon.

Furthermore, my analyses revealed another two species that were closely related to frogs previously known as *C. crassiovis*. Thus, with evidence of molecular data, morphology of adults and larvae, as well as geographical distribution, the new genus *Sumaterana* was proposed to amend the taxonomic position of *C. crassiovis* and the two new congeneric species (Chapter 2).

This study gives new insights into the current diversity of the species with their unique larval forms and their geographical distributions. To date, the Cascade Frogs assemblage comprises four genera with 76 described species and three candidate species. My molecular phylogenetic analyses could not resolve the paraphyly of *Huia*. My analyses (Chapter 2 and 4) demonstrated similar result to previous studies (e.g., Stuart 2008, Wiens 2009, Pyron and Wiens 2011) for: (1) the position of *Huia* in the phylogenetic trees, (2) the unstable arrangement of some branches (e.g., *Clinotarsus*), and (3) the low support values in some of the clades (see Fig 10 Chapter 1, Fig. 2 Chapter 2, Fig. 1 Chapter 4). The present study expands this unclear picture insofar as *Huia* frogs on Sumatra and Java were revealed to be more diverse than previously known (see Chapter 4). Future studies that intend to unravel the *Huia* enigma will require sufficient geographic samples across the distributional range for all *Huia* species (*H. cavitympanum* from Borneo, *H. melasma* from mainland Asia, and *H. masonii* from Java), where hidden diversity within this genus is anticipated. For example, Manthey and Denzer (2014) already tentatively suggested to separate *H. javana* as valid species from *H. masonii*; currently only *H. masonii* is recognized (Frost 2018). Furthermore, the position of *H. modiglianii*, the second species of *Huia* on Sumatra, has never been investigated in any genetic study and needs to be addressed. Manthey and Denzer (2014) assessed the original description of *H. modiglianii* as vague and they assume that this insufficient original description has led to confusion in the species' identification, such as in Kurniati (2009). Resolving phylogenetic uncertainties within *Huia* by no doubt require great efforts, Thus, no taxonomic amendment concerning *Huia* was suggested in this study with respect to the problem's complexity.

Tadpole morphology has proven useful for diagnosing *Huia* species from one to another (see also Shimada et al. 2015 for *Meristogenys*' larvae). Within the five recognized *Huia* species, however, tadpoles of *H. melasma* (Thailand) and *H. modiglianii* (Sumatra) remain unknown (Manthey and Denzer 2014). My study demonstrated that incorporating tadpole data is just as important as collecting adult data, particularly when adults are highly similar to one another in morphology (e.g., DNA barcoding of adults and larvae of *Sumaterana*; Chapter 2). This study also corroborated and expanded (by *Sumaterana*) the conclusion of Manthey and Denzer (2014) that the tadpoles of the four recognized Cascade Frogs genera (*Amolops*, *Huia*,

Meristogenys, and *Sumaterana*) can be distinguished by the shape of their jaw sheaths (Fig. 1).

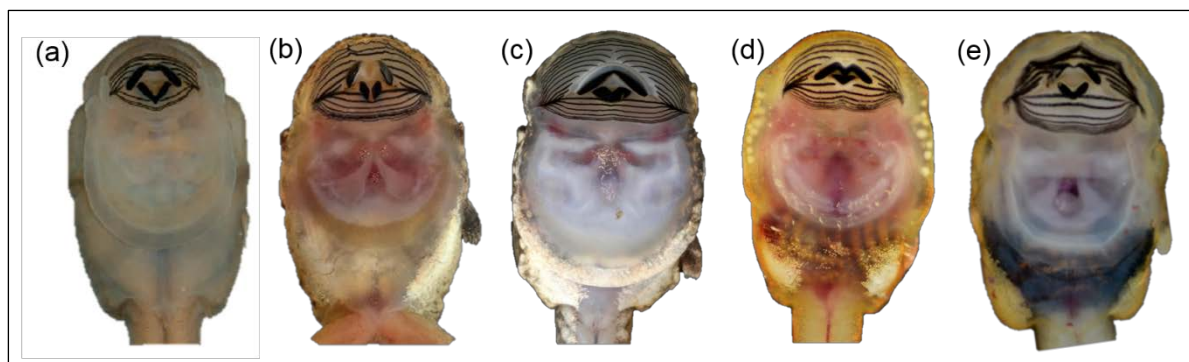


Figure 1 Different jaw sheaths shown by representative species of the four Cascade Frogs genera: (a) *Amolops panhai*, (b) *Meristogenys jerboa*, (c) *Huia cavitympanum*, (d) *H. sumatrana*, (e) *Sumaterana crassiovis*. Photos: Matsui and Nabhitabhata 2006 (a), A. Haas (b–c), U. Arifin (d–e).

In the case of *Sumaterana*, proposing a new genus of frogs possessing gastromyzophorous tadpoles while *Huia* remains an open problem within the phylogeny of the Asian ranid frogs was challenging. Establishing *Sumaterana* might be considered controversial by some because another taxonomic option would have been possible, i.e., proposing a clade comprising *Clinotarsus*, *Huia*, *Meristogenys*, and *Sumaterana* under a single name *Clinotarsus*, the oldest available name. However, valuable biological information associated with the current monophyletic groups would have been dissolved in this process: (1) island endemism (e.g., *Sumaterana* - Sumatra, *Meristogenys* - Borneo), (2) differences in adult and tadpole morphology, and (3) tadpole peculiarities – the species of *Clinotarsus* do not possess larvae with an abdominal sucker. Weighing pros and cons, establishing a genus *Sumaterana* was considered the better option, in order to ensure taxonomic stability (Arifin et al. 2018a).

Apart from the abovementioned main results from this study, the phylogenetic trees reconstructed in this study (see Chapter 2 and 4) also corroborated previous hypotheses concerning the arrangement of the Cascade Frogs in a more inclusive phylogeny (e.g., Stuart 2008, Wiens et al. 2009, Kurabayashi et al. 2010, Pyron and Wiens 2011). On one hand, *Amolops* was more closely related to other frogs within the family Ranidae (e.g., *Amnirana*, *Babina*, *Chalcorana*, *Hydrophylax*, *Hylarana*, *Odorrana*, *Phelophylax*, *Pulchrana*) and not to other species of Cascade Frogs (*Huia*, *Meristogenys*, and *Sumaterana*). On the other hand, *Clinotarsus* (no gastromyzophorous tadpoles) was nested within a clade comprising *Huia*, *Meristogenys*, and *Sumaterana* (all having abdominal sucker larvae). According to these evidence, Gan et al. (2015) and (Arifin et al. 2018a) hypothesized that the frogs with abdominal sucker larvae might have evolved independently twice in this ranid assemblage, once in the most recent common ancestor of the group comprising *Huia*, *Sumaterana*, and *Meristogenys*, and again in the genus of *Amolops*. Although tadpoles from both clades show similar morphological and anatomical characters (Noble 1929, Gan et al. 2015), the available molecular evidence implies separate origins and parallel evolution of these characters. In case

of *Clinotarsus*, this scenario would mean that gastromyzophorous larvae have been lost secondarily (Arifin et al. 2018a).

Concerning the unstable branches and low support values in parts of the clades comprising *Clinotarsus*, *Huia*, *Meristogenys*, and *Huia* (see Fig 10 Chapter 1, Fig. 2 Chapter 2, Fig. 1 Chapter 4). I believe these might not be influenced by the length of the sequences or the number of taxa included in the study. Previous studies included only a limited number of Cascade Frogs (especially for *Huia*, only one sample per species), but with different lengths of sequences. Amongst available studies, the shortest sequence length was ~1834 bps (Stuart 2008) and the longest ~12,712 bps (Pyron and Wiens 2011). My study fell in between the two (it being the most comprehensive taxon sampling with a total of 7,582 bps sequence length). All studies, however, demonstrate similar results concerning the instability of certain clades. These short-unstable branches and poorly supported nodes could be attributed to rapid radiation (see Whitfield et al. 2008, Pyron 2014). Furthermore, my divergence time analyses estimated that the most recent common ancestor of *Clinotarsus*, *Huia*, *Meristogenys*, and *Sumaterana* diversified during the Eocene (Fig. 3 Chapter 4). During the Eocene, amphibian diversification experienced an elevated speciation rate (Roelants et al. 2007). Various other taxa also underwent rapid radiation during this period, e.g., birds (Barker et al. 2004), chameleons (Tolley et al. 2013), snakes (Kelly et al. 2009). It is very likely that the biogeographic history of the region plays an important role in the diversification of certain species.

The phylogenetic systematics of Cascade Frogs remains a challenge and their taxonomy is far from stable. Improved geographic sampling could reveal that Cascade Frogs have hidden diversity (see also Chan et al. 2017, 2018). This diversity needs to be addressed with appropriate methods to accurately identify species boundaries (Chan et al. 2017, more detail discussion below). Especially resolving the problems with *Huia* systematics is critical for establishing a solid phylogenetic hypothesis and taxonomy of the rapid with gastromyzophorous tadpoles within the family Ranidae.

II Amphibian diversity on Sumatra and biodiversity discovery through time

In 1923, Van Kampen recorded 61 amphibian species from Sumatra, and to date, the number of Sumatran amphibians is 104 species (Frost 2018), an increase of 41.3% in almost a century. In only the past decade, 22 species of amphibians (approximately 51.2% of the total increase) have been recognized and described from Sumatra (see Table 1). Thus, on average, approximately two or three species of Sumatran amphibians are described every year. This study, however, also shows that a total of approximately one year's fieldwork can possibly contribute to the recognition of at least one genus (*Sumaterana*) and three species (*S. dabulescens*, *S. montana*, and *Pulchrana fantastica*) new to science from the island (Arifin et

al. 2018a-b, Chapter 2 and 3). Additionally, three distinct lineages within *Huia sumatrana* were also identified as candidate species (see Vieites et al. 2009 for definition) by genetic divergence in this study, awaiting to be confirmed true species (Chapter 4). Furthermore, from the same collaborative field expedition, one genus (*Sigalegalephrynus*) and two new species (*S. mandailinguensis* and *S. minangkabauensis*) of Sumatran bufonids (Smart et al. 2017) has been described. The publications and rates at which new species were described (including my study) are further evidence that Sumatra (and Sundaland in general) has a very high potential for future species discoveries (Iskandar and Colijn 2000, Stuart et al. 2006, Inger et al. 2009, Teynie et al. 2010, Arifin et al. 2018a-b).

Table 1 Amphibian species described from Sumatra in the last decade (2008–2018; Frost 2018, accessed in November 2018)

Year	Species
2009	Ranidae (N=2): <i>Chalcorana parvaccola</i> , <i>C. rufipes</i>
2010	Bufonidae (N=1): <i>Duttaphrynus totol</i> Microhylidae (N=1): <i>Leptobrachium wayseputiensis</i>
2011	Dicroglossidae (N=1): <i>Limnonectes sisikdagu</i> Rhacophoridae (N=1): <i>Rhacophorus pseudacutirostris</i>
2012	Ranidae (N=1): <i>Pulchrana rawa</i>
2014	Rhacophoridae (N=4): <i>Chiromantis badalika</i> , <i>C. nauli</i> , <i>Polypedates pseudotilopus</i> , <i>Rhacophorus bengkuluensis</i>
2015	Rhacophoridae (N=1): <i>Rhacophorus indonesiensis</i>
2017	Bufonidae (N=2): <i>Sigalegalephrynus mandailinguensis</i> , <i>S. minangkabauensis</i> Rhacophoridae (N=4): <i>Philautus amabilis</i> , <i>P. polymorphus</i> , <i>P. thamyridion</i> , <i>P. ventrimaculatus</i>
2018	Megophryidae (N=1): <i>Megophrys lancip</i> Ranidae (N=3): <i>Pulchrana fantastica</i> , <i>Sumaterana dabulescens</i> , <i>S. montana</i>

Sumatra is topographically heterogeneous. Numerous types of ecosystems in low to high altitude (up to 3,805 m a.s.l.) provide plentiful habitats and microhabitats (Bihari and Lal 1989, Whitten et al. 2000) that are suitable for amphibians. Especially in areas that have never been sampled before (e.g., Aceh), many more species are very likely awaiting to be discovered. In my study, *Sumaterana dabulescens* was described from Aceh and it is endemic to the region (Chapter 2). *Pulchrana fantastica* (Chapter 3) was also described from Aceh. Large scale and strategic sampling efforts are paramount in revealing the true faunal diversity and distribution patterns on Sumatra Island. The cumulative total of Sumatra's amphibians undoubtedly continues to increase every year (Stuart et al. 2006, Inger et al. 2009, Teynie et al. 2010).

The cumulative curve for the total number of documented amphibian species for Southeast Asian increased particularly in Sundaland, mainland Asia, Sulawesi, and the Philippines (Brown and Stuart 2012; Fig. 2). Interestingly, Brown and Stuart (2012) suggested that species accumulation in these areas has experienced a dramatically steep increase only in the last two decades. During this period, more sampling efforts were carried out compared to previous decades. Surprisingly, mainland Asia had the highest species diversity and fastest recent discovery rate compared to Sundaland and oceanic islands (Fig. 2; Brown and Stuart 2012). Brown and Stuart (2012) suggested numerous explanations for this phenomenon. Amongst

them, probably the most critical is the more intensive sampling efforts performed in the

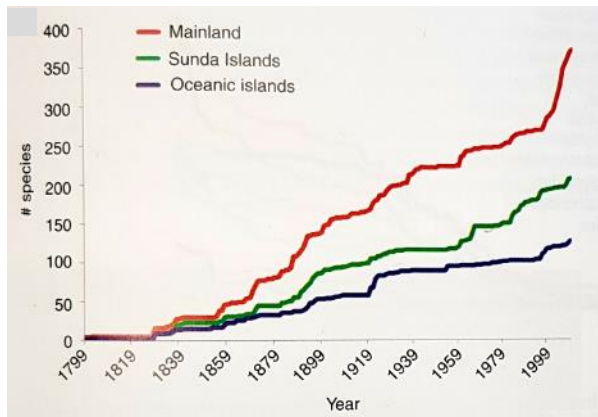


Figure 2 Species accumulation curves of Southeast Asian Amphibian descriptions in Asia mainland, Sunda Island, and Oceanic islands (Brown and Stuart 2012).

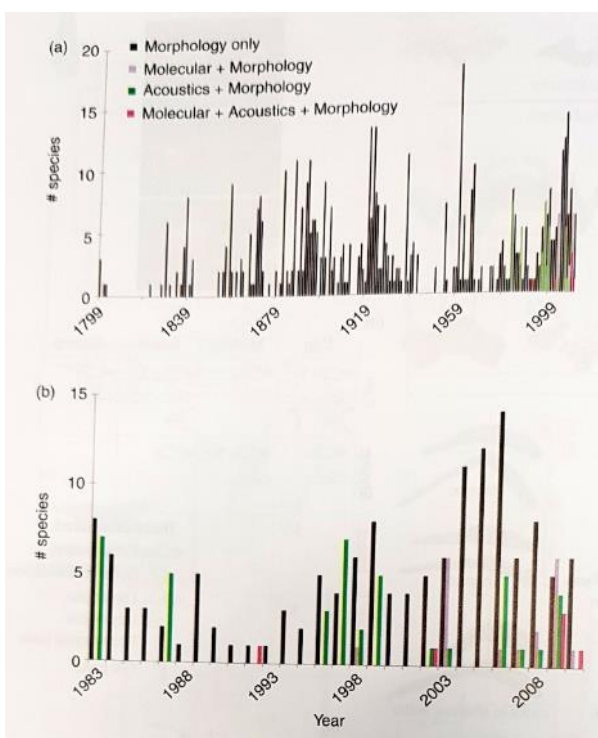


Figure 3 Number of amphibian species in Southeast Asia described over the past two centuries (a) and the expansion of described species with more than one data type. (Brown and Stuart 2012)

mainland (Stuart and Bain 2008) compared to in the Indonesian islands (Brown 2009). Assuming the same relative quantity of hidden diversity in Indonesia and mainland Asia, the species discovery in those regions could potentially increase at the same rate if Indonesia received equal sampling efforts as mainland Asia.

Higher species accumulation in mainland Asia compared to archipelagic or oceanic islands is to some degree due to previously overlooked species diversity (Brown and Stuart 2012). Amphibian species in the tropics often exhibit cryptic morphologies or similar morphological characters (Stuart et al. 2006), and therefore were often treated as a single species with a wide distribution range (Stuart et al. 2006, Bickford et al. 2007). *Chalcorana chalconota* for example, has previously treated as a single species that widely distributed in Southeast Asia until Inger et al. (2009) demonstrated that these frogs comprises at least seven species based on molecular and morphological data. This suggest that integrative taxonomic approaches are the key

to accelerate the number of species discoveries in this region. Integrative taxonomy refers to taxonomic approaches

that integrate all available data sources, such as genetic, morphology, behavior, ecology (Padial et al. 2000, Dayrat 2005, Schlick-Steiner et al. 2010). Previously (over the past 210 years), taxonomic studies for frogs were exclusively based on morphological characters (Brown and Stuart 2012). This approach, however, has limitation in the tropical regions where the diversity of countless of amphibians remain hidden or undiscovered (e.g., Emerson and Iskandar 2000, Elmer et al. 2007, Veites et al. 2009, McLeod 2010, Brown and Stuart 2012, Nishikawa et al. 2012, Guarnizo et al. 2015). Dring (1983, 1987) was one of the first proponents of integrative taxonomy in Southeast Asia. He delimited amphibian species with

morphology and bioacoustics data. Since then, the application of more than one data type (e.g., morphology, molecular, ecology, behavior, bioacoustics) for species description has been widely applied (Fig. 3, Brown and Stuart 2012). As a consequence, the total number of species diversity from the region has accelerated (Joppa et al. 2011, Brown and Stuart 2012). This holds true not only for amphibians, but also other taxa, such as mammals (Gaubert et al. 2005), insects (Gibbs 2009), snails (Walther et al. 2016). However, there is no general consensus on outlining minimum or maximum number of characters that are sufficient to delineate a species. Thus, each particular group of taxa might vary in the number of combined adequate character sets that delimit species (Valdecasas et al. 2008, Padial and De La Riva 2010).

Integrative taxonomy for Southeast Asian reptiles has also produced a considerable increase in species discoveries through time (e.g., Grismer et al. 2013, Loredó et al. 2013, Welton et al. 2014). Numerous reptile species from the Sunda region and mainland Asia have been described continuously over the past two decades, for example: *Amphiesma* from Sumatra David and Das 2003; *Cyrtodactylus* from Sulawesi Hayden et al. 2008; *Cyrtodactylus* from Vietnam Geissler et al. 2009; *Cnemaspis* from Malaysia, Thailand, and Indonesia Grismer et al. 2014; *Cyrtodactylus* from Sumatra Harvey et al. 2015; *Bronchocela* from Malaysia Grismer et al. 2015; *Trimeresurus* from Sumatra Wostl et al. 2016. Interestingly, some reptile species have also been described from regions, such as Singapore that no longer possess pristine forests (see Grismer et al. 2012). This shows that bio-discovery efforts in tropical regions should be undertaken both in unexplored areas as well as well explored areas.

Today molecular approaches often served as a primary tool to delimit species (e.g., Yang and Ranala 2010, Fujita et al. 2012, Puillandre et al. 2012). Molecular phylogenetic analyses are often used as the backbone for taxonomic descriptions (Jörger and Schrödl 2013). Exclusivity criteria (e.g., monophyly or degree of genetic clustering) are a significant consideration in order to determine the status of taxon using this approach (Knowles and Carstens 2007). The molecular approach has been developed constantly to overcome errors in tree reconstruction and tree resolution has improved (Phillipe et al. 2006). Phillipe et al. (2006) suggested that large scale sequencing is inevitably, in order to produce well-resolved phylogenies. To date, the application of the phylogenomic approach in the tropics where speciation of morphologically similar species or cryptic is commonly observed, has become indispensable in addition to dense geographic taxon sampling of a region; yet, other supporting evidence remains an integral part of species delimitation (e.g., ecology, bioacoustics, behavior). Temperate regions are known to have less diversity and generally have been more thoroughly explored compared to the tropics (e.g., Pyron and Wiens 2013). New species discoveries are less likely to happen there. However, even in temperate region, cryptic speciation can be

demonstrated if a broad toolset is applied. For example, Dufresnes et al. (2018) recognized cryptic speciation in Italian tree frogs based on evidence from mitochondrial phylogenetic, nuclear phylogenomics, hybrid zone population genomic, niche modeling analyses, and biometric assessments.

With the advent of next generation sequencing, various phylogenomic methods have become available for solving phylogenetic problems, including identifying species boundaries. A proper and accurate method needs to be carefully selected, in order to effectively solve a particular research question. A recent study (Singhal et al. 2018) proposed a framework for resolving cryptic species by integrating genomic and morphological data with data on hybridization and introgression from contact zones (Fig. 4). Singhal et al. (2018) suggested that some cryptic species lineages might exhibit temporary genetic differentiation and would become lost through hybridization with congeneric lineages. In this scenario, data on hybridization and introgression from a contact zone would become very important in delimiting species, for example in the case of lizards of the Australian Wet Tropics (Singhal et al. 2018).

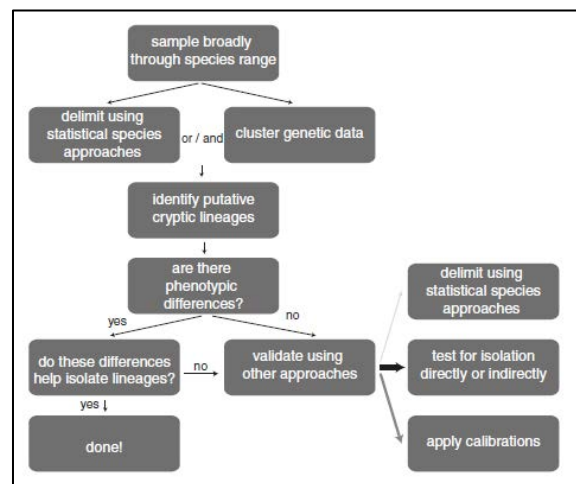


Figure 4 A flowchart outlining a possible research approach to validating cryptic lineages proposed by Singhal et al. (2018)

This raises the question if traditional Sanger sequencing and commonly used species delimitation methods in the long term are less effective than phylogenomic methods to solve cryptic species problems, especially in tropical regions. Chan et al. (2017) demonstrated in *Amolops* populations from Malaysia that both genomic and commonly used species delimitation methods are effective in assessing lineage separation, with consideration on the presence-absence of gene flow in the population. Chan et al. (2017) suggested that lineage independence is the only necessary property of a species. According to these authors, species delimitation frameworks should strictly focus on assessing lineage separation and/or cohesion.

In my study, traditional Sanger sequencing has successfully resolved some of the phylogenetic problems of Sumatran Cascade Frogs and delimited frog species with substantial morphological similarity on Sumatra with strong evidence (*Sumaterana*, Chapter 2). Parts of the clade comprising *Sumaterana*, *Huia*, *Meristogenys*, and *Clinotarsus*, however, had low support values and unstable sister group relationships. Furthermore, the old problem of *Huia* paraphyly was not resolved by my analyses. Similar result were obtained in previous studies for *Huia*, *Meristogenys*, and *Clinotarsus* (Stuart 2008, Wiens 2009, Pyron and Wiens 2011). The phylogenomic methods and/ or the framework proposed by Chan et al. (2017) and Singhal

et al. (2018) appear to be a proper means to address these open problems and to disentangle phylogenetic problems within this group of frogs. Furthermore, current evidence concerning amphibian diversity and distribution should probably be revisited with these new approaches (Dufresnes 2018).

III Biogeography and diversification patterns of Sumatran amphibians

The ecoregions with the highest species richness span along the equator (Das and Paul Van Dijk 2013), and this is also true for amphibians (Pyron and Wiens 2013), possibly because of tropical rainforests, aseasonal climate, high precipitation, and complex vegetation. Structural complexity and climatic conditions have created high levels of species richness in lowland and low elevation rainforests (Das and Paul Van Dijk 2013). Furthermore, Pyron and Wiens (2013) demonstrated that in tropical regions the speciation rate (for amphibians) is much higher than the extinction rate, whereas the opposite patterns were observed in temperate regions. In the tropics, mountain regions provide a wide variety of life supporting environments that have been continuously available through climatic alteration. As a consequence, newly formed species in the tropics have more opportunities to survive over geologic time compare species in temperate regions (Hewitt 2000). Limited dispersal from the tropics to temperate regions concentrates diversity in the tropics (Pyron and Wiens 2013).

Sumatra lies on the equator with topographically diverse and rich distinct habitats being found across the island (van Schaik and Mirmanto 1985, Whitten et al. 2000). High levels of species diversity and endemism on the island have been predicted (e.g., Roos et al. 2004, Muchlisin and Azizah 2009), including amphibians (e.g., Teynie et al. 2010). The number of species per island is calculated as a function of area (size of the island) and number of available habitat on the island (Kohn and Walsh 1994). Based on this hypothesized, the total of 104 amphibian species that have been recorded to date for the island of Sumatra (Frost 2018) is relatively low for the size of the island (approximately 473,481 km²; see Simberloff 1976, MacArthur and Wilson 2001, Kier et al. 2009). Java has 81 amphibian species and Borneo has 198 species (Frost 2018), although the sizes of these islands are approximately one third and more than twice that of Sumatra, respectively.

The proportion of endemic species of amphibians on Sumatra is very low (25.6%) compared to Java (34.3%) or Borneo (62.4%; Frost 2018). Among endemic species on Sumatra, the number of micro-endemics (found only in a small region or narrow distribution range of the island [see Caesar et al. 2017], such as *Chalcorana parvaccola*, *Chiromantis baladika*, *Sigalegalephrynus minangkabauensis*, *Sumaterana dabulescens*, is higher than the number of island endemics (observed across Sumatra, such as *S. crassiovis*, *Huia sumatrana*, *Rhacophorus catamitus*). Apart from endemic species, numerous amphibian species on

Sumatra are also observed in the neighboring islands of Borneo, Java, and the Malay Peninsula (mainland Asia; Table 2), implying there was a connection within these landmasses.

This pattern is also shown in Sumatran reptiles. The Reptiles Database (Uetz et al. 2018) has recorded a total of 275 species of reptiles from Sumatra. This number is only 68 species more than on Java and 35 species less than on Borneo, respectively (Uetz et al. 2018). Its endemism is also considerably lower compared to the two neighboring islands (approximately 22.1%), which is less than that of anurans. Wilting et al. (2012) suggested that in the past century Sumatra experienced more local extinction than Borneo and other regions. In contrast, mammals and birds show higher numbers of endemism on Sumatra compared to Java, although considerably lower than on Borneo (Natus 2005). Natus (2005) hypothesized that Sumatran mammalian endemics evolved from an earlier migration of species from Java and became isolated on Sumatra. Due to long period of isolation, the islands off the western coast of Sumatra have more bird endemics compared to the islands off the eastern coast. This has contributed to the total number of endemism on Sumatra as a whole (Natus 2005). It has been hypothesized that distribution patterns including the number of endemics in the Sunda region have been influenced significantly by multiple land connections and multiple periods of isolations due to sea level changes (Lohman et al. 2011, Morley 2012, de Bruyn et al. 2013). Land connections served as land bridges that allowed for faunal exchange among the Sunda islands (e.g., Heaney 1986, Lohman et al. 2011). The number of colonization, extinction, and speciation of the species on the island are significantly correlated with isolation of each island (Heaney 1986).

Table 2 Example of amphibian species that occur both on Sumatra and its neighboring islands (Frost 2018, accessed in November 2018). Star (*) indicated provisional distribution.

Geographical range	Species
Sumatra+Java	<i>Chalcorana chalconota</i> , <i>Ingerophrynus biporcatus</i> , <i>Kalophrynus minusculus</i> , <i>Limnonectes macrodon</i> , <i>Microhyla palmipes</i> , <i>Polypedates pseudotilopus</i> *
Sumatra+Borneo	<i>Occidozyga baluensis</i> , <i>Phrynomis juxtasper</i> , <i>Philautus kerangae</i> , <i>Philautus refugii</i> , <i>Rhacophorus angulirostris</i>
Sumatra+the Malay Peninsula	<i>Limnonectes khasianus</i> , <i>Microhyla heymonsi</i> , <i>Microhyla inomata</i> , <i>Microhyla superciliaris</i> , <i>Pulchrana centropeninsularis</i> , <i>Phrynomis pulchra</i> , <i>Rhacophorus norhayati</i> *, <i>Theioderma leporosum</i> ,
Sumatra+Borneo+the Malay Peninsula	<i>Amnirana nicobariensis</i> , <i>Ansonia leptopus</i> , <i>Ichthyophis nigroflavus</i> , <i>Ingerophrynus divergens</i> , <i>Ingerophrynus quadriporcatus</i> , <i>Kaloula pulchra</i> , <i>Kurixalus appendiculatus</i> , <i>Leptobrachium hendricksoni</i> , <i>Limnonectes blythii</i> , <i>Megophrys nasuta</i> , <i>Microhyla berdmorei</i> , <i>Nyctixalus pictus</i> , <i>Odorrana hosii</i> , <i>Pelophryne signata</i> *, <i>Philautus larutensis</i> , <i>Polypedates colletti</i> , <i>Polypedates macrotis</i> , <i>Phrynomis asper</i> , <i>Pseudobufo subasper</i> , <i>Pulchrana glandulosa</i> , <i>Pulchrana signata</i> , <i>Rhacophorus pardalis</i> , <i>Rhacophorus nigropalmatus</i> , <i>Theioderma asperum</i> *
Sumatra+Java+Borneo	<i>Leptobrachium hasseltii</i> , <i>Polypedates leucomystax</i> ,
Sumatra+Java+the Malay Peninsula	<i>Ingerophrynus parvus</i>
Sumatra+Java+Borneo+the Malay Peninsula (mainland)	<i>Duttaphrynus melanostictus</i> , <i>Fejervarya cancrivora</i> , <i>Hylarana erythraea</i> , <i>Kalophrynus pleurostigma</i> , <i>Kaloula baleata</i> , <i>Limnonectes malesianus</i> , <i>Megophrys montana</i> , <i>Occidozyga sumatrana</i> , <i>Pulchrana baramica</i> ,

In the period of the Last Glaciation Maxima (LGM), the sea level was at its lowest (120 m below present day) and therefore major parts of the Sundaland were exposed (Cannon et al. 2009). The climate was considerably cooler and drier than before (Morley 2012). The major event during this time was the formation of a Paleo-drainage systems across Sundaland (Voris 2000, Sathiamurthy and Voris 2006). These Pleistocene drainage systems had impact on biodiversity patterns in the region in that they potentially served as multiple bridges or dispersal routes between the Greater Sunda Islands (Voris 2000, Sathiamurthy and Voris 2006). The freshwater riverine faunas of many of today's rivers were connected to different river systems within the Greater Sunda Islands in the Pleistocene but are at present separated by sea (Parenti 1991, Zakaria-Ismail 1994, Voris 2000, Sathiamurthy and Voris 2006, de Bruyn et al. 2013).

According to this river-as-bridge hypotheses, the Pleistocene drainage systems is suggested to have played a role in the diversification patterns of the freshwater fauna in Sundaland. The Mekong mud snakes (Lukoschek et al. 2011) and freshwater fishes (de Bruyn et al. 2013) were two taxa that have demonstrated diversification patterns that have been significantly influenced by the Pleistocene drainage systems. Genetic variance of both taxa was strongly partitioned geographically, in accordance to the Sundaland drainage systems. However, this was not the case for frogs with gastromyzophorous tadpoles in the present study (see Chapter 4). Frogs with abdominal sucker tadpoles are highly dependent on cascading stream habitats but show no congruence with the Paleo-river systems on their patterns of distribution.

The most parsimonious scenarios to explain this pattern is that *Huia* and *Sumaterana* diversified on Sumatra much earlier than the occurrence of the Paleo-drainage systems in the Pleistocene (Chapter 4). Molecular clock analyses estimate the most recent common ancestor (MRCA) of *Huia* and *Sumaterana* had first colonized the island of Sumatra during Mid-Late Oligocene (27.65 Ma and 25.11 Ma, respectively; see Chapter 4). In the Late Oligocene, the sea level experienced deep drops, approximately 250 m below present sea level (Monk et al. 1997). Thus, much of Sundaland was terrestrial, including major parts of Sumatra and the western part of Java, allowing migration of taxa (Hall 2012, 2013). Furthermore, ancestral area analyses in this study suggested the MRCA of *Huia* reached Sumatra from the south, via Lampung province, whereas *Sumaterana* entered the island from the north, via Aceh province (see Chapter 4).

Although my finding demonstrated that distribution patterns of *Huia* and *Sumaterana* were not genetically structured according to the Paleo-drainage systems, my analyses show that both genera were partitioned into northern and southern lineages, with Sumatera Barat province as the border for the two regions (Chapter 4). The distributional patterns has also been reported for three species of Sumatran *Rhacophorus* (O'Connell et al. 2018a-b). O'Connell et al.

(2018a-b) show genetic partitioning between population in the northern (Aceh to Sumatera Barat provinces, approximately the region above Mount Kerinci) and southern region (West Sumatra to Lampung, approximately all region below Mount Kerinci). Whitten et al. (2000) also suggested north-south partition of several mammal species on the island of Sumatra with Lake Toba as the zoogeographic boundary: e.g., Thomas's langur - *Presbytis thomasi* and white-handed gibbon - *Hylobates lar* (north); Horsfield's tarsier - *Tarsius bancanus* and Tapir – *Tapirus indicus* (south). Confirming Whitten et al. (2000), Nater (2011) suggested that major rivers, mountain ridges, and the Toba caldera have influenced population structure of the Sumatran orangutans (*Pongo abelli*). Wilting et al. (2012) speculated this might be related to the recolonization of Sumatra after the super volcanic eruption of Toba. Nevertheless, it needs to be clarified as my finding and O'Connell et al. (2018a-b) show that the border between the northern and southern group was in Sumatera Barat province, but no evidence for precise location, whereas Toba region was claimed to be the border for mammals population (Whitten 2000, Nater 2011). Toba super volcanic eruption took place at approximately 73 ka (Rampino and Self 1992, 1993) and might have influenced the composition of the Sumatran fauna (e.g., extinction and recolonization; Wilting et al. 2012). The divergence time estimation for *Huia* and *Sumaterana* suggested that the two genera have experienced rapid divergence from the Early Pliocene on (Fig. 3 Chapter 4). Thus, the Paleo-climatic and geological events during this period (Morley 2012, Hall 2012, 2013) may have played a major role in the early divergence within these frogs.

IV Significance for conservation

Tropical forests serve as both cradles of biodiversity and promoters of diversification (Acebey et al. 2003; Couvreur et al. 2011). They also offer invaluable life support services, raw natural resources, and cultural necessities that are economically priceless (Costanza et al. 1997, Ferraz et al. 2014). Indonesia, being the third most biodiverse country after Brazil and Colombia (Conservation International 2014), plays an important role in providing those ecosystem services. Unfortunately, deforestation is currently a major issue for biodiversity loss in the country (Sala et al. 2000, Sodhi and Brook 2006, Sodhi et al. 2008), in addition to other factors, such as human population growth, wild fires, overexploitation, invasive species, pollution, and climate change (e.g., Iskandar and Erdelen 2006, Bickford et al. 2012).

Indonesia has experienced an unprecedented loss of primary forest (Margono et al. 2014), which has now surpassed Brazil (PRODES 2018). Between 2000 and 2012, that speed of loss was estimated at a rate of 47,600 ha/year. Within this same period, a staggering 2,857 kha of primary forest loss was recorded in Sumatra, the highest deforestation rate among the five

largest islands in Indonesia. Approximately 1,205 kha of which was lowland forest (Margono et al., 2014).

Primary forest loss by deforestation or habitat degradation is the paramount problem for the remaining tropical forest in Southeast Asia.

Approximately three quarters of pristine forest in Southeast Asia could potentially disappear by the year 2100 (Sodhi et al.

2004, Rowley et al. 2010). As a consequence, about 13–85% of the known species are expected to face extinction by the same year (Bickford et al. 2012). Moreover, numerous species might be extinct before they have been discovered (Giam et al. 2010). This situation is a major biodiversity crisis that warrants immediate conservation actions (Pangau-Adam et al. 2015, Wong et al. 2013). Singapore for instance, has experienced approximately 95% habitats loss over 183 years and consequently at least 28% of its biodiversity was locally extinct (Brook and Sodhi 2003). Conserving Southeast Asian forests is currently of the highest priority (Trainor 2007, Sodhi and Brook 2008); there is no substitute for primary forests when it comes to maintaining tropical biodiversity (Gibson et al. 2011).

Amphibians are one of the most widespread animal groups that can be observed in almost any type of terrestrial ecosystem on every continent except Antarctica (Pyron 2014), with tropical region harbouring most of the species (e.g., Pyron and Wiens 2013). They occupied an important, mid-trophic level position in the ecosystem (see Whiles et al. 2006) and are also very vulnerable taxon (e.g., Foden et al. 2013, Pacifici et al. 2015) to environmental changes, such as deforestation and habitat degradation (Duellman 1999, Zhelev et al. 2013, Correia et al. 2014) in general. Distributional changes, population changes, extinction probability, vulnerability indices and other relative scoring systems are some of the measured criteria used to assess vulnerability of taxa (Pacifici et al. 2015). The majority of amphibians require forested environments and/ or specific water regimens (Bain and Hurley 2004).

While amphibian decline is currently a major issue globally (e.g., Houlahan et al. 2000, Collins and Storer 2003, Beebee et al. 2005, Collins et al. 2009, Ramsey et al. 2010), rapid deforestation could significantly accelerate amphibian decline worldwide, as amphibians are already at a critical stage today (Stuart et al. 2004, Harper et al. 2007, Whittaker et al. 2013). The IUCN (2017) has estimated that 2,067 species of the globally known 6,533 taxa are currently threatened, and it is very troubling that almost 2% of these threatened species are found in Indonesia. Reliable and detailed information concerning the status of most Indonesian amphibians is not available, and the actual number of threatened species is likely much higher.

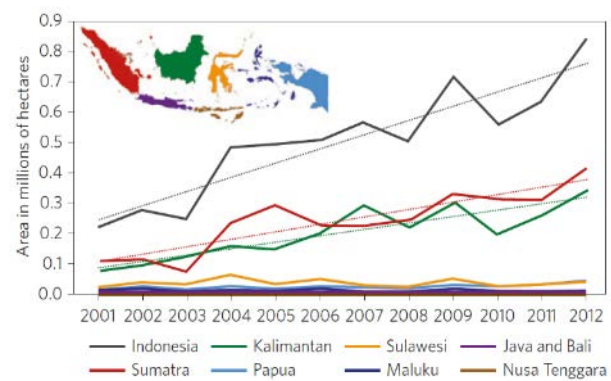


Figure 5 Annual primary forest cover loss for Indonesia during period 2000–2012 (Margono et al. 2014).

Moreover, as has been discussed above, factual information on how many amphibian species actually exist in Indonesia is not available. Today, Frost (2018) lists 7,935 species of amphibian worldwide. Chapman (2009), however, estimated that up to 15,000 species of extant amphibians' might exist. That would mean that our current species inventory represents only about 67% of the total species number (Scheffers et al. 2012). Documenting species diversity of amphibians and their distribution patterns (e.g., Chapter 2 and 3 of this study, Inger et al. 2009, McLeod et al. 2011, Wostl et al. 2017), are prerequisites for conservation. In other words, with regard to the biodiversity crisis to date, accurate taxonomy and diversity estimates for amphibians will become increasingly important (Brown and Stuart 2012). As a consequence, conservation management strategies for each taxa in the region need to carry out appropriate planning (Rowley et al. 2010, Brown and Stuart 2012).

More studies are urgently needed that uncover species diversity of anurans in Southeast Asia. Discovering unknown species, as well as rediscovering known species that reported as extinct species (Ladle et al. 2011, Scheffers et al. 2011), will help to underline the remarkable biological diversity and uniqueness of each species (Scheffers et al. 2012). A better understanding of amphibian communities would generate important input to conservation strategies, e.g., which location should be protected, how big is the area, what strategic action should be taken (Scheffers et al. 2012). Basic information concerning species diversity and distribution across particular geographical regions, including species richness, endemism, and similarity of fauna among sites can be analyzed to determine priority areas for conservation (Azevedo-Ramos and Galatti 2002). According to my study, for example, due to its restricted distribution range, *Sumaterana dabulescens* should receive conservation priority compared to *S. montana* and *S. crassiovis*. Other than this, Aceh province should be prioritized as conservation area because it has more diversity (e.g., the three species of *Sumaterana* can be found in Aceh) than other regions and the forest is threatened by deforestation due to palm oil field expansions.

References

- Acebey A, Gradstein SR, Krömer T (2003) Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *Journal of tropical ecology*, 19(1), 9–18.
- Arifin U, Smart U, Hertwig ST, Smith EN, Iskandar DT, Haas A (2018a) Molecular phylogenetic analysis of a taxonomically unstable ranid from Sumatra, Indonesia, reveals a new genus with gastromyzophorous tadpoles and two new species. *Zoosystematics and Evolution*, 94, 163–193.

- Arifin U, Cahyadi G, Smart U, Jankowski A, Haas A (2018b) A new species of the genus *Pulchrana* Dubois, 1992 (Amphibia: Ranidae) from Sumatra, Indonesia. *Raffles Bulletin of Zoology*, 66, 277–299.
- Azevedo-Ramos C, Galatti U (2002) Patterns of amphibian diversity in Brazilian Amazonia: conservation implications. *Biological Conservation*, 103(1), 103–111.
- Bain RH, Lathrop A, Murphy RW, Orlov NL, Cuc HT (2003) Cryptic species of a cascade frog from Southeast Asia: taxonomic revisions and descriptions of six new species. *American Museum Novitates*, 1–60.
- Bain RH, Hurley MM (2011) A biogeographic synthesis of the amphibians and reptiles of Indochina. *Bulletin of the American Museum of Natural History*, 1–138.
- Barker FK, Cibois A, Schikler P, Feinstein J, Cracraft J (2004) Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences*, 101(30), 11040–11045.
- Beebee TJ, Griffiths RA (2005) The amphibian decline crisis: a watershed for conservation biology?. *Biological conservation*, 125(3), 271–285.
- Bickford D, Lohman DJ, Sodh, NS, Ng PK, Meier R, Winker K, Ingram KK, Das I (2007) Cryptic species as a window on diversity and conservation. *Trends in ecology & evolution*, 22(3), 148–155.
- Bickford DP, Poo S, Posa MRC (2012) Southeast Asian biodiversity crisis. *Biotic Evolution and Environmental Change in Southeast Asia*, 79–114.
- Bihari M, Lal CB (1989) Species composition, density and basal cover of tropical rainforests of central Sumatra. *Tropical Ecology* 30(1): 118–137.
- Brook BW, Sodhi NS, Ng PK (2003) Catastrophic extinctions follow deforestation in Singapore. *Nature*, 424(6947), 420–423.
- Brown RM (2009) *Frogs*. *Encyclopedia of Islands*. University of California Press, Berkeley, 347–351.
- Brown RM, Stuart BL (2012) Patterns of biodiversity discovery through time: an historical analysis of amphibian species discoveries in the Southeast Asian mainland and island archipelagos. *Biotic evolution and environmental change in Southeast Asia*, 348–389.
- Caesar M, Grandcolas P, Pellens R (2017) Outstanding micro-endemism in New Caledonia: More than one out of ten animal species have a very restricted distribution range. *PloS one*, 12(7), e0181437.

- Cannon CH, Morley RJ, Bush AB (2009) The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance. *Proceedings of the National Academy of Sciences*, 106(27), 11188–11193.
- Chan KO, Alexander AM, Grismer LL, Su YC, Grismer JL, Quah ES, Brown RM (2017) Species delimitation with gene flow: A methodological comparison and population genomics approach to elucidate cryptic species boundaries in Malaysian Torrent Frogs. *Molecular ecology*, 26(20), 5435–5450.
- Chan KO, Abraham RK, Grismer JL, Grismer L (2018) Elevational size variation and two new species of torrent frogs from Peninsular Malaysia (Anura: Ranidae: *Amolops* Cope). *Zootaxa*, 4434(2), 250–264.
- Chapman AD (2009) Numbers of living species in Australia and the world.
- Conservation International (2018) Biodiversity hotspots regions. (Accessed on November 2018)
- Costanza R, d'Arge R, De Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The value of the world's ecosystem services and natural capital. *Nature*, 387(6630), 253.
- Collins JP, Storfer A (2003) Global amphibian declines: sorting the hypotheses. *Diversity and distributions*, 9(2), 89–98.
- Collins JP, Crump ML, Lovejoy III TE (2009) *Extinction in our times: global amphibian decline*. Oxford University Press.
- Correia LO, Siqueira S, Carneiro PLS, Bezerra MA (2014) Evaluation of the use of *Leptodactylus ocellatus* (Anura: Leptodactylidae) frog tissues as bioindicator of metal contamination in Contas River, Northeastern Brazil. *Anais Da Academia Brasileira De Ciencias*, 86(4), 1549–1561. DOI: 10.1590/0001-3765201420130357.
- Couvreur TL, Forest F, Baker WJ (2011) Origin and global diversification patterns of tropical rain forests: inferences from a complete genus-level phylogeny of palms. *BMC biology*, 9(1), 44.
- Das I, van Dijk PP (2013) Species richness and endemism of the herpetofauna of South and Southeast Asia. *Raffles Bulletin of Zoology*, 29, 289–277.
- David P, Das I (2003) A new species of the snake genus *Amphiesma* (Serpentes: Colubridae: Natricinae) from western Sumatra, Indonesia. *Raffles Bulletin of Zoology*, 51(2), 413–420.
- Dayrat B (2005) Towards integrative taxonomy. *Biological journal of the Linnean society*, 85(3), 407–417.

- De Bruyn M, Rüber L, Nylinder S, Stelbrink B, Lovejoy NR, Lavoué S, Tan HH, Nugroho E, Wowor D, Ng PKL, Siti Azizah MN, Rintelen TV, Hall R, Carvalho G (2013). Paleo-drainage basin connectivity predicts evolutionary relationships across three Southeast Asian biodiversity hotspots. *Systematic Biology*, 62(3), 398–410.
- Dring J (1983) Some new frogs from Sarawak. *Amphibia-Reptilia*, 4(2), 103–115.
- Dring J (1987) Bornean treefrogs of the genus *Philautus* (Rhacophoridae). *Amphibia-Reptilia*, 8(1), 19–47.
- Duellman WE (1999) Global distribution of amphibians: patterns, conservation, and future challenges (pp. 1–30). Johns Hopkins University Press, Baltimore, MD, USA.
- Dufresnes C (2018) Patterns of amphibian diversity in the Western Palearctic. Short Note. *The Herpetological Bulletin* 145, 28–30.
- Dufresnes C, Mazepa G, Rodrigues N, Brelsford A, Litvinchuk SN, Sermier R, Lavanchy G, Betto-Colliard C, Blaser O, Borzée A, Cavoto E, Fabre G, Ghali K, Grossen C, Horn A, Leuenberger J, Phillips BC, Saunders PA, Savary R, Maddalena T, Stöck M, Dubey S, Canestrelli D and Jeffries DL (2018) Genomic evidence for cryptic speciation in tree frogs from the Apennine Peninsula, with description of *Hyla perrini* sp. nov. *Frontiers in Ecology and Evolution*, 6:144. doi: 10.3389/fevo.2018.00144.
- Elmer KR, Dávila JA, Lougheed SC (2007) Cryptic diversity and deep divergence in an upper Amazonian leaf litter frog, *Eleutherodactylus ockendeni*. *BMC Evolutionary Biology*, 7(1), 247.
- Emerson SB, Inger RF, Iskandar D (2000) Molecular systematics and biogeography of the fanged frogs of Southeast Asia. *Molecular Phylogenetics and Evolution*, 16(1), 131–142.
- Ferraz SF, Ferraz KM, Cassiano CC, Brancalion PHS, da Luz DT, Azevedo TN, Tambosi LR, Metzger JP (2014) How good are tropical forest patches for ecosystem services provisioning?. *Landscape ecology*, 29(2), 187–200.
- Foden WB, Butchart SH, Stuart SN, Vié JC, Akçakaya HR, Angulo A, Donner SD, Katariya V, Bernard R, Holland RA, Hughes AF, O'Hanlon SE, Garnett ST, Şekercioğlu ÇH, Mace GM (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PloS one*, 8(6), e65427.
- Fujita, M K, Leaché, A D, Burbrink, F T, McGuire, J A, & Moritz, C (2012) Coalescent-based species delimitation in an integrative taxonomy. *Trends in ecology & evolution*, 27(9), 480–488.

- Frost DR (2018). Amphibian Species of the World: an Online Reference. Version 6.0 (Accessed on November 2018). Electronic Database accessible at <http://research.amnh.org/herpetology/amphibia/index.html>. American Museum of Natural History, New York, USA.
- Gaubert P, Taylor PJ, Veron G (2005) Integrative taxonomy and phylogenetic systematics of the genets (Carnivora, Viverridae, Genetta): a new classification of the most speciose carnivoran genus in Africa. In African Biodiversity (pp. 371–383). Springer, Boston, MA.
- Gan L, Hertwig ST, Das I, Haas A (2015) The anatomy and structural connectivity of the abdominal sucker in the tadpoles of *Huia cavitympanum*, with comparisons to *Meristogenys jerboa* (Lissamphibia: Anura: Ranidae). *Journal of Zoological Systematics and Evolutionary Research* 54(1): 1–14.
- Geissler P, Nazarov R, Orlov NL, Boehme W, Phung TM, Nguyen Q, Ziegler T (2009) A new species of the *Cyrtodactylus irregularis* complex (Squamata: Gekkonidae) from southern Vietnam. *Zootaxa*, 2161(1), 20–32.
- Giam X, Ng TH, Yap VB, Tan HT (2010) The extent of undiscovered species in Southeast Asia. *Biodiversity and Conservation*, 19(4), 943–954.
- Gibbs J (2009) Integrative taxonomy identifies new (and old) species in the *Lasioglossum* (*Dialictus*) *tegulare* (Robertson) species group (Hymenoptera, Halictidae). *Zootaxa*, 2032, 1–38.
- Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE, Sodhi NS (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478(7369), 378.
- Grismer LL, Wood Jr PL, Lim KK (2012) *Cyrtodactylus majulah*, a new species of bent-toed gecko (Reptilia: Squamata: Gekkonidae) from Singapore and the Riau Archipelago. *The Raffles Bulletin of Zoology*, 60(2), 487–499.
- Grismer LL, Wood Jr PL, Anuar S, Muin MA, Quah ES, McGuire JA, Brown RM, Tri NV, Hong Thai P (2013) Integrative taxonomy uncovers high levels of cryptic species diversity in *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) and the description of a new species from Peninsular Malaysia. *Zoological Journal of the Linnean Society*, 169(4), 849–880.
- Grismer LL, Wood PJJ, Anuar S, Riyanto A, Ahmad N, Muin MA, Sumontha M, Grismer JJ, Chan KO, Quah ESH, Pauwels OS (2014) Systematics and natural history of Southeast

- Asian Rock Geckos (genus *Cnemaspis* Strauch, 1887) with descriptions of eight new species from Malaysia, Thailand, and Indonesia. *Zootaxa*, 3880(1), 1–147.
- Grismer LL, Wood Jr PL, Lee CH, Quah ES, Anuar S, Ngadi E, Sites Jr JW (2015) An integrative taxonomic review of the agamid genus *Bronchocela* (Kuhl, 1820) from Peninsular Malaysia with descriptions of new montane and insular endemics. *Zootaxa*, 3948(1), 1–23.
- Guarnizo CE, Paz A, Muñoz-Ortiz A, Flechas SV, Méndez-Narváez J, Crawford AJ (2015) DNA barcoding survey of anurans across the Eastern Cordillera of Colombia and the impact of the Andes on cryptic diversity. *PLoS One*, 10(5), e0127312.
- Hall R (2012) Sundaland and Wallacea: geology, plate tectonics and palaeogeography. *Biotic evolution and environmental change in Southeast Asia*, 32–78.
- Hall R (2013) The palaeogeography of Sundaland and Wallacea since the Late Jurassic. *Journal of Limnology*, 72(s2), 1.
- Harper GJ, Steininger MK, Tucker CJ, Juhn D, Hawkins F (2007) Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental conservation*, 34(4), 325–333.
- Harvey MB, O'Connell KA, Barraza G, Riyanto A, Kurniawan N, Smith EN (2015) Two new species of *Cyrtodactylus* (Squamata: Gekkonidae) from the Southern Bukit Barisan Range of Sumatra and an estimation of their phylogeny. *Zootaxa*, 4020(3), 495–516.
- Hayden CJ, Brown RM, Gillespie G, Setiadi IM, Linkem CW, Iskandar DT, Umilaela, Bickford DP, Riyanto A, Mumpuni, McGuire JA (2008) A new species of bent-toed gecko *Cyrtodactylus* Gray, 1827, (Squamata: Gekkonidae) from the island of Sulawesi, Indonesia. *Herpetologica*, 64(1), 109–120.
- Heaney LR (1986) Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. *Biological journal of the Linnean Society*, 28(1–2), 127–165.
- Hewitt G (2000) The genetic legacy of the Quaternary ice ages. *Nature*, 405(6789), 907.
- Houlahan JE, Findlay CS, Schmidt BR, Meyer AH, Kuzmin SL (2000) Quantitative evidence for global amphibian population declines. *Nature*, 404(6779), 752.
- Inger RF, Stuart BL, Iskandar DT (2009) Systematics of a widespread Southeast Asian frog, *Rana chalconota* (Amphibia: Anura: Ranidae). *Zoological Journal of the Linnean Society*, 155(1), 123–147.

- Iskandar DT, Colijn E (2000) Preliminary Checklist of Southeast Asian and New Guinean Herpetofauna: Amphibians. I. Research and Development Centre for Biology, Indonesian Institute of Sciences.
- Iskandar DT, Erdelen WR (2006) Conservation of amphibians and reptiles in Indonesia: issues and problems. *Amphibian and reptile Conservation*, 4(1), 60-87.
- IUCN (2017) IUCN Red List of Threatened Species, Version 2017.1. www.iucnredlist.org. (Accessed 1 June 2017)
- Jiang K, Wang K, Yan F, Xie J, Zou DH, Liu WL, Jiang JP, Che J (2016) A new species of the genus *Amolops* (Amphibia: Ranidae) from southeastern Tibet, China. *Zoological Research*, 37(1), 31.
- Joppa LN, Roberts DL, Myers N, Pimm SL (2011) Biodiversity hotspots house most undiscovered plant species. *Proceedings of the National Academy of Sciences*, 108(32), 13171–13176.
- Jörger KM, Schrödl M (2013) How to describe a cryptic species? Practical challenges of molecular taxonomy. *Frontiers in zoology*, 10(1), 59.
- Kelly CM, Barker NP, Villet MH, Broadley DG (2009) Phylogeny, biogeography and classification of the snake superfamily Elapoidea: a rapid radiation in the late Eocene. *Cladistics*, 25(1), 38–63.
- Kier G, Kreft H, Lee TM, Jetz W, Ibisch PL, Nowicki C, Mutke J, Barthlott W (2009) A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences*, 106(23), 9322–9327.
- Knowles LL, Carstens BC (2007) Delimiting species without monophyletic gene trees. *Systematic biology*, 56(6), 887–895.
- Kohn DD, Walsh DM (1994) Plant species richness--the effect of island size and habitat diversity. *Journal of Ecology*, 367–377.
- Kurabayashi A, Yoshikawa N, Sato N, Hayashi Y, Oumi S, Fujii T, Sumida M (2010) Complete mitochondrial DNA sequence of the endangered frog *Odorrana ishikawae* (family Ranidae) and unexpected diversity of mt gene arrangements in ranids. *Molecular Phylogenetics and Evolution* 56(2): 543–553.
- Kurniati H (2009) Morphological variations of Sumatran torrent frogs, *Huia sumatrana* (Yang, 1991) and *H. modiglianii* Doria, Salvidio and Tavan, 1999. *Zoo Indonesia*, 18(1), 9–20.

- Ladle R, Jepson P, Malhado A, Jennings S, Barua M (2011) Perspective: the causes and biogeographical significance of species' rediscovery. *Frontiers of Biogeography*, 3(3).
- Lohman DJ, de Bruyn M, Page T, von Rintelen K, Hall R, Ng PK, Shih HAT, Carvalho GR, von Rintelen T (2011) Biogeography of the Indo-Australian archipelago. *Annual Review of Ecology, Evolution, and Systematics*, 42.
- Loredo AI, Wood Jr PL, Quah ES, Anuar SH, Greer L, Norhayati A, Grismer LL (2013) Cryptic speciation within *Asthenodipsas vertebralis* (Boulenger, 1900)(Squamata: Pareasidae), the description of a new species from Peninsular Malaysia, and the resurrection of *A. tropidonotus* (Lidth de Jude, 1923) from Sumatra: an integrative taxonomic analysis. *Zootaxa*, 3664(4), 505–524.
- Liu W, Yang D, Ferraris C, Matsui M (2000) *Amolops bellulus*: A new species of stream-breeding frog from western Yunnan, China (Anura: Ranidae). *Copeia*, 2000(2), 536–541.
- Lukoschek V, Osterhage JL, Karns DR, Murphy JC, Voris HK (2011) Phylogeography of the Mekong mud snake (*Enhydris subtaeniata*): the biogeographic importance of dynamic river drainages and fluctuating sea levels for semiaquatic taxa in Indochina. *Ecology and evolution*, 1(3), 330–342.
- MacArthur RH, Wilson EO (2001) *The theory of island biogeography* (Vol. 1). Princeton University Press.
- Manthey U, Denzer W (2014) Südostasiatische Anuren im Fokus Spezies der Gattung *Huia* (sensu lato) Yang, 1991 (Amphibia: Anura: Ranidae). *Sauria* 36(4): 31–48.
- Margono, BA, Potapov, PV, Turubanova, S, Stolle, F and Hansen, MC (2014) Primary forest cover loss in Indonesia over 2000-2012. *Nature Climate Change*, 4(8), 730–735.
- Matsui M, Nabhitabhata J (2006) A new species of *Amolops* from Thailand (Amphibia, Anura, Ranidae). *Zoological science*, 23(8), 727–732.
- McLeod DS (2010) Of least concern? Systematics of a cryptic species complex: *Limnonectes kuhlii* (Amphibia: Anura: Dicroglossidae). *Molecular Phylogenetics and Evolution*, 56(3), 991–1000.
- McLeod DS, Horner SJ, Husted C, Barley A, Iskandar DT (2011) Same-same, but different": an unusual new species of the *Limnonectes kuhlii* complex from West Sumatra (Anura: Dicroglossidae). *Zootaxa*, 2883(1), 52–64.
- Morley RJ (2012) A review of the Cenozoic palaeoclimate history of Southeast Asia. In *Biotic Evolution and Environmental Change in Southeast Asia*, eds DJ Gower et al. The Systematic Association, Cambridge University Press, pp.79–114.

- Monk KA, de Fretes Y, Reksoduharjo-Lilley G (1997) The ecology of Nusa Tenggara and Maluku. Oxford University Press. Oxford.
- Muchlisin ZA, Azizah S (2009) Diversity and distribution of freshwater fishes in Aceh waters, northern Sumatra Indonesia. *International Journal of Zoological Research*, 5(2), 62–79.
- Nater A, Nietlisbach P, Arora N, van Schaik CP, van Noordwijk MA, Willems EP, Singleton I, Wich SA, Goossens B, Warren KS, Verschoor EJ, Persitasari-Farajallah D, Pamungkas J, Krützen M (2011) Sex-biased dispersal and volcanic activities shaped phylogeographic patterns of extant orangutans (genus: *Pongo*). *Molecular Biology and Evolution*, 28(8), 2275–2288.
- Natus IR (2005) Biodiversity and endemic centres of Indonesian terrestrial vertebrates. PhD Thesis, University of Trier, Germany.
- Nishikawa K, Matsui M, Yong HS, Ahmad N, Yambun P, Belabut DM, Sudin A, Hamidy A, Orlov NL, Ota H, Yoshikawa N, Tominaga A, Shimada T (2012) Molecular phylogeny and biogeography of caecilians from Southeast Asia (Amphibia, Gymnophiona, Ichthyophiidae), with special reference to high cryptic species diversity in Sundaland. *Molecular Phylogenetics and Evolution*, 63(3), 714–723.
- Noble GK (1929) The adaptive modifications of the arboreal tadpoles of *Hoplophryne* and the torrent tadpoles of *Staurois*. *Bulletin American Museum of Natural History* 58: 291–334.
- O'Connell KA, Smith EN, Shaney KJ, Arifin U, Kurniawan N, Sidik I, Fujita MK (2018a) Coalescent species delimitation of a Sumatran parachuting frog. *Zoologica Scripta*, 47(1), 33–43.
- O'Connell KA, Hamidy A, Kurniawan N, Smith EN, Fujita MK (2018b) Synchronous diversification of parachuting frogs (Genus *Rhacophorus*) on Sumatra and Java. *Molecular phylogenetics and evolution*, 123, 101–112.
- Orlov N L, Le Nguyen N, Ho TC (2003) A new species of cascade frog from North Vietnam (Ranidae, Anura). *Russian Journal of Herpetology*, 10(2), 123–134.
- Pacifici M, Foden WB, Visconti P, Watson JE, Butchart SH, Kovacs KM, Scheffers BR, Hole DG, Martin TG, Akcakaya HR, Corlett RT, Huntley B, Bickford D, Carr JA, Hoffmann AA, Midgley GF, Kelly PP, Pearson RG, Williams SE, Willis SG, Young B, Rondinini C (2015) Assessing species vulnerability to climate change. *Nature climate change*, 5(3), 215.
- Padial JM, Miralles A, De la Riva I, Vences M (2010) The integrative future of taxonomy. *Frontiers in Zoology* 7(16): 1–14. <https://doi.org/10.1186/1742-9994-7-16>.

- Padial JM, De La Riva I (2010) A response to recent proposals for integrative taxonomy. *Biol Journal of Linnaean Society*, 101(3):747–756.
- Pangau-Adam M, Mühlenberg M, Waltert M (2015) Rainforest disturbance affects population density of the northern cassowary *Casuarius unappendiculatus* in Papua, Indonesia. *Oryx*, 49(04), 735–742.
- Parenti LR (1991) Ocean basins and the biogeography of freshwater fishes. *Australian Systematic Botany*, 4(1), 137–149.
- Philippe H, Telford MJ (2006) Large-scale sequencing and the new animal phylogeny. *Trends in Ecology & Evolution*, 21(11), 614–620.
- PRODES (Monitoramento da floresta amazonica Brasileira por satellite) (2018) INPE-Instituto Nacional de Pesquisas Espaciais. Available from <http://www.obt.inpe.br/prodes/index.php>. Accessed on October 2018.
- Puillandre N, Lambert A, Brouillet S, Achaz G (2012) ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology*, 21(8), 1864–1877.
- Pyron RA, Wiens JJ (2011) A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution*, 61(2), 543–583.
- Pyron RA, Wiens JJ (2013) Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. *Proceeding of the Royal Society B* 280: 20131622. <http://dx.doi.org/10.1098/rspb.2013.1622>
- Pyron RA (2014) Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians. *Systematic Biology*, 63(5), 779–797.
- Rampino MR, Self S (1992) Volcanic winter and accelerated glaciation following the Toba super-eruption. *Nature*, 359(6390), 50.
- Rampino MR, Self S (1993) Climate-volcanism feedback and the Toba eruption of ~ 74,000 years ago. *Quaternary Research*, 40(3), 269–280.
- Ramsey JP, Reinert LK, Harper LK, Woodhams DC, Rollins-Smith LA (2010) Immune defenses against *Batrachochytrium dendrobatidis*, a fungus linked to global amphibian declines, in the South African clawed frog, *Xenopus laevis*. *Infection and Immunity*, 78(9), 3981–3992.

- Roelant K, Gower DJ, Wilkinson M, Loader SP, Biju SD, Guillaume K, Moriau L, Bossuyt F (2007) Global patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences*, 104(3), 887–892.
- Roos MC, Keßler PJ, Robbert Gradstein S, Baas P (2004) Species diversity and endemism of five major Malesian islands: diversity–area relationships. *Journal of Biogeography*, 31(12), 1893–1908.
- Rowley J, Brown R, Bain R, Kusriani, M Inger R, Stuart B, Wogan G, Thy N, Chan-ard T, Trung CT, Diesmos A, Iskandar DT, Lau M, Tzi Ming L, Mackhai S, Truong NQ, Phimmachak S (2010) Impending conservation crisis for Southeast Asian amphibians. *Biology Letters*, 6(3), 336–338.
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science*, 287(5459), 1770–1774.
- Sathiamurthy E, Voris HK (2006) Maps of Holocene sea level transgression and submerged lakes on the Sunda Shelf. *Tropical Natural History*, (2), 1–44.
- Scheffers BR, Yong DL, Harris JBC, Giam X, Sodhi NS (2011) The world's rediscovered species: back from the brink?. *PloS one*, 6(7), e22531.
- Scheffers BR, Joppa LN, Pimm SL, Laurance WF (2012) What we know and don't know about Earth's missing biodiversity. *Trends in Ecology and Evolution*, 27(9), 501–510.
- Schlick-Steiner BC, Steiner FM, Seifert B, Stauffer C, Christian E, Crozier RH (2010) Integrative taxonomy: a multisource approach to exploring biodiversity. *Annual Review of Entomology* 55: 421–438.
- Shimada T, Matsui M, Sudin A, Mohamed M (2007) Identity of larval *Meristogenys* from a single stream in Sabah, Malaysia (Amphibia: Ranidae). *Zoological Journal of the Linnaean Society*, 151(1), 173–189.
- Shimada T, Matsui M, Yambun P, Sudin A (2011) A taxonomic study of Whitehead's torrent frog, *Meristogenys whiteheadi*, with descriptions of two new species (Amphibia: Ranidae). *Zoological Journal of the Linnaean Society*, 161(1), 157–183.
- Shimada T, Matsui M, Nishikawa K, Eto K (2015) A New Species of *Meristogenys* (Anura: Ranidae) from Sarawak, Borneo. *Zoological Science*, 32(5), 474–484.

- Simberloff D (1976) Experimental zoogeography of islands: effects of island size. *Ecology*, 57(4), 629–648.
- Singhal S, Hoskin CJ, Couper P, Potter S, Moritz C (2018) A framework for resolving cryptic species: a case study from the lizards of the Australian Wet Tropics. *Systematic biology*, 67(9), 1061–1075.
- Smart U, Sarker GC, Arifin U, Harvey MB, Sidik I, Hamidy A, Kurniawan N, Smith EN (2017) A new genus and two new species of arboreal toads from the highlands of Sumatra with a phylogeny of Sundaland toad genera. *Herpetologica* 73: 63–75. <https://doi.org/10.1655/Herpetologica-D-16-00041>.
- Sodhi NS, Koh LP, Brook BW, Ng PKL (2004) Southeast Asian biodiversity: an impending disaster. *Trends in Ecology and Evolution*, 19, 654–660. (doi:10.1016/j.tree.2004.09.006)
- Sodhi NS, Brook BW (2006) Southeast Asian biodiversity in crisis. Cambridge University Press.
- Sodhi NS, Bickford D, Diesmos AC, Lee TM, Koh LP, Brook BW, Sekercioglu CH, Bradshaw CJ (2008) Measuring the meltdown: drivers of global amphibian extinction and decline. *PLoS one*, 3(2), e1636.
- Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues AS, Fischman DL & Waller RW (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, 306: 1783–1786.
- Stuart BL, Inger RF, Voris HK (2006) High level of cryptic species diversity revealed by sympatric lineages of Southeast Asian forest frogs. *Biology Letters*, 2(3), 470–474.
- Stuart BL (2008) The phylogenetic problem of *Huia* (Amphibia: Ranidae). *Molecular Phylogenetic and Evolution* 46(1): 49–60. <https://doi.org/10.1016/j.ympev.2007.09.016>
- Stuart BL, Bain RH, Phimmachak, S., & Spence, K. (2010). Phylogenetic systematics of the *Amolops monticola* group (Amphibia: Ranidae), with description of a new species from northwestern Laos. *Herpetologica*, 66(1), 52–66.
- Teynie A, David P, Ohler A (2010) Note on a collection of amphibians and reptiles from Western Sumatra (Indonesia), with the description of a new species of the genus *Bufo*. *Zootaxa*, 2416(1), 1–43.
- Tolley KA, Townsend TM, Vences M (2013) Large-scale phylogeny of chameleons suggests African origins and Eocene diversification. *Proceedings of the Royal Society of London B: Biological Sciences*, 280(1759), 20130184.

- Trainor CR (2007) Changes in bird species composition on a remote and well-forested Wallacean Island, South-East Asia. *Biological Conservation*, 140(3–4), 373–385.
- Uetz P, Freed P, Jirí Hošek (2018) eds. *The Reptile Database*, <http://www.reptile-database.org>, accessed 1 November 2018.
- Valdecasas AG, Williams D, Wheeler QD (2008) 'Integrative taxonomy' then and now: a response to Dayrat (2005). *Biological Journal of Linnaean Society*, 93(1): 211–216.
- Van Kampen PN (1923) *The amphibia of the Indo-Australian archipelago*. EJ Brill, Ltd.
- Van Schaik CP, Mirmanto E (1985) Spatial variation in the structure and litterfall of a Sumatran rain forest. *Biotropica*, 196–205.
- Vieites DR, Wollenberg KC, Andreone F, Köhler J, Glaw F, Vences M (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Sciences*, 106(20), 8267–8272.
- Voris HK (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography*, 27(5), 1153–1167.
- Walther F, Neiber MT, Hausdorf B (2016) Species complex or complex species? Integrative taxonomy of the land snail genus *Rossmassleria* (Gastropoda, Helicidae) from Morocco and Gibraltar. *Systematics and Biodiversity*, 14(4), 394–416.
- Welton LJ, Travers SL, Siler CD, Brown RM (2014) Integrative taxonomy and phylogeny-based species delimitation of Philippine water monitor lizards (*Varanus salvator* Complex) with descriptions of two new cryptic species. *Zootaxa*, 3881(3), 201–227.
- Whiles MR, Lips KR, Pringle CM, Kilham SS, Bixby RJ, Brenes R, Connelly S, Colon-Gaud JC, Hunte-Brown M, Huryn AD, Montgomery C, Peterson S (2006) The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. *Frontiers in Ecology and the Environment*, 4(1), 27–34.
- Whitfield JB, Kjer KM (2008) Ancient rapid radiations of insects: challenges for phylogenetic analysis. *Annual Review of Entomology*, 53, 449–472.
- Whittaker K, Koo MS, Wake DB & Vredenburg VT (2013) Global Declines of Amphibians. In: Levin SA (ed.) *Encyclopedia of Biodiversity*. Second Edition, Volume 3. Academic Press, Waltham, MA. Pp. 691–699.
- Whitten T (2000) *The Ecology of Sumatra*, vol. 1. Periplus Edition, Jakarta, Indonesia.

- Wiens JJ, Sukumaran J, Pyron RA, Brown RM (2009) Evolutionary and biogeographic origins of high tropical diversity in Old World frogs (Ranidae). *Evolution: International Journal of Organic Evolution* 63(5): 1217–1231.
- Wilting A, Sollmann R, Meijaard E, Helgen KM, Fickel J (2012) Mentawai's endemic, relictual fauna: is it evidence for Pleistocene extinctions on Sumatra? *Journal of Biogeography*, 39(9), 1608–1620.
- Wong, WM, Leader-Williams, N and Linkie, M (2013) Quantifying changes in sun bear distribution and their forest habitat in Sumatra. *Animal Conservation*, 16(2), 216–223.
- Wostl E, Sidik I, Trilaksono W, Shaney KJ, Kurniawan N, Smith E N (2016) Taxonomic Status of the Sumatran Pitviper *Trimeresurus (Popeia) toba* David, Petri, Vogel & Doria, 2009 (Squamata: Viperidae) and Other Sunda Shelf Species of the Subgenus *Popeia*. *Journal of Herpetology*, 50(4), 633–641.
- Wostl E, Riyanto A, Hamidy A, Kurniawan N, Smith EN, Harvey MB (2017) A taxonomic revision of the *Philautus* (Anura: *Rhacophoridae*) of Sumatra with the description of four new species. *Herpetological Monographs*, 31(1), 98–141.
- Yang DT (1991) Phylogenetic systematics of the *Amolops* group of ranid frogs of southeastern Asia and the Greater Sunda Islands. *Fieldiana: Zoology New Series* 63: 1–42. <https://doi.org/10.5962/bhl.title.2854>
- Yang Z, Rannala B (2010) Bayesian species delimitation using multilocus sequence data. *Proceedings of the National Academy of Sciences*, 200913022.
- Zakaria-Ismail M (1994) Zoogeography and biodiversity of the freshwater fishes of Southeast Asia. In *Ecology and conservation of Southeast Asian marine and freshwater environments including wetlands* (pp. 41–48). Springer, Dordrecht.
- Zhelev, ZM, Popgeorgiev, GS, Angelov, MV (2013) Investigating the Changes in the Morphological Content of the Blood of *Pelophylax ridibundus* (Amphibia: Ranidae) as a Result of Anthropogenic Pollution and Its Use as an Environmental Bioindicator. *ACTA Zoologica Bulgarica*, 65(2), 187–196.

Contribution to thesis chapters

The following table summarizes my contributions to published articles and manuscript included in this thesis:

Chapter 2 – Molecular phylogenetic analysis of a taxonomically unstable ranid from Sumatra, Indonesia, reveals a new genus with gastromyzophorous tadpoles and two new species (published)

Chapter 3 – A new species of the genus *Pulchrana* Dubois, 1992 (Amphibia: Ranidae) from Sumatra, Indonesia (published)

Chapter 4 – Genetic structure of two genera of Sumatran frogs trace back to ancient volcanic islands origins rather than Paleo-drainage systems (manuscript)

Contribution to	Chapter 2	Chapter 3	Chapter 4
Study design	lead	lead	lead
Data collection	lead	lead	lead
Data analyses	lead	lead	lead
Writing the manuscript	lead	lead	lead

Eidesstattliche Versicherung

Declaration on oath

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

I hereby declare, on oath, that I have written the present dissertation by my own and have not used other than the acknowledged resources and aids.

Hamburg, den 30.11.2018

A handwritten signature in black ink, consisting of a stylized 'U' followed by a series of loops and a final flourish.

Umilaela Arifin



“Untuk Tuhan, Bangsa, dan Almamater”