Title

Historical Biogeography of Sumatra and Western Archipelago, Indonesia: Insights from the flying lizards in the genus Draco (Iguania: Agamidae)

Permalink

https://escholarship.org/uc/item/05v6062g

Author

Lawalata, Shobi

Publication Date

2011

Historical Biogeography of Sumatra and Western Archipelago, Indonesia: Insights from the flying lizards in the genus *Draco* (Iguania: Agamidae)

By

Shobi Zenobia Sarenha Lawalata

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Integrative Biology

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Jimmy A. McGuire, Chair

Professor Craig C. Moritz

Professor Rauri Bowie

Professor Rosemary Gillespie

Fall 2011

Historical Biogeography of Sumatra and Western Archipelago, Indonesia: Insights from the flying lizards in the genus *Draco* (Iguania: Agamidae)

by Shobi Zenobia Sarenha Lawalata

Abstract

Historical Biogeography of Sumatra and Western Archipelago, Indonesia: Insights from the flying lizards in the genus *Draco* (Iguania: Agamidae)

by

Shobi Zenobia Sarenha Lawalata

Doctor of Philosophy in Integrative Biology

University of California, Berkeley

Professor Jimmy A. McGuire, Chair

The island arc west of the island of Sumatra in Indonesia, here referred to as the Western Archipelago, is home to many endemic flora and fauna. Despite their importance in the biogeographic theater of insular Southeast Asia, little scientific attention has been given to these islands, with the exception of the four islands that comprise the Mentawai group. In this dissertation, I used the evolutionary history of the flying lizards in the genus *Draco* to elucidate the biogeographical history of Western Archipelago relative to its neighboring mega-island Sumatra. In Chapter 1, I provide an updated checklist of the herpetofauna of the islands in the archipelago—a list that had not been revisited or updated in the last 20 years. My visit to the islands of Western Archipelago proved to add considerably to our knowledge of the herpetofauna occurring in the area. In Chapter 2, I present a revision of the molecular phylogeny of the genus *Draco* by incorporating sequence data from nuclear markers. And finally, in Chapter 3 I looked at the phylogenetics and population genetics of the most widely distributed species of flying lizards in Sunda Shelf—*Draco sumatranus* the common flying lizards—to discern the historical process by which they colonized the islands of the Western Archipelago. Using one mitochondrial locus and nine nuclear loci, I employed phylogenetic and coalescent-based population genetic methods to reconstruct the evolutionary history of *Draco sumatranus*. My results suggest that the islands of Simeulue, Nias, Siberut, Sipora, North & South Pagai and Enggano are monophyletic, but the Batu and Banyak Islands themselves are more closely related to Northwest Sumatran populations. This divergence is inferred to have occurred ~550,000 years ago. These findings reject the hypothesis of independent overwater dispersal onto each island, and support the hypothesis that the Western Archipelago had been colonized via the Batu and Banyak Islands and was subsequently isolated by a vicariant event—most likely related to the Pleistocene changes in sea levels. I also uncovered deep divergences of Sumatran *D. sumatranus* populations that cannot be adequately explained simply by the emergence of the Sunda Shelf basin during the last glacial maxima, or the modern-day geography of the island. This hints at the cryptic diversity harbored within Sumatra, and merits a more rigorous study of the island's biogeography.

Dedicated to Benjamin Dobbs.

TABLE OF CONTENTS

ACKNOWLEDGMENTS

If I were to do grad school all over again, I would absolutely come back and apply to be Jim McGuire's student. In 2004, as I was trying to figure out what I wanted to do with my life, Jim invited me to go on one of his field trips. This was my first experience of doing extensive fieldwork—a 40-day whirlwind tour of Sulawesi with Jim and his field crew—and the experience left such a mark on me that I was convinced it is something I would love to do for the rest of my life. I am forever indebted for Jim's invaluable assistance as I embarked on my own fieldwork later on—not only were his endless energy and determination indispensable, but through my close interactions with him I learned and grew a lot as a field biologist. The level of support I experienced as his student was simply outstanding, and not just financially (for which I am also eternally thankful). I'm sure Jim has no idea how many times his encouraging words, said with such conviction, had kept me chugging along even when I wasn't sure I had it in me. His passion and enthusiasm for science is infectious, and his insistence in adhering to the highest academic and intellectual standards continually challenged me to bring out the best in me. I leave the McGuire lab with a heavy heart, but with much delight I look forward to many more field trips and collaborations with Jim.

I owe a huge gratitude to my dissertation committee members for their invaluable advice and their trust in my abilities. I also thank them for putting up with my plea for last minute advising. Craig Moritz always provided his input with such great interest in my project, and his encouraging words invariably leaves me feeling better about myself after each meeting with him. Rosemary Gillespie lent her keen meticulousness and a fresh perspective into my dissertation, rooted deeply in her extensive knowledge and experience in island biogeography. Rauri Bowie made time to read and provide useful comments, and made my dissertation infinitely better despite his unbelievably busy semester of dissertation reading and intensive field season. Chelsea Specht and Anthony Barnosky sat in my qualifying exam committee, and I cannot be gladder that despite their expertise and knowledge, they are some of the most approachable people in the field. I truly learned a lot from my interaction with them. I enjoyed and gained a lot of experience from working with Claire Kremen and Per Palsbøll while teaching the Conservation Biology course. Former undergraduate advisors Noviar Andayani and Jatna Supriatna inspired me to get into evolutionary biology, and I continue to look up to them for guidance.

Before I go on to thank colleagues and lab mates, a special mention is truly deserving of the following people for their exceptional generosity with their time and knowledge while I bugged them endlessly with questions: Matthew Fujita, Jonathan Fong, and Sonal Singhal. Not only this dissertation would have taken twice as long to finish without their assistance, they also prove to be wonderful friends who have shown me steadfast love and support in all aspects of my life, more than I ever deserve.

I will be forever thankful that I was a part of the Museum of Vertebrate Zoology community—the most fertile ground for academic growth and learning, filled with amazing people who are especially good at what they do and love sharing their knowledge freely. I have enjoyed much banter—scientific or otherwise—with its wonderful people past and present, all of whom have been remarkably warm and supportive. These include, but are not limited to Dave Wake, Jim Patton, Eileen Lacey, Kevin & Karen Rowe, Sarah Werning, Verna Bowie, Maria Tonione, Carol Spencer, Rayna Bell, Anna Ippolito, Ted Papenfuss, and Michelle Koo. I thank my lab mates past and present in the McGuire lab for creating such a lively intellectual atmosphere and a wonderful sense of camaraderie in the lab: Becky Chong, Adam Leache, Matthew Brandley, Tom Devitt, Guin Wogan, Chris Witt, Brian Stuart, Corrine Richards, Alison Davis, Sean Reilly, Dan Portik, and newcomers Sarah Hykin and Phillip Skipwith. My office mates past and present in 3172 VLSB earn a special mention for being my little family in the MVZ. Not only do they make great intellectual sparring partners, they all have a special place in my heart for the companionship and emotional support that they provided over the years: Juan Parra, Sean Rovito, Matthew MacManes, Elaine Vo, and Roberta Damasceno. My laboratory work would not have gone as smoothly had it not been for our very capable lab manager Lydia Smith, and I also thank the formidable Maria Tonione and Joshua Penalba for their willingness to entertain even my stupidest questions in the lab. I have had the pleasure of training and working with many talented and motivated undergrads in the lab: Molly Gleeson, Juli Goldenberg, Nicholas Fletcher, Derek Moriyama, Sarah Hykin, Leselle Norville, and my own awesome assistants, Matthew Ogbuehi and Jennifer Kim, whose help had been invaluable.

My fieldwork is admittedly no small feat, and for its successful completion I thank the following people. Collaborator and mentor Dr. Djoko Iskandar (Bandung Technological Institute) freely lent his tremendous expertise in Indonesian herpetofauna, and hosted and fed me many times, absolutely free of charge and without hesitation. I thank Ibu Dewi Roesma (of Universitas Andalas) for opening up her home to me and my field crew, providing us with motherly care when we were tired, beaten and so far away from home. I was lucky to have been aided by the most competent and dedicated field assistants throughout my field expeditions: Jarot Arisona, Mistar Kamsi, Umilaela Arifin, Angga Rachmansah, Muhammad Rasit, Rosita Elianur, David Gusman, Mika Riski Puspaningrum, Irfan Fitriawan, Reksa Kurnia Robi, Riski Ramadhan, Andrian Saputra, Fadly Febriansyah, Dimar Adhi Perdana, and Pak D.T. Tjong from Universitas Andalas. Andrew Gottscho and Nicholas Fletcher flew themselves out to Indonesia from the United States to help me with my fieldwork, and I am forever indebted for their invaluable assistance. I thank Bang Boice and Bang Joel from Conservation International Indonesia for driving me around Padang on their expense when I first arrived there with absolutely no working knowledge of the city, and letting me crash the office floor and their home when I was cash-strapped. I also thank the local undergraduate students who contributed their passion, time and energy to help me collect my precious samples: Wawan and Dio from Bengkulu, and Edwin and Resa from Universitas Andalas.

I thank the following institutions for funding my scientific endeavors or simply providing me with means to get by: Department of Integrative Biology, Museum of Vertebrate Zoology, National Science Foundation, The International House, and the National Geographic Society.

Behind the academic scene, making a tremendous difference in my life, is a support network on which I have come to rely over the years. It's made up of friends and family who have been rooting for me unfailingly, and if it hadn't been for them I probably would have been tempted to throw in the towel a long time ago. My family—parents Brian & Agustien Lawalata, brother Jehoshua and sister in-law Anneke and my two nephews Denzel and Elden—cheered me on and made so many selfless sacrifices to get me where I am today. I cannot be more excited to be coming home to such a loving family. The family that I married into—parents in-law Greg and Darleen Dobbs, sister in-law Julie Polson, her husband Burt and children Abbie and Jake, brother in-law Rob McBlair and his wife Kelly and children Emily and Chloe—took me in and treated me as one of their own practically from Day 1, and they leave me no doubt that I am sincerely loved. ~~Mr. & Mrs.~~ Mom & Dad Dobbs have my most sincere gratitude for taking my husband and me under their wings and supported us when we were in an unfortunate financial place; without them my graduate career would have had a very different, much sadder ending. When I first landed in the United States years ago, alone and awkward, unsure how to fit in, these people befriended me and stayed true throughout the years, and I hope they will remain in my life for many more years to come: Pedro Gardete, Bianca Cerchiai, Christophe Choumert, Can Erdonmez, Charlene Ng, Becky Chong, Rosie Sejung-Chae. My closest friends from Indonesia cheered me on constantly despite the distance and infrequent communication, and I can't wait to once again be in their amazing company: Dhamar Pramudhito, Heri, Gianina Miranda, Kartika Simatupang.

When I was desperate about the prospect of finishing my lab work in time, my husband, best friend, and better half Benjamin Dobbs without hesitation decided to drop everything going on in his life to work shoulder-to-shoulder with me through grueling12-hour days, seven days a week for three months straight—just one of the countless selfless acts he had done for me over the years. I thank him for the unconditional love, for his faith in what I can do, for putting up with me when I'm stressed out and not at my best behavior, and for tirelessly telling me, "It's gonna be OK."

I no doubt have missed a few names, but I hope all of these people know who they are and what they mean to me. There is no way I can pay everyone back the kindness that they provided me even if I tried, but I know for sure I can always pay it forward towards others, and let kindness beget kindness.

CHAPTER 1

AN UPDATED CHECKLIST OF THE HERPETOFAUNA OF THE WESTERN ARCHIPELAGO, INDONESIA

INTRODUCTION

On the western margin of Indonesia lies Sumatra, the 5th largest island in the world and a major component of Sundaland biodiversity hotspot. Along Sumatra's west coast sits a chain of comparatively smaller islands, although by no means small (the island of Nias is home to ~750,000 people). This archipelago is composed of seven major islands from North to South in the following order: Simeulue (1,982 km^2), Nias (4,048 km^2), Siberut (4,030 km^2), Sipora (651.55 km^2), North and South Pagai (1,521 km^2 combined), and Enggano (0.4 km^2). Throughout this chapter, I will refer to this chain of islands as the Western Archipelago.

The Western Archipelago is situated roughly between 85–150 km off the west coast of Sumatra, separated by a deep-water channel called the Mentawai Strait (Figure 1). Geologically, the islands were formed together with the Nicobar and the Andaman islands to the north when the entire arc was raised from the ocean floor due to the thrust generated by the collision of Indo-Australian plate with Eurasian plate, ca. 60 million years ago (Whitten et al. 2000). Bathymetry studies show that the floor of the strait lies more than 200 m below current sea level except at two places where the water is shallower (Ladage et al. 2006). These two points, which now exist as two clusters of small islands (the Batu Islands on the south and Banyak Islands on the north), indicate where the historical land bridge connections between Sumatra and the Western Archipelago may have occurred. These bathymetry readings combined with results from studies on Pleistocene sea level fluctuations suggest that Simeulue, Nias and Enggano have probably never had a land connection with mainland Sumatra, whereas the Mentawai islands were probably joined to the mainland between 250,000 and one million years ago (Dring et al. 1989; Voris 2000).

Having been separated from Sumatra for an extended period of time, the Western Archipelago harbors a wealth of endemic species. For example, the Mentawai Islands, which are restricted to the four islands at the center of the chain (Siberut, Sipora, North Pagai and South Pagai) have long been known for their four endemic primate species, which have received notable scientific attention with regards to their ecology, behavior, and phylogeny (e.g. Roos et al. 2003; Tilson 1977; Whittaker 2005, 2009). However, the remainder of the biota inhabiting the islands has been only poorly studied. These islands were mentioned in older records inventorying the herpetofauna of Sundaland and the Indo-Australian Archipelago (e.g. deRooj 1917; vanKampen 1923), while more recent publications have updated lists of species occurrence and provided records of newly described species from the area (mostly on the basis of historical museum specimens rather than recent fieldwork; e.g. Das 2005; Das & Lim 2005; Dring et al 1989). Since then, surprisingly very little scientific attention has been given to these islands.

In this chapter, I will provide an updated inventory of the herpetofauna of the Western Archipelago based on surveys I conducted while collecting samples for my dissertation research on the historical biogeography of the region. Though unlikely to be comprehensive given the extent of the archipelago and the duration of field time on the islands, this list is the most comprehensive accounting of the amphibian and reptile diversity of the archipelago yet compiled.

MATERIALS & METHOD

Specimen collecting was conducted in two phases: I first made a reconnaissance visit to the Mentawai Islands in June of 2007, and returned between June–September 2009 with more manpower to perform more extensive collecting on all of the islands in the Western Archipelago, with the exception of Enggano. However, I also included records from a collection made in 2002 from the island of Enggano by Dr. Jimmy A. McGuire and colleagues. The habitats we sampled on all islands were patches of old growth forests within walking distance of human settlements, as well as secondary growth and disturbed habitats in the form of coconut groves and/or farmlands in the vicinity of villages. Night collecting was typically conducted along streams, rivers or creeks.

Specimens were obtained using a method loosely based on the visual encounter surveys method (Crump & Scott 1994; Rödel and Ernst 2004). Collecting sites were I tentatively identified prior to the field surveys, but locality choices were, by necessity, influenced by the presence of infrastructure (i.e. accessibility and accommodation), and were generally discovered by interviewing local inhabitants. A list of general sampling localities on each island is given in Table 1. Once a prospective site was identified, our team would walk along a trail while scanning the environs for any visible herpetofauna. We also turned rocks and logs, dug through leaf litter, peeled bark, and excavated burrows, termite mounds and tree hollows. We also conducted night surveys, employing a similar survey technique while using headlamps to discover active and sleeping amphibians and reptiles. Many anurans were located via eyeshine. We also used acoustic cues to locate frogs. Because my surveys were focused on geographical coverage of the entire archipelago, we rarely stayed for very long at any given locality and we therefore did not have an opportunity to sample using more systematically, such as with pitfall trap arrays. Specimens were primarily captured by hand, although plastic plugs shot from blowguns were also used to stun fast-moving or otherwise unreachable arboreal species. Snake tongs were used to capture venomous snakes. During the course of our survey, XX specimens were collected for depositon in the MZB and MVZ collections. During specimen preparation, liver samples were taken from every specimen through a small lateral or ventral incision and stored in 95% ethanol or RNA preservation buffer. For every specimen, data on date, time, habitat type and geographical coordinates at the time of capture were recorded. GPS coordinates (WGS 84 datum) were recorded using Garmin GPSmap 60CSx hand-held receivers. This information was supplemented with data on sex, tail length, snout-vent length, and live weight of every specimen at the time it was sacrificed. We obtained photographs of representatives of many species using Nikon D70 or Canon Rebel XSi digital cameras. Voucher specimens were preserved for each species.

RESULTS

We documented a total of 88 species of reptiles and amphibians from the Western Archipelago, including 26 frog species (four families), 36 lizard species (three families), 24 snakes species (five families), and 2 turtles (one family). We did not find any caecilians, even though they have been documented to occur in the area (Boulenger 1894, van Kampen 1923; Dring et al. 1989). Many of these specimens represent new occurrence records for the area, and we also discovered at least two new species of lizards.

SPECIES ACCOUNTS

Below I provide accounts of species that we collected or encountered during my surveys. In cases where there seems to be superficial resemblance to described taxa but where comparisons were rendered difficult by the unavailability of comparative material, by discordance with my own field observation, or by pending taxonomic revisions, I flagged the situation by inserting the clause "cf." (from the Latin word *confer* = "compare") into the species name. Specimens that do not seem to match any known species and thus presumed to be new to science are listed using the abbreviation "sp. nov." followed by the island of origin (e.g. an undescribed species of *Aphaniotis* from the island of Simeulue would be listed as *Aphaniotis* sp. nov. Simeulue). Relative abundance is noted as "abundant" when we experienced many encounters throughout a locality, "common" when the species is usually present at a locality, "infrequent" when only few individuals were seen, "rare" when the species is recorded only once, or "indeterminate" in cases where my field experience and knowledge of the local population was insufficient to allow classification.

AMPHIBIA, ANURA

TRUE TOADS, FAMILY BUFONIDAE

Ingerophrynus biporcatus (Gravenhorst, 1829)

Common name: Double-crested toad.

Description: Moderate-sized with a stout body. Two elongated supraparietal ridges between the eyes (hence the species' name). Small and distinct parotoid glands are present. The skin is wrinkled and covered with tubercles. The tympanum is visible and may be circular or somewhat elliptical. The toes are half-webbed except for the fourth toe. Dorsal coloration is brown (may be a reddish or grayish shade), mottled with darker blotches (AmphibiaWeb).

Occurrence & relative frequency: Banyak Islands (rare).

Habits & collection: We found one exemplar of this species (JAM 11116) while night collecting along a creek that was surrounded by a narrow gallery forest. This species has not been recorded to occur from these islands before.

Taxonomic comment: This species was known as *Bufo biporcatus* prior to revision by Frost et al. 2006.

Ingerophrynus claviger (Peters, 1863)

Common name: N/A.

Description: This is a medium-sized toad with a stout habit and a head that is more broad than narrow. On the head, one can see the canthal, supratympanic, supraorbital and parietal ridge. Of these, the last two are joined together forming an almost straight line that is highly elevated towards the back. The finger and toe tips are blunt. The first finger extends longer than the second, which is shorter than the fourth. The toes are almost half webbed. The upper part of the body has conical warts. The parotoids are small and oblong or roundish. The color is brown, with black spots above (vanKampen 1918).
Occurrence & relative frequency: Nias (common).
Habits & collection: We found this species to be common while collecting in disturbed secondary growth habitat away from water. They were typically found on the ground, actively foraging at night. My finding confirmed their presence on Nias, where their occurrence had been questioned previously. We collected 21 specimens: JAM 10107–8, 10188–10197, 10235–6, 10241–2, 10255–6, 10270–1, and 10284.
Taxonomic comment: This species was known as *Bufo claviger* prior to revision by Frost et al. 2006.

Duttaphrynus melanostictus (Schneider, 1799)

Common name: Southeast Asian Toad, Asian Common Toad, Spectacled Toad
Description: This is a medium-sized toad with a stout habit. Several bony ridges present on the head: along the edge of the snout (canthal ridge), in front of the eye (pre-orbital), above the eye (supra-orbital), behind the eye (post-orbital), and a short one between the eye and ear (orbito-tympanic). The eardrum or tympanum is very distinct and is at least as wide as two-thirds the diameter of the eye. The first finger is often longer than the second and the toes at least half-webbed. A warty tubercle is found just before the junction of the thigh and shank (sub-articular tubercle) and two moderate ones are on the shank (metatarsus). There are no skin folds along the tarsus. Dorsal side is covered with spiny warts. Parotoid glands are present and prominent, kidney-shaped or elliptical and elongated. The dorsal side is yellowish or brownish and the spines and ridges are black, and the underside is unmarked or spotted. Males have a subgular vocal sac and black nuptial pads on the inner fingers (from Boulenger 1890).
Occurrence & relative frequency: Simeulue (abundant), Nias (common), Siberut (common).
Habits & collection: A human commensal, we encountered this species in great abundance near human settlements, hopping on the ground at night. We collected two specimens from Simeulue (JAM 9986–7), two specimens from Siberut (SZL 039–40), and one specimen from Sipora (SZL 055).
Taxonomic comment: This species was known as *Bufo melanostictus* prior to revision by Frost et al. 2006.

Pelophryne signata (Boulenger, 1894)

Common name: Saint Andrew's dwarf toadlet.
Description: These are very small toads (SVL 14–18 mm) with moderately stout body and slender limbs. Fleshy webbings are present on the hands reaching the tip of the first finger, but leaving half of the outer fingers free. On the feet, the webbing is thick and reaches the tips of the first two toes only. A yellow or cream-colored band is present from

below the eye, passing above the armpit and along the side of body (Manthey & Grossman 1997).

Occurrence & relative frequency: Siberut (infrequent), Sipora (common), South Pagai (common).

Habits & collection: This species live in flat or hilly primary or old secondary forests with good canopy cover, up to 1,000 m in elevation. We have found them on the ground, or perched on leaves and branches of low-lying vegetation. We collected three specimens from Siberut (JAM 10390, 10395 & 10433), nine specimens from South Pagai (JAM 10548–9, 10560–2, 10628–30, and 10679–81), and 23 specimens from Sipora (JAM 10771–10785, 10842, and 10880–10887).

Taxonomic comment: Manthey & Grossman (1997) noted that *Pelophryne signata* and *P. brevipes* were synonymized by Inger (1966), but the two reappeared as valid species in Inger & Stuebing (1997). My specimens were examined by D.T. Iskandar and determined to belong to *P. signata*.

THE NARROW-MOUTHED FROGS – FAMILY MICROHYLIDAE

Kalophrynus punctatus Peters, 1871

Common name: Spotted sticky frog.

Description: A medium-sized frog that secretes a substance that makes it sticky to the touch. The body is triangular in shape, with slender limbs. The pupil is horizontal. The tongue is entire and free behind, with a toothless palate. A more or less distinct dermal ridge runs across the palate behind the choanae, and two other ones in front of the pharynx. Of these two, the posterior one is always denticulate but the other ones may or may not be denticulate. The tympanum is usually distinct. The fingers are free, while toes are webbed; the toe tips lack regular disks. The outer metatarsals are united. The clavicles are present. The omosternum is present. The terminal phalanges are club-shaped. Fingers and toes remarkably short; fourth finger extending as far as second; third toe not extending beyond fifth. Color is dark brown above, punctated with black (vanKampen 1923).

Occurrence & relative abundance: Batu Islands (infrequent), Sipora (infrequent), South Pagai (infrequent).

Habits & collection: This species is a forest-floor dweller, and is already known to occur on Siberut, Sipora, and Batu Islands (aside from Sumatra, Malay Peninsula and Indochina). We typically found them on the forest floor on well-drained soil, both during the day and at night. We collected four specimens from Pini island (part of the Batu Islands; JAM 10931, 10967, 11013 & 11077), two specimens from Sipora (JAM 10852–3), and three specimens from South Pagai (JAM 10618; JAM 10701–2).

Microhyla heymonsi Vogt, 1911

Common name: Arcuate-spotted pygmy frog, Dark-sided chorus frog.

Description: A tiny frog with wedged-shaped body and pointed snout. The tips of fingers and toes disc-shaped with marginal folds, and the toes are webbed at the base. The skin on the back is smooth to finely granulated, with a weak fold from eye to arm. Dorsal coloration varies from cream to brown to rusty red with a vertebral line dividing the body from the tip of the snout to the anus. There is a small black, circular, elevated

spot in the middle of the back, often with a second, somewhat smaller spot between the shoulders. The color of the sides (from the tip of the snout to the base of the leg) is dark brown to black, contrasting sharply with the lighter coloration of the back. The belly and chest is dirty white, the throat is grayish brown, and the inside of the legs are darck and mottled. The arms are gray to pale brownish (Manthey & Grossman 1997).
Occurrence & relative abundance: Nias (infrequent).
Habits & collection: My collection from the island of Nias represents a new record for this species on a Western Archipelago island. We collected four specimens (JAM 10117, JAM 10277–10279) from secondary growth forest adjacent to agricultural fields and human settlements at an altitude of < 100 m above sea level. This species is also known to inhabit disturbed areas such as riverbanks and grassy fields and gardens (Manthey & Grossman 1997).

Microhyla palmipes Boulenger, 1897

Common name: Palmated chorus frogs.
Description: Small frog; snout-vent length typically ~18 mm. The head and mouth are small. There is a small rounded tubercle on the upper eyelid, but otherwise this frog has smooth skin. Its fingers and toes have small, dilated tips, and circum-marginal grooves. The toes are 2/3 to 3/4 webbed. This species is brown in color, with a double arrowhead pattern on the back, and darker, blackish sides (AmphibiaWeb).
Occurrence & relative abundance: South Pagai (rare).
Habits & collection: This species is common on Java and Bali, but has never been recorded from any of the islands west of Sumatra. We collected one specimen (JAM10700) during night collecting from a patch of old, marshy secondary forest not far from the beach.

Phrynella pulchra Boulenger, 1887

Common name: Malacca frog.
Description: Body is slightly wedge-shaped, with short snout and small mouth. First finger as long as the second, finger ends in a widened spatula shape, with enlarged subarticular tubercle at the base, one on the inner two fingers, two on the outer fingers. Toe tips only slightly widened. Dorsal body with numerous scattered, small and large tubercles. There is a weak skin fold connecting the eye to the arm. Color is gray, black, brown or green on top with symmetrical dark spots, some surrounded by pale red lines. Red or yellow belly and underside of the legs. The throat of both sexes is mottled black or brown; cloaca in the center of a dark brown spot (Manthey & Grossman 1997).
Occurrence & relative abundance: Nias (rare), Siberut (common), South Pagai (rare).
Habits & collection: These frogs are known to be tree-hole dwellers. On Siberut we collected them from the hollow trunks of sago palms at sea level, having determined their location based on acoustic cues. Their calls can be heard frequently all over sago plantations, suggesting they are common in the area. We collected one specimen from Nias (JAM 10276), 11 specimens from Siberut (SZL 024–034), and one specimen from South Pagai (JAM 10537).

TRUE FROGS – FAMILY RANIDAE

Fejervarya limnocharis (Gravenhorst 1829)

Common name: Asian Grass Frog, Common Pond Frog, Field Frog, Grass Frog, Indian Rice Frog, Rice paddy frog.

Description: A small frog with long and narrow head and slender, oval body. The toes are pointed, and less than half webbed. The fingertips are also pointed. Visible tympanum. Skin is finely pebbled, with a series of low, interrupted ridges running down the back, which turns into a line of bumps both on the rump and the sides. A fold of skin is present behind the eye and over the tympanum. Coloration is rusty brown to brownish grey on top, with blotches of darker color on the back. A marking in the shape of U or W is usually present across the shoulders. May or may not have a light streak down the middle of the back, extending from the tip of the snout to the anus. The lips have conspicuous vertical brown and white bars (Manthey & Grossman 1997).

Occurrence & relative abundance: Nias (indeterminate).

Habits & collection: Even though this species is a human commensal and is otherwise ubiquitous, they are not known to occur in the islands of Western Archipelago. We only encountered one individual of *Fejervarya limnocharis*, and cannot determine their relative abundance because we did not sample rice paddies, where they are commonly found in great numbers. We collected one specimen (JAM 10116).

Limnonectes cf. *blythii* (Boulenger, 1920)

Common name: Blyth's river frog, Malayan giant frog.

Description: Robust body (SVL 85–260 mm) with massive head; long snout that is slightly pointed; robust and powerful limbs. First finger longer than second, fingers and toes with rounded, slightly enlarged ends. All toes are fully webbed. Rear part of the upper eyelid is granulated. Tympanum is visible and with distinct, widely curving tympanic fold that ends near the forearm. Smooth underside. Dorsal coloration is various shades of reddish brown, olive brown, greenish or grayish brown, with or without bright vertebral stripe. Throat is whitish to light gray (Manthey & Grossman 1997).

Occurrence & relative abundance: Banyak Islands (infrequent).

Habits & collection: This species is common along rivers and streams in lowland forests but can also be found in disturbed areas as well as hilly forest. They are found on the ground along stream or riverbanks, but can also be spotted great distances from water. Even though they can often be found in great abundance, we only encountered and collected two specimens of this species, JAM 11158–9.

Taxonomic comment: This species is known to be a species complex containing several lineages (Emerson & Ward 1998, Emerson et al. 2000).

Limnonectes cf. *kuhlii* (Tschudi, 1838)

Common name: Kuhl's creek frog

Description: Short body with stout, powerful limbs. Head of the male very broad, with slightly rounded snout, eyes slightly upward. Finger tips are rounded, first finger as long as the second; second and third fingers with marginal folds; pointed toe tips without marginal folds, toes fully webbed. Skin on the upperside rough with scattered shallow tubercles, or with a network of tiny wrinkles. Lower legs are covered with thorny protuberances. Ventrum almost smooth; tympanum not visible, with well-defined, straight or slightly curved tympanum fold. Dorsal coloration is reddish to brownish, or yellowish to greenish, mostly with darker spots, occasionally with vertebral stripe. Ventral side is whitish with numerous small pale gray spots, and the underside of the thigh is pale reddish (vanKampen 1923).

Occurrence & relative abundance: Sipora (common), South Pagai (common).

Habits & collection: This species is very widespread, with distribution ranging from continental Indochina to virtually all the major islands of Sunda Shelf. They are usually found along the banks or on the rocks in fast-moving creeks or streams. We collected 23 specimens from Sipora (JAM 10750–64, 10769–70, and 10829–10834), and eight specimens from South Pagai (JAM 10585–91, and 10639).

Taxonomic comment: This species almost certainly represents a complex of more than one species containing many taxa with more restricted distributions (McLeod 2010; vanDijk et al. 2011).

Limnonectes macrodon (Dumeril & Bibron, 1841)

Common name: Fanged river frog, Brown mountain frog, Javan giant frog, Malaya wart frog, stone creek frog.

Occurrence & relative abundance: Siberut (infrequent).

Description: A large frog that is a member of the creek ranid frogs. The head is wider than the body, and the tips of the fingers are distinctly enlarged. The tympanum is distinct and the vomerine teeth are arranged in two oblique series. The fingers are unwebbed and the toes are broadly webbed. Finger 1 is longer than finger 2, and fingers 2 and 4 are subequal in length. The outer metatarsal tubercles are absent (Inger & Stuebing 2005; vanKampen 1923).

Habits & collection: This species is found in sympatry, inhabiting the same habitat types as other creek frogs that we found in this survey (see above and below). Four specimens were collected from Siberut (JAM 10363–4, 10416–7).

Limnonectes microdiscus (Boetger, 1892)

Common name: Pygmy creek frog, Indonesian wart frog.

Description: Vomerine teeth in two oblique series. The lower jaw has two acute, tooth-like processes in the male that are less prominent in the female. Head is as long as broad, with rounded snout that is vertically truncate or slightly projecting. The canthus rosalis is distinct, and obtuse, loreal region oblique, feebly concave. The fingertips are weakly expanded or with very small disks, as are the toes. The first finger extends as far as or beyond the second, which is shorter than fourth. The third toe is longer than fifth. The toes are 2/3 to 3/4 webbed. The subarticular tubercles are moderate; inner metatarsal tubercle is small, oblong; the outer metatarsal tubercle is absent. The back and sides smooth or with some rounded warts or longitudinal ridges. The color is brown or olive above, marbled or spotted with black. Sometimes a broad, black cross-bar is present between the eyes. A broad, light vertebral line or two broad dorsolateral stripes may be present; lips with dark vertical bars; limbs with numerous, narrow, black cross-bands; posterior surface of thighs dark marbled; white beneath, throat and breast often powdered or marbled with blackish (van Kampen 1923).

Occurrence & relative abundance: Nias (common), Batu Islands (infrequent), Sipora (rare).

Habits & collection: This species is found near moving water (streams or creeks) in primary or mature secondary forests. Our collection originated from Nias (JAM10109–11, 10183, 10274), Batu Islands (JAM10958–9), and Sipora (JAM10861).

Limnonectes cf. *shompenorum* (Das, 1996)

Common name: Shompen creek frog.

Description: A large, stout ranid species that can be distinguished from other creek frogs in having the following suit of characters: (1) head narrower than body, and longer than broad, (2) interorbital distance greater than the upper eyelid width, (3) fingers with movable dermal fringe, (4) tips of fingers weakly enlarged, (5) finger 4 longer than finger 2, (6) fully webbed toes, (7) dark horizontal loreal stripes, (8) partially pigmented eggs.

Occurrence & relative abundance: Simeulue (abundant), Banyak Islands (abundant), Nias (abundant), Batu Islands (abundant), Siberut (common), Sipora (abundant), South Pagai (abundant), Enggano (common).

Habits & collection: This species is very abundant near moving bodies of water in primary or old secondary forests as well as near agricultural fields. They are usually found on rocks or in holes in the earth walls that make up the riverbank. My collection includes 23 specimens from Simeulue (JAM 9980–4, 10019–27, 10064–72), 13 specimens from Banyak Islands (JAM 11093–4, 11114, 11146–9, and 11168–71), 23 specimens from Nias (JAM 10112, 10163–82, and 10272–3), 19 specimens from Batu Islands (JAM 10970, 10976–86, 11012, and 11063–8), eight specimens from Siberut (JAM 10434–41), 21 specimens from Sipora (JAM 10748–9, 10765–8, 10819–28, and 10856–60), and 31 specimens from South Pagai (JAM 10495–503, and 10565–84). J.A. McGuire collected fifteen specimens from Enggano (JAM4167–71, 4189–96, 4339, 4403).

Taxonomic comment: Personal correspondence with B. Tapley revealed that his record of *L.* cf. *shompenorum* collected from the Banyak Islands (Tapley & Muurman 2011) have been determined by the species author (I. Das) not to be *L. shompenorum* despite overall similarities. As is the case with many widespread species, this species is likely to be an aggregate of multiple lineages.

Occidozyga cf. *sumatrana* (Peters, 1887)

Common name: Sumatran puddle frog.

Description: Small, squat and stocky with short, fat hind limbs. Toes are fully webbed with round tips. Very similar in appearance to young *Limnonectes kuhlii* except that the distance between the eyes is about the same or narrower than the width of the eyelid, and the inside of the tip of lower jaw only has one tooth-like projection instead of a pair as in *L. kuhlii*. The skin on the back and upper surfaces has corrugated appearance with occasional rounded bumps. Uniformly dark grey to brown in color, but occasionally may have a wide light-colored stripe down the middle of the back. The underside of the head is commonly mottled dark grey, and the belly and underside of the thighs have some yellowish tinge (Inger & Stuebing 2005).

Occurrence & relative abundance: Batu Islands (abundant), Sipora (rare).

Habits & collection: This species is common at low elevations in mud puddles (including pig wallows and animal footprints that had filled with rain water) or in marshy areas. They do not appear to live in groups. Adults sit or float almost submerged in water and can be difficult to spot until they start moving. We were only able to collect one individual from the island of Sipora, JAM 10789, but made a larger collection from the Batu Islands (JAM 10961, 10987–97, and 11052–62) where they are highly abundant in the marshy forests of Pulau Pini.

Rana glandulosa (Boulenger, 1882)

Common name: Rough-sided frog.
Description: Medium- to large-sized frog with broad head and prominent eyes. The toes are only half-webbed, and have thickened, triangular pads on the tips. The fingers are long and similarly padded as the toes. Large tympanum. The skin is covered by rough, slightly raised bumps that are most prominent on the sides of the body and the tops of the legs. There is a short tympanic fold between the back of the eye and above the tympanum. Dorsal coloration is brown to dark brown with spots on the back. The chin, throat, chest and belly are whitish with many brown spots. Red-colored iris is prominent.
Occurrence & relative abundance: Batu Islands (abundant).
Habits & collection: This species is very abundant in the lowland marshy forests on Pulau Pini (part of the Batu Islands). Males are typically spaced apart and called singly. We were able to collect a good series of 22 specimens: JAM 10932–40, 10971–5, and 11020–7.

Hylarana chalconota (Schlegel 1837; sensu Inger et al. 2007)

Common name: Schlegel's frog, brown stream frog, copper-cheeked frog, white-lipped frog.
Description: A larger member of the *chalconota* species group (SVL 37–55mm). Head triangular; snout slightly projecting; tympanum slightly depressed relative to surface of temporal region; pineal body faintly visible, slightly anterior to or in line with front corners of upper eyelids; dorso-lateral fold narrow; skin of back granular in females, with many fine spinules in males; crossbars on hind limb visible in about half of preserved individuals; rear of thigh brown with obscure, rounded light markings (Inger et al. 2007).
Occurrence & relative abundance: Nias (common), Siberut (abundant), Sipora (common), South Pagai (common).
Habits & collection: This species can thrive both in primary forest habitats as well as disturbed areas and around human settlements (e.g. in yards and gardens). They are usually found perched on small twigs and leaves in shrubs and small trees. We were able to collect 14 specimens from Nias (JAM 10098–104, 10199–204, and 10283), 22 specimens from Siberut (JAM 10354–62, 10297–403, and 10442–7), 10 specimens from Sipora (JAM 10790–7, 10835 and10851), and 11 specimens from South Pagai (JAM 10490–4, and 10648–53).
Taxonomic comment: We follow the taxonomy of Inger et al. 2007 in which the species *Hylarana chalconota* sensu lato was divided into seven different lineages based on morphological characters, geographical distribution and molecular phylogenetic evidence. The specimens identified to be in this group are largely true to the authors' description of *H. chalconota*.

Hylarana nicobariensis (Stoliczka, 1870)

Common name: Cricket frog.

Description: A small to medium sized frogs with long, narrow, pointed head. Tympanum is visible. The legs are slender, and the fingers and toes are extremely long with slightly enlarged tips. The toes are only about ½ webbed, and the longest toe extends far beyond the webbing. The skin on the back is finely pebbled, with a distinct ridge of skin folded along each side of the back. The back is brown with dark spots; the entire upper lip is white. Many individuals have a darker brown marking that extends from the tip of the snout, across the side of the face and over the eye to the tympanum (Inger & Stuebing 2005).
Occurrence & relative abundance: Nias (common), Siberut (abundant), Sipora (abundant), South Pagai (abundant), Enggano (abundant).
Habits & collection: This species is highly abundant and widely distributed. They thrive in disturbed habitat and can often be found along logging roads and in roadside ditches, especially in thick grassy aquatic vegetation. Despite this abundance, however, males don't seem to call in groups. We were able to obtain a large series of this species: 12 specimens from Nias (JAM 10106, 10113–5, 10205–7, and 10265–9), 18 specimens from Siberut, four specimens from Sipora (JAM10838, 10891–3), and 18 specimens from South Pagai (JAM 10474–89, and 10593–4). J.A. McGuire collected 71 specimens from Enggano (JAM4143–66, 4197–98, 4234–5, 4295–318, 4320–38).

Hylarana parvaccola (Inger, Stuart & Iskandar 2006)
Common name: N/A
Description: This species is easily distinguishable at a glance as the small, more brightly colored form of the *Rana chalconota* group (SVL of females < 45 mm, of males < 40 mm). Dark spots are present on back. Nuptial pad of males are not constricted. Habitus slender, head very slightly wider than trunk, with long legs. The head is triangular, longer than broad; the snout is narrowly rounded, projecting slightly beyond lower jaw. The tympanum is distinct. The fingers are long, without webbing. Tips of toes expanded into discs smaller than those of fingers, but with circummarginal grooves; webbing extensive. The skin is granular on the back, in males the granules are tipped with small, colorless spinules. The rear of abdomen is rugose, the rest of venter is smooth. Males have paired vocal sac openings on floor of mouth. Males have whitish velvety nuptial pad on dorsal and medial surfaces of first finger. A weak humeral gland is detectable by folding back skin of upper arm (Inger et al. 2007).
Occurrence & relative abundance: Banyak Islands, Batu Islands (abundant), Sipora, South pagai.
Habits & collection: This species is often found in sympatry with their larger form, *H. chalconota*, although in some instances not nearly as abundant. We were able to obtain the following specimens: two individuals from Banyak Islands (JAM 11160–1), 26 individuals from Batu Islands (JAM 10941–51, 10998–11002, 11011, and 11028–36), one individual from Sipora (JAM 10837), and 15 individuals from South Pagai (JAM 10601–3, 10619–24, and 10703–8).

Hylarana siberu (Dring, McCarthy & Whitten 1990)
Common name: Siberut island frog.
Description: (from Dring et al. 1989) A species of the section *Hylarana*; supratympanic and dorsolateral ridges absent; digital discs one and one half times the width of digit; first

finger longer than second; third and fifth toes webbed to distal tubercle. The color of the dorsum is black with red dorsolateral stripes, yellow spots on lips, limbs and lower flanks. Males have large humeral gland and paired subgular vocal sacs, but no nuptial pads or dorsal spinules; female with dorsal asperities and unpigmented eggs.

Occurrence & relative abundance: Siberut (infrequent), Sipora (infrequent), South Pagai (infrequent).

Habits & collection: We encountered this species at low elevations on the ground in humid secondary growth or selectively logged forest close to water. They were often hiding in the understory of brushes and scrubs, with males sometimes calling from holes in the soil that form the riverbanks. We never found them in groups; they are typically found as solitary male or female. My collection included two individuals from Siberut (JAM 10365 and 10451), one individual from Sipora (JAM 10855), and eight individuals from South Pagai (JAM 10592 and10692–8).

Odorrana hosii (Boulenger, 1891)

Common name: Poisonous rock frog.

Description: This frog has a robust body with long, slender legs; males measure 50–60 mm, females 85–100 mm. The dorsal coloration is dark green with brown sides, while the underside is pale. The limbs are marked with dark crossbars. The finger- and toe-tips bear grooved discs.

Occurrence & relative abundance: Sipora (abundant), South Pagai (abundant).

Habits & collection: This frog is often found at night perching 1–2 m high on shrubs in or at medium to large rocky streams or on vegetation overhanging the river's edge. We were able to obtain a good series of specimens: 26 specimens from Sipora (JAM 10735–47, 10807–18, and 10836) and 19 specimens from South Pagai (JAM 10595–600, 10604–12, 10625–7, and 10675).

THE AFRO-ASIAN TREE FROGS – FAMILY RHACOPHORIDAE

Nyctixalus pictus (Peters, 1871)

Common name: Cinnamon tree frog.

Description: (from Inger & Stuebing 2005) This species is a small frog with a relatively long snout and long hind limbs. The eardrum is visible and slightly smaller than the diameter of the eye. The tips of the fingers and toes are expanded into round pads that are smaller than the eardrum. The toes are about half-webbed and the fingers lack webbing. The skin of the back, head, and the upper surfaces of the limbs is rough, with many small spiny bumps. The color of the upper surfaces and sides tend to be cinnamon brown, though some individuals are red or even orange. Scattered over the dorsum are small, glossy white spots that form a broken line from the edge of the snout, along the edge of the upper eyelid, and continue part way down the side of the back. The upper half of the iris of the eye is also white; the lower half is brown (Inger & Stuebing 2005).

Occurrence & relative abundance: Nias (rare), Siberut (common), Sipora (common), South Pagai (common).

Habits & collection: This species inhabits primary and old secondary forests, both on flat and hilly terrains from sea level all the way to 1,650m (Manthey & Grossman 1997). Adults are usually found on leaves of shrubs and small trees 1–3m above ground. We were able to collect one specimen from Nias (JAM 10198), five specimens from Siberut (JAM 10366, 10418, 10448–50), five specimens from Sipora (JAM 10786–8, 10889–90), and three specimens from South Pagai (JAM 10631, 10677, and 10699).

Polypedates leucomystax (Gravenhorst, 1829)

Common name: Common tree frog.
Description: This is a small to medium-sized frog with a slender body and long, slender hind limbs. The sides of the snout are sharp, but the tip is blunt. The skin is smooth except for a curved fold over the tympanum. The fingers and toes have enlarged disks, and the fingers lack webbing. The color varies from light beige to dark tan on the head, back and legs. Most individuals have four narrow dark stripes running down the back, while the rest have some scattered brown spots (Inger & Stuebing 2005).
Occurrence & relative abundance: Nias (common), Siberut (infrequent), Sipora (common), South Pagai (common).
Habits & collection: This species is very common in lowland areas up to 750m, and can be found both in disturbed habitat as well as old secondary forests, but rarely in primary forests. Males form calling groups near and around standing water. Specimens collected: Six individuals from Nias (JAM 10095–7, 10105, 10208, and 10280), one individual from Siberut (JAM 10421), 10 individuals from Sipora (JAM 10870–9), and 21 individuals from South Pagai (JAM 10504–13, 10613–7, and 10655–60).

Polypedates macrotis (Boulenger, 1891)

Common name: Dark-eared tree frog.
Description: A medium-sized to large frog with a triangular head and large eyes. The skin is smooth, although some individuals may have very small bumps on the back. There is often a narrow whitish ridge of skin along the outer edge of the forearm. Fingers and toes with enlarged disks. Fingers without webbing. This species is tan to brown on the head, back and legs. Some have a pair of wide black stripes down the back. There is a distinct dark brown band from the eye, covering the eardrum and becoming narrower as it continues along the side. The underside of the head is heavily mottled with brown (Inger & Stuebing 2005).
Occurrence & relative abundance: Siberut (infrequent), Sipora (infrequent).
Habits & collection: This species is a lowland inhabitant of good primary and secondary disturbed forests, often over standing water at forest edges, or near ditches with nearby shrubs. Specimens collected: three individuals from Siberut (SZL 041–3), and two specimens from Sipora (SZL 060-1).

Rhacophorus appendiculatus (Günther, 1858)

Common name: Frilled tree frog.
Description: A small species of tree frog with a triangular head and almost conical tip to the snout in males. In females, the snout has an enlarged conical projection, giving them an odd “boat-nosed” appearance. The toes are about ¾ webbed, with the ends of several toes projecting beyond the webbing. The two outer fingers are partially webbed, but the others are free. The skin of the dorsal surfaces is covered with many irregular small bumps, which tend to be larger on the sides. The outer edges of the forearm and the leg have a narrow, wavy-edged fringe of skin. A narrow flap of skin also runs across

the body just below the vent. Coloration on dorsal side is grey green to brown or tan, with variable dark markings. The undersides of the head and body are whitish, with a very slight yellowish tinge. Some individuals have a pinkish tinge on the front of the thigh. Females are larger than males (Inger & Stuebing 2005; Manthey & Grossman 1997).

Occurrence & relative abundance: Siberut (abundant), Sipora (abundant), South Pagai (abundant).

Habits & collection: This species lives in primary or old secondary forests at low elevations, usually in large groups. It has also been found in peat swamps as well as well-drained forests. Males call from low marshy areas or at slight depressions in the forest floor where rainwater accumulates. Males typically perch on twigs and leaves of small trees and shrubs up to 3 m above ground, often in large groups. We only encountered one individual on Siberut (JAM 10408), however when these animals were found in great abundance, we collected a sizeable series: 26 specimens from Sipora (JAM 10898–915 and 10917–24), and 25 specimens from South Pagai (JAM 10517–31 and 10661–70).

Rhacophorus cf. *pardalis* Günther, 1858

Common name: Harlequin tree frog, gliding tree frog, panther tree frog.

Description: Small to medium in size, with males reaching 39-55 mm and females 55-71 mm. Snout is rounded. Third, fourth, and fifth fingers are fully webbed and bear expanded discs. The outer edges of the hand and forearm have a wide flap of skin. Toes are fully webbed. The heel has a rounded flap of skin. Dorsum is smooth, venter is coarsely granular (Inger & Stuebing 2005). Males have nuptial pads (Harvey et al. 2002). Dorsum is tan to reddish brown, often with an X-shaped darker marking on the back. Several white spots are often present, with some individuals having yellow or blue spots on the dorsal surfaces. Flanks are yellowish with black spots. Venter is yellowish with orange reticulation. Webbing is orange-red (Inger & Stuebing 2005).

Occurrence & relative abundance: Nias (infrequent), Batu Islands (rare), Siberut (rare), Sipora (infrequent).

Habits & collection: We typically were able to find this species in primary or old secondary forests with good canopy cover. They are found as solitary individuals, often perched atop high branches or palm fronds (up to 4–5 m above ground). We collected two specimens from Nias (JAM 10301–2), one specimen from Batu Islands (JAM 11070), one specimen from Siberut (JAM 10432), and four specimens from Sipora (JAM 10894–7).

REPTILIA, SQUAMATA

AGAMAS AND DRAGONS – FAMILY AGAMIDAE

Aphaniotis acutirostris Modigliani, 1889

Common name: Indonesian earless agama

Description: This species has strongly compressed body, with long and slender limbs, and a fifth toe that is longer than the first. Their dorsal scales are small and interspersed with larger ones. A dorsal crest is present, with a slight gular sac. The tympanum is

hidden. The snout is pointed, and much longer than the diameter of the orbit. Above the rostral, a convex scale can be found projecting anteriorly (deRooij 1915).
Occurrence & relative abundance: Banyak Islands (common), Nias (common), Batu Islands (rare), Siberut (common), Sipora (infrequent), SOUTH, NORTH OR BOTH?? Pagai (infrequent).
Habits & collection: This species is typically found on the trunk of trees in primary or secondary growth with good canopy cover, not too high above ground (up to ~3m). My collection includes 17 specimens from Banyak Islands (JAM 11105–9, 11129–37, and 11196–7), 13 specimens from Nias (JAM 10122–25, 10136, 10162, 10223, 10228–9, and 10251–4), one specimen from the Batu Islands (JAM 10960), 11 specimens from Siberut (JAM 10345–8, 10386–9, and 10419–20), four specimens from Sipora (JAM 10799–800, 10848–9), and three specimens from South Pagai (JAM 10552, 10642 and 10686).

Aphaniotis sp. nov. Simeulue

Common name: Simeulue earless agama.
Description: This species is very similar in appearance to *A. acutirostris*, with the exception of the presence of a single, enlarged scale on the tip of the snout—especially prominent in the males.
Occurrence & relative abundance: Simeulue (abundant).
Habits & collection: This species seems to have diverged from *A. acutirostris* on the island of Simeulue following a long period of isolation. They are found in primary and mature secondary forests, active during the day on the trunks of small- to large-sized trees at heights of <3 m above ground. We collected a substantial series of this Simeulue-endemic species: JAM 9998–10018, and 1039–60.

Bronchocela cristatella Kuhl, 1820

Common name: Green crested lizard.
Description: This species of lizard is easy to spot because of its uniform bright green coloration that is occasionally accompanied with a blue tinge on the head. The males have a prominent neck crest. The body is strongly compressed and covered in small, keeled scales. The ventral scales are large and strongly keeled. The tail is compressed at the base, and very long (generally at least 3 times the SVL if fully intact). They are capable of changing colors to yellowish, grey-brown or black (deRooij 1917).
Occurrence & relative abundance: Banyak Islands (common), Nias (common), Siberut (common), Sipora (common), South Pagai (common).
Habits & collection: This species can be found in primary and secondary forests, but my most frequent encounters took place in open, disturbed areas (like logged forest patches or on trees near houses and agricultural fields). Specimens collected: two from Banyak Islands (JAM 11181, 11199), 13 from Nias (JAM 10081, 10088, 10137, 10139, 10142, 10148–9, 10233, 10238, 10243–44, 10248, 10286), four from Siberut (JAM 10344, 10381, 10396, 10422), one from Sipora (JAM 10729), two from South Pagai (JAM 10541, 10691).

Draco cristatellus Günther, 1872

Common name: Crested flying dragon, crested flying lizard.

Description: A member of the flying lizards, *Draco cristatellus* can be easily identified from the other *Draco* species in the region by its stocky build, keeled head scales, the presence of a tubercle at the posterior corner of the orbit, a strong statistical mode of five ribs supporting the patagium, the presence of a lacrimal bone, and its large triangular dewlap covered with small scales. A prominent crest is present along the length of the tail, made up of long, separated triangular scales. Their coloration is mostly dark reddish brown with some black spots, a black spot on the head between the orbits. The dewlap is the shape of inverted sail, in males with varying degrees of yellow tint on the tip, white in females. The neck lappets also show some yellow coloration in males.

Occurrence & relative abundance: Banyak Islands (infrequent), Batu Islands (rare), Siberut (infrequent), Sipora (infrequent), South Pagai (infrequent).

Habits & collection: This species can be found in lowland areas in primary and secondary forests, but it also frequents trees in open agricultural fields such as coconut groves. They have been found in sympatry with *Draco sumatranus* on beaches along coastlines. My collection is scant: three specimens from Banyak Islands (JAM 11194–5, 11203), one specimen from the Batu Islands (JAM 11076), two from Siberut (SZL 001, 017), one from Sipora (SZL 047), and one from South Pagai (JAM 10533–4).

Draco melanopogon Boulenger, 1887

Common name: Black-bearded gliding lizard.

Description: This species of flying lizard is easy to distinguish even from a distance due to its green body coloration, very slender habitus, small head, and slender limbs. The turret-like nostrils are oriented posterodorsally on the snout, a strong statistical mode of five ribs support the patagium, and lacrimal bones are present. The gular sac or dewlap is long, thin, and jet-black in males, whereas the smaller gular pouch in females is gray in coloration. The patagial membranes are primarily black, with yellow spots above.

Occurrence & relative abundance: Banyak Islands (common), Batu Islands (infrequent).

Habits & collection: This species is a forest-obligate and is common in lowland areas, never found disturbed or human-altered landscapes. We found them both on hilly, cool and shaded forests as well as hot, marshy swamp forests. They are absent from most of the islands of the Western Archipelago with the exception of the Batu and Banyak island groups, from which we were able to make a small collection: six specimens from Banyak Islands (JAM 11090 and 11118–23), and five specimens from the Batu Islands (JAM 10964–5 and 11007–9).

Draco modiglianii Vinciguerra, 1892

Common name: Modigliani's flying dragon.

Description: This species is endemic to the island of Enggano and is the only species of flying lizard known from the island. It has nostrils that are directed laterally, a strong statistical mode of six ribs supporting the patagium, and naked tympanum; lacrimal bones are absent. The color is bright green in males, with patagial membranes that are reddish-brown, marbled with indistinct lighter spots (deRooij 1915).

Occurrence & relative abundance: Enggano (abundant).

Habits & collection: This species thrives both in forests as well as in human-altered environments. It is endemic to the island of Enggano, where it can be found in great abundance. J.A. McGuire was able to make a substantial collection from his visit in 2003: JAM 4116–40, 4187, 4210, 4227–32, 4253–69, 4280–8, 4291, 4344–67.

Draco obscurus Boulenger, 1887

Common name: Dusky flying lizards.
Description: This species of flying lizard is easily distinguishable from other *Draco* species because of its conspicuous color pattern and dewlap morphology. The dorsal side of the neck lappet is grey, decorated with bright orange spots, while the underside is bright orange or dark crimson in color. The patagial membranes are maroon to reddish orange distally, yellowish tan basally, with a series of radiating black bands extending to the maroon distal margin. The gular sac in males is elongated, gray in color, and slightly enlarged distally with conspicuously enlarged pavementous scales; the gray of the dewlap contrasts sharply with the maroon on the underside of the throat lappets. Like the distal tip of the dewlap, the throat lappets have conspicuously enlarged scales relative to their neighbors. *Draco obscurus* has a strong statistical mode of five ribs supporting the patagium, lacrimal bones are present, and the turret-like nostrils are oriented posterodorsally.
Occurrence & relative abundance: Banyak Islands (common), Batu Islands (infrequent), Siberut (common), Sipora (common), North & South Pagai (common).
Habits & collection: This species is known to inhabit primary and secondary rain forests up to elevation of about 900 m above sea level, but can occasionally be found in open, disturbed areas adjacent to a forest patch. We were able to collect a good series of this species: 14 from the Banyak Islands (JAM 11080–5, 11128, 11184–90), three from the Batu Islands (JAM 11017–8, 11075), 10 from Siberut (JAM 10335–40, 10342–3, 10382–3), 12 from Sipora (JAM 10732–4, 10841, 10844–7, 10925–8), five from North Pagai (SZL 081–5) and 15 from South Pagai (JAM 10536, 10538–40, 10551, 10553–7, 10643–7).

Draco quinquefasciatus Linnaeus, 1758

Common name: Five-banded gliding lizard.
Description: This species possesses a patagium with a brilliant pattern of five concentric black rings alternating with rust orange decorating its patagial membranes. The coloration of the patagium is more vivid in females than males, though the general pattern is quite similar. The gular sac is very thin and elongated, in the shape of an inverted triangle. Male gular sacs are yellow in color, while in females they are greenish with yellow streaks. The patagium is supported by a strong statistical mode of six ribs, lacrimal bones are present, and the turret-like nostrils are oriented posterodorsally.
Occurrence & relative abundance: Banyak Islands (common), Batu Islands (infrequent).
Habits & collection: This species is common in flat lowland forests, usually on the trunk of medium to small-diameter trees. On the Batu Islands, we found them inhabiting wet, marshy forests. My collection from the Western Archipelago includes five specimens from the Batu Islands (JAM 10962–3, 11010, 11015–6) and eight specimens from the Banyak Islands (JAM 11086–9, 11124–7).

Draco sumatranus Schlegell, 1844

Common name: The common flying lizard, Sumatran flying lizard.

Description: This highly ubiquitous species is slightly stocky in appearance, with nostrils that point laterally. The head scales are keeled, and it has a small tubercle at the posterior corner of the orbit as well as a few small tubercles on each side of the neck. The gular sac is the shape of an inverted triangle that is bright yellow in males and bluish white in females. The head of male individuals sometimes show a tint of bright turquoise, invariably with a black spot between the eyes. The color of the dorsum is grayish brown, and the patagial membranes are black with yellow to rusty orange spotting. The patagium is supported by a strong statistical mode of six ribs. Lacrimal bones are lacking.
Occurrence & relative abundance: Banyak Islands (common), Nias (abundant), Batu Islands (common), Siberut (abundant), Sipora (abundant), South Pagai (abundant).
Habits & collection: This species is known to occur in primary as well as secondary forests, particularly near the edges where there is plenty of sunlight, but they are most easily encountered in open, disturbed habitat such as coconut groves or even in trees around human settlements. We were able to collect a substantial series: 10 specimens from the Banyak Islands (JAM 11091–2, 11165–6, 11191–3, 11200–2), 29 specimens from Nias (JAM 10080, 10082–94, 10135, 10138, 10140, 10144, 10150–8, 10230–2), 10 specimens from the Batu Islands (JAM 10966, 11003–6, 11014, 11071–4), six specimens from Siberut (JAM 10328–32, 10462), 10 specimens from Sipora (JAM 10719–28), and 20 specimens from South Pagai (JAM 10463–73, 10532, 10542–6, 10687–90).

Draco sp. nov. Simeulue

Common name: Shobi's kick-ass giant green sumatranus-like Draco
Description: This species seems to have diverged from *D. sumatranus*, retaining much of the pattern of the patagial membranes and dewlap shape and colors, but rather than being pale gray or tan dorsally it is vivid green in coloration. Females are stockier in build, with a more rounded gular sac that is bluish white and is marked with streaks of black. The patagium is supported by a strong statistical mode of six ribs. Lacrimal bones are lacking.
Occurrence & relative abundance: Simeulue (abundant), Lasia (abundant).
Habits & collection: This is a newly discovered and yet to be described endemic species that occurs on the island of Simeulue and its satellite islands. They are very abundant in coconut groves along the coast, and we were able to collect a substantial series from Simeulue (20 individuals: JAM 9957–9970, 9972–7) as well as from Lasia, a smaller island South of Simeulue (10 individuals: JAM 9988–97).

Gonocephalus chamaeleontinus (Laurenti, 1768)

Common name: Chameleon forest dragon.
Description: This medium to large-sized lizard has a compressed body, covered with small uniform or unequal scales. The tympanum is distinct and it has a strong transverse gular fold. The males have gular sac and a prominent dorsal crest. No preanal or femoral pores are present. *Gonocephalus chamaeleontinus* is distinguishable from other large agamids based on its strongly raised supraciliary border, and a dorsal crest that is much lower than the nuchal crest. The ventral scales are smooth, and the nuchal crest begins at the occiput. The color is light greenish above, with dark brown reticulations and transverse bands and dark lines radiating from the eye. The tail has alternating light and dark rings. The underside is olive or brownish (from deRooij 1915).

Occurrence & relative abundance: Banyak Islands (common), South Pagai (common).
Habits & collection: This species is usually found inhabiting lowland primary or old secondary forests, not too far from water (creeks or streams). We typically found them sleeping at night on branches ~1–2 m above ground. My collection consists of six specimens from the Banyak Islands (JAM 11110–3, 11139–40) and nine specimens from South Pagai (JAM 10550, 10564, 10638, 10641, 10682–5, 10711).

Gonocephalus grandis (Gray, 1845)

Common name: Giant forest dragon, sailfin lizard, angle-head lizard, river dragon.
Description: This magnificent species of forest lizard has a compressed body with prominent dorsal crest in males that extends along the head, body and tail (hence the name "sailfin lizard"), formed from long narrow scales that are united except at the tips. It can be distinguished from other large agamids by its supraciliary border that is only moderately raised, dorsal scales that are equal in size, and smooth, non-keeled ventral scales. The neck and dorsal crests are separated by a deep notch, with the dorsal crest a little lower than the neck crest. The color is green, brown or blue dorsally, uniform or with dark transverse bands. The flanks can be decorated with pale brown or yellowish round spots. Females and young animals have a dark band behind they eye that passes through the ear. The lower parts are brownish or yellowish (deRooij 1915).
Occurrence & relative abundance: Banyak Islands (infrequent), Nias (common).
Habits & collection: This species is diurnal and inhabits primary rainforests up to ~1,400m altitude, although we also have encountered them in patches of tree stands in disturbed areas (e.g. on a university campus), always in association with streams or creeks. They are easily spotted sleeping at night, perched on twigs or branches above water. We were able to collect two specimens from the Banyak Islands (JAM 11151–2) and 12 specimens from Nias (JAM 11018–21, 10209–14, 10263–4).

GECKOS – FAMILY GEKKONIDAE

Cnemaspis dezwaani Das, 2005

Common name: deZwaan's rock gecko.
Description: This is a small species of *Cnemaspis* (SVL to 31.4 mm), diagnosable by the following combination of characters: two semicircular supranasals that are separated by a single scale; three postnasals bounding the nasal; four scale rows separating the orbit from the supralabials; posteriorly, each postmental is bounded by three smooth, rounded and juxtaposed scales; scattered spinose paravertebral rows of tubercles on dorsum; pectoral and abdominal scales not elongated, imbricate, bearing a single keel; tail segmented, with enlarged flattened scales forming whorls, a single spinose postcloacal spur present; median subcaudals enlarged, unicarinate; supralabials (to midorbit position) 6; infralabials 7; lamellae under toe IV 18–19; adult males with 4–6 pairs of preanal pores and 3 femoral pores (Das 2005).
Occurrence & relative abundance: Nias (infrequent).
Habits & collection: We discovered this species on the trunk and leaves of smaller shrubs inside a small patch of mixed agricultural trees (rubber, cacao, etc.). We collected two specimens: JAM 10126 and 10127.

Cnemaspis modiglianii (2005)

Common name: Modigliani's rock gecko.
Description: This is a small species of *Cnemaspis* (SVL to 33.7 mm), diagnosable by the following combination of characters: supranasals separated by a single scale; five postnasals bounding the nasal; two scale rows separate the orbit from supralabials; postmentals bounded by three smooth, rounded and juxtaposed scales; no paravertebral rows of tubercles on dorsum; pectoral and abdominal scales distinctly elongated and imbricate, bearing a single keel; spinous processes on lateral surface of body; ventral surface of tail smooth; median subcaudals enlarged, unicarinate; supralabials (to midorbit position) 6–7; infralabials 6–8; lamellae under toe IV 16–18; and adult males with paired preanal pores, no preanal depression and four pairs of femoral pores (Das 2005).
Occurrence & relative abundance: Enggano (common).
Habits & collection: J.A. McGuire collected a large series representing this species from Enggano, where they are abundant on the trunks of moderate to large trees generally below 2 meters above the ground (JAM 4199–209, 4233, 4246–52, 4270–9, 4383–6, 4391–400, 4401–2).

Cnemaspis whittenorum Das 2005

Common name: Whitten's rock gecko.
Description: A small species of *Cnemaspis* (SVL to 31.5 mm), diagnosable from conspecific species in showing the following combination of characters: supranasals separated by a single scale; two postnasals bounding the nasal; postmental is bounded by four smooth, rounded and juxtaposed scales; no paravertebral rows of tubercles on dorsum; pectoral and abdominal scales distinctly elongated and imbricate, bearing a single keel; spinous processes on lateral surface of body; median subcaudals enlarged, unicarinate (Das 2005).
Occurrence & relative abundance: Siberut (infrequent), South Pagai (rare).
Habits & collection: This species was described to occur in hilly lowland evergreen forests with some peat swamps. My sampling locality can be described as a patch of old growth forest surrounded by logged fields. We found only three exemplars of this species, on Siberut (JAM 10384–5) and Sipora (JAM 10712).

Cyrtodactylus consobrinus (Peters, 1871)

Common name: Peter's forest gecko.
Description: This species has strong digits that are cylindrical or depressed at the base and laterally compressed distally. The outermost phalanges form an angle to the rest of the digit, hence the name bent-toed gecko. It is distinguishable from other *Cyrtodactylus* in having an angular series of 9–11 preanal pores and no pubic groove. The body is dark brown above with 8 or 9 narrow white, black-edged cross lines that are much narrower than the dark brown section separating them. The head is also brown with a network of narrow white lines. The upper lip has white spots (deRooij 1915).
Occurrence & relative abundance: Banyak Islands (rare).
Habits & collection: This species is quite common on the nearby "mainland" island of Sumatra, but is not frequently encountered across the Mentawai Strait. It is typically found in lowland primary forests or mature secondary forests. We found only one

specimen on Tuangku Island (one of the Banyak Islands), on the trunk of a tree in a mature secondary forest not too far away from a stream (JAM 11153).

Cyrtodactylus cf. *lateralis*

Common name: Spiny forest gecko, sumatran bow-fingered gecko.
Description: This species has strong digits that are cylindrical or depressed at the base and laterally compressed distally. The outermost phalanges form an angle to the rest of the digit, hence the name bent-toed gecko. *Cyrtodactylus lateralis* is differentiated from the presence of lateral fold with larger and smaller pointed tubercles. The tail is equipped with whorls of keeled spiny tubercles, with small ventral scales (deRooij 1917).
Occurrence & relative abundance: Banyak Islands (infrequent).
Habits & collection: While we frequently encountered this species on Sumatra, it is not as ubiquitous on the islands of Western Archipelago. We collected two specimens from the Banyak Islands (JAM 11095–6) on the trunk of a strangler fig in a patch of secondary forest at sea level, where they seemed to have made a nest inside the hollow of the tree.
Taxonomic comment: This species was tentatively identified as *C. lateralis* based on the presence of spiny tubercles on the dorsum, but recent evidence reveals that the species may be a complex consisting of several lineages (D.T. Iskandar, pers. comm.).

Cyrtodactylus marmoratus (Gray, 1831)

Common name: Javan bent-toed gecko.
Description: This species of bent-toed gecko can be distinguished from the presence of 4–6 femoral pores and 12 or 13 preanal pores on the males that are arranged in a longitudinal groove. The tail is covered below with small scales. The body is light brown above with dark brown spots, sometimes forming cross bands on the back (deRooij 1915).
Occurrence & relative abundance: Enggano (rare).
Habits & collection: Despite substantial searching, we collected only one juvenile specimen under a decomposing log on Enggano Island (JAM 4188).

Cyrtodactylus cf. *quadrivirgatus* (Taylor, 1962)

Common name: Taylor's bent-toed gecko, Marbled forest gecko.
Description: This small species has slender digits which lack expanded pads; the fingers and toes are well adapted for gripping on fissured tree bark or other rough surfaces. The reddish-brown eyes have vertical pupils and are fringed with a series of pointed yellow scales. The body is medium brown in color, pale cream or pale grey, patterned with four buff or dark brown lateral stripes that may be semi-continuous or completely broken into irregular blotches. The tail is patterned with dark and light bands of roughly equal thickness.
Occurrence & relative abundance: Banyak Islands (common), Nias (common), Batu Islands (common), Siberut (common), Sipora (common), South Pagai (common).
Habits & collection: This species is commonly encountered at night, perched on leaves or small branches of trees and vines not too high above ground. It lives in primary as well as secondary forests. We were able to collect a substantial series due to their abundance: Banyak Islands (JAM 11097–104, 11138, 11154–7, 11175–7), Nias (JAM

10128, 10215–22, 10257–60) Batu Islands (JAM 10952–5, 11039–11047), Siberut (JAM 10374–80, 10391, 10409–13), Sipora (JAM 10801–5, 10839, 10863–9), South Pagai (JAM 10672–4, 10709–10).
Taxonomic comment: This species is known to consist of several lineages. D.T. Iskandar (pers. comm.) is actively working on the group's systematics.

Cyrtodactylus sp. nov. "Large"

Common name: N/A
Description: This species has the appearance of *C. quadrivirgatus* in its coloration, but the snout-vent length is almost twice the size of the typical *C. quadrivirgatus*.
Occurrence & relative abundance: Banyak Islands (infrequent), Sipora (rare).
Habits & collection: We encountered two specimens on the Banyak Islands (JAM 11172–3), and one on Sipora (JAM 10862). The number of tubercles that are present on the dorsum of these animals from the two localities suggest further that they may represent different undescribed species.

Gehyra mutilata (Wiegmann, 1834)

Common name: Four-clawed gecko, stump-toed gecko, tender-skinned house gecko, sugar lizard.
Description: This species has strongly expanded digits that are webbed at the base. The distal phalanges are free, elongate, compressed, and clawed. The body has no folds between the armpit and groin, and the inner pair of chin shields is very large with quadrangular rostral. The color is pinkish grey above, and it can be uniform or with darker brown variegation or round white spots arranged in longitudinal series (deRooij 1915).
Occurrence & relative abundance: Siberut (rare).
Habits & collection: This species is a human commensal, and on adjacent Sumatra is frequently encountered on walls inside people's homes. However, we encountered this species crawling along an earthen bank near a logged forest patch. Our specimen from the island of Siberut (JAM 10370) represents the only record of this species from the Western Archipelago.

Gekko monarchus (Schlegel, 1836)

Common name: Spotted house gecko.
Description: This species of gecko has strongly expanded digits, free/webbed, clawed and with undivided lamellae below. The eyes have vertical pupil. The rostral scales border the nostril, and the male has 16–20 femoral pores on each side. The tympanum is 1/3 time the orbit width. The color is brown or grey, with darker spots that are arranged in a double row along the middle of the back. The tail has alternating darker and lighter sections. The underside is whitish, and each scale is dotted with dark brown (deRooij 1915).
Occurrence & relative abundance: Simeulue (infrequent), Batu Islands (rare), Nias (infrequent).
Habits & collection: This species is known to inhabit a diversity of habitats, from people's homes to disturbed forests. My collection of two specimens from the island of Simeulue (JAM 10036–7) was obtained from locals who found them inside their homes.

Likewise, on the Batu Islands (JAM 11019) we found the species crawling on the roof of a bamboo-thatched building. On the island of Nias (JAM 10239–40), we found two specimens on tree trunks inside a secondary forest patch at low-elevation.

Gekko smithi Gray, 1842

Common name: Smith's green-eyed gecko, large forest gecko.
Description: This is a large species of gekko. The head is concave, the ear opening is oval and oblique, less than half the diameter of the orbit. The head is covered with small polygonal scales, the largest being on the snout. The snout is very large, twice as broad as high. The body is long and covered in flat granules and ten or twelve longitudinal series of conical tubercles. The ventral scales are large and imbricate. Males have 11–16 preanal pores in short angular series. The tail is cylindrical, annulate, covered with quadrangular smooth scales that are larger on the underside. The limbs are long with free digits that are strongly dilated. The lamellae below are undivided and curved. The coloration is greenish-gray above, with some variegated darker tints, usually with transverse rows of white spots. The tail is banded with alternating light and dark colors (modified from deRooij, 1917). .
Occurrence & relative abundance: Banyak Islands (infrequent), Nias (rare), Siberut (rare).
Habits & collection: This is an arboreal species inhabiting humid primary as well as secondary forests at lower elevations. We found specimens invariably while night collecting. They are often seen on the trunk of larger trees, up to ~10 m above the ground. The species is vocal and its loud call can be heard from great distance in the forest. Our collection came from the Banyak Islands (JAM 11144, 11145), Nias (JAM 10261), and Siberut (JAM 10371).

Hemidactylus craspedotus Mocquard, 1890

Common name: Frilled forest gecko.
Description: This species has a narrow snout, longer than the distance between the eye and the ear-opening. The ear opening is small, oval, horizontal. The head scales are small, with the largest scales being on the snout. The body is dorso-ventrally compressed, and from the armpits to the groin there is a membrane that borders the flanks. Another membrane covers the neck, extending from the corner of the mouth to the forelimb. The body is covered above with fine granules, intermixed with small unequal round tubercles that are irregularly distributed. The tail is very depressed, bordered on each side by a broad fold with sharp denticulated lateral edge, anteriorly covered with transverse series of tubercles. The limbs are also bordered on both sides by a membrane. The color is grey-brown above, mottled with brown. The tail has brown cross bars. The lower parts are yellowish grey, speckled with blackish towards the sides. The tail has orangish red tint along the middle (modified from de Rooij 1915).
Occurrence & relative abundance: Banyak Islands (infrequent).
Habits & collection: This species is a forest dweller, although on the Banyak Islands we found one specimen on a coconut tree not too far away from a secondary forest patch. My collection consists of two specimens from the Banyak Islands (JAM 11142, 11163).

Hemidactylus frenatus Duméril & Bibron, 1836

Common name: Common house gecko.
Description: Snout longer than the distance between the eye and the ear-opening, one time and one third to one time and a half the diameter of the orbit; forehead concave; ear-opening small, roundish. Head covered with small granules, largest on the snout. Rostral quadrangular, nearly twice as broad as high, with median cleft above; nostril bordered by the rostral, the first labial and three nasals. Ten to twelve upper and eight or ten lower labials; mental large, triangular or pentagonal; two or three pairs of chin-shields, the median in contact behind the mental. Body is granular with more or less numerous, sometimes absent, irregularly scattered, round, convex tubercles, which are smaller than the ear-opening. Ventral scales cycloid, imbricate. Male with an uninterrupted series of 28—36 femoral pores. Tail is rounded, feebly depressed, covered above with very small smooth scales and 6 longitudinal series of keeled tubercles, below with a median series of transversely dilated plates. Limbs moderate; digits dilated, free, inner with sessile claw; 4– 5 lamellae under the inner digits, 7 to 9 under the 4th finger, 9 or 10 under the 4th toe. The color is grayish or pinkish brown above, uniform or with dark markings; head variegated with brown; a brown streak, light-edged above on the side of the head, passing through the eye, sometimes continued along the side of the body. Lower parts are whitish, sometimes dotted with brown (de Rooij 1915).
Occurrence & relative abundance: Sipora (common), North Pagai (common), Enggano (common).
Habits & collection: This species is known to inhabit people's homes. We encountered an abundance of them, but collected only a few. My collection came from Sipora (JAM 10930), North Pagai (JAM 10713), and Enggano (JAM 4113–4, 4215, 4219–22, 4292–4).

Hemidactylus platyurus (Schneider, 1792)

Common name: Flat-tailed house gecko.
Description: This species of house gecko has a snout that is longer than the distance between the eye and the ear opening, roughly 1.5 times the diameter of the orbit. The body is depressed, and covered above with uniform small granules that are largest on the snout. A dermal expansion stretches from the axilla to the groin, and another flap extends along the posterior side of the hind limb. The ventral scales are cycloid and imbricate. Males have an uninterrupted series of 34–36 femoral pores. The tail is depressed, flat inferiorly, with sharp denticulated lateral edge, and covered above with uniform small granules, below with a median series of transversely dilated plates. The limbs are moderate, depressed. The fingers and toes are strongly dilated, about half-webbed. There are 3 to 6 lamellae under the inner digits, and 7 to 9 under the median ones. The coloration is grey above, marbled with darker grey. Typically with a dark streak from eye to shoulder (deRooij 1915).
Occurrence & relative abundance: Nias (common), Sipora (common), North Pagai (common).
Habits & collection: Just like the other species of house gecko *Hemidactylus frenatus*, *H. platyurus* is extremely common and can be seen inside most houses in human settlements. We collected a few specimens from Nias (JAM 10133), Sipora (JAM 10929), and North Pagai (JAM 10714–8).

Hemiphyllodactylus typus Bleeker 1860

Common name: Indopacific tree gecko, common dwarf gecko.

Description: Head more long than broad, oviform; snout as long as the distance between the eye and the ear-opening, 1.5 times the diameter of the eye; ear-opening very small, oval, oblique. Rostral broad, nearly pentagonal; nostril bordered by the rostral, the first labial, a supranasal and two or three small scales. Eleven upper and as many lower labials; mental small, triangular; no chin-shields. Body long and slender; covered with small granular scales, those on the snout and the limbs somewhat enlarged. Limbs slender; digits very unequal, free (fig. 30); inner rudimentary; four pair of lamellae under the other digits. Ventral scales larger, smooth, imbricate. Male with an angular series of 15 preanal pores. Tail cylindrical, slender, covered with small scales. Brown above, marbled with darker; a dark streak from the tip of the snout to the shoulder, passing through the eye; a series or found whitish spots beginning behind the eye and continued along each side of the body to the tail. Tail lighter than brown above with two whitish elongate spots at the base, white below for 2/3 of its length. Lower parts of the body are whitish, speckled with brown (deRooij 1915).

Occurrence & relative abundance: Banyak Islands (rare), Enggano (infrequent).

Habits & collection: This small, nocturnal species is an inhabitant of both Banyak Islands (JAM11143), Enggano (JAM4223, 4289, 4373).

Lepidodactylus lugubris (Duméril & Bibron, 1836)

Common name: Mourning gecko, common smooth-scaled gecko.

Description: Head much longer than broad; snout as long as the distance between the eye and the ear-opening, one time and a half the diameter of the orbit; ear-opening small, oval. Head covered with very small granular scales, slightly enlarged on the snout. Rostral twice as broad as deep; nostril bordered by the rostral, the first labial and three small scales. Eleven or twelve upper and as many lower labials; mental small, triangular; no chin-shields. Body long, covered with small granules. Ventral scales somewhat larger and flat. Male with 11 preanal pores in an angular series. Tail cylindrical, covered with uniform small scales. Limbs short, fore limb not measuring half the distance between axilla and groin; digits free, inner rudimentary; 4 or 5 divided lamellae under the median toes. Brown above, with small round yellowish spots; a dark streak from the tip of the snout to the shoulder, passing through the eye, bordered above by light brown; a small light spot on each digit. Lower parts dirty white, dotted with brown (deRooij 1915).

Occurrence & relative abundance: Enggano (infrequent)

Habits & collection: This species dwells in plains of flat lowland areas, not too far from coastal areas. It can also be found on crop trees in plantations or inside houses. J.A. McGuire collected two specimens from the island of Enggano (JAM 4217–8). They were collected from the beach on a pandanus plant, and from the roof of a house.

Ptychozoon kuhlii Stejneger, 1902

Common name: Kuhl's flying gecko.

Description: This medium-sized gecko is readily recognizable due to the many fringes on its body—an innovation to help generate lift as a gliding mechanism. The hands and feet are fully webbed, and it has a pair of skin flaps or patagia along the lateral sides of the body. The tail is crenulated with large semi-circular fringes along the sides, and the tail ends in a paddle-shape. The color is usually gray to tan, with W-shaped transverse bands running along the body. The tail has alternating bands of light and dark patches.

Occurrence & relative abundance: Simeulue (rare), (Banyak Islands (rare), Siberut (rare), Enggano (abundant).

Habits & collection: This species lives in primary as well as old secondary forests from lowlands up to 1,600 m elevation. Their coloration allows them to blend in relatively well on the barks of tree trunks, where they are usually found quite high above the ground (~3–10m or more). My collection came from Simeulue (JAM 10035), the Banyak Islands (JAM 11164), Siberut (JAM 10349). J.A. McGuire collected a substantial series from Enggano (JAM 4172–86, 4212–4, 4241–3, 4290, 4368, and 4409).

SKINKS – FAMILY SCINCIDAE

Dasia olivacea (Gray, 1839)

Common name: Olive tree skink.

Description: This species of tree skink has a robust, stocky built with strong limbs. The snout is long and depressed, and the lower eyelid is scaly. The supranasals are present, often separated. The body has 28–30 scales around mid-body, dorsals and laterals with three to nine strong keels. The nuchal scales are smooth or feebly keeled, dorsals larger than ventrals. The tail is nearly 1 1/3 the length of head and body. The limbs are strong, the hind limb reaches the wrist; digits moderate, strongly compressed distally, fourth toe with 17–20 smooth lamellae below. The color is olive or brownish above, with transverse series of light, dark-edged spots; sometimes a light dorsolateral band is present on the posterior part of the body and on the tail; sutures between the head-shields black; with a black spot on parietals and nuchals. Lower parts are greenish. The young specimens have markedly different coloration, with transverse wide bands of black alternating with narrower greenish ones, and a scarlet tail (deRooij 1915).

Occurrence & relative abundance: Simeulue (common), Banyak Islands (common), Nias (common), Siberut (common), Sipora (common).

Habits & collection: The olive tree skink inhabits the canopy of coastal forests and offshore islands. It is more commonly encountered, however, on the trunks of coconut palms on the shoreline adjacent to such forests. It is a fully arboreal species that rarely descends to the ground. The species is common, but we only made a small collection from Simeulue (JAM 9971, a juvenile), Banyak Islands (JAM 11079), Nias (JAM 10145–6), Siberut (JAM 10333), and Sipora (JAM 10731, 10843).

Eutropis multifasciatus (Kuhl, 1820)

Common name: Many-lined sun skink, many-striped skink, common sun skink.

Description: This species of kink has a short, obtuse snout. The lower eyelid is scaly; with a lart ear-opening large. The parietal scales are separated. The body has 30–34 scales around the middle. The tail is about one time and a half the length of head and body. It has a robust build with strong limbs. The hind limbs do not reach the axilla. The digits are long and compressed, with smooth lamellae below. The color is olive-brown above. It can be uniform, or the scales can be bordered laterally with black, forming longitudinally oriented lines. Sometimes a light dorso-lateral band or a light,

yellow or reddish stripe is present on each side towards the head. The flanks are dark brown with light, black-edged spots. The lower parts are greenish (deRooij 1915).
Occurrence & relative abundance: Nias (common), Batu Islands (common), Siberut (common), Sipora (common), South Pagai (common), Enggano (common).
Habits & collection: This species is a common inhabitant of a variety of disturbed and undisturbed habitats. We have found them in gardens as well as on the forest floor, and they are known from sea-level to 1,800m above sea level (Manthey & Grossman 1997). We did not make a big collection of this species primarily because they are difficult to capture: eight from Nias (JAM 10184–7, 10245–7, 10249), one from the Batu Islands (JAM 11038), five from Siberut (JAM 10334, 10367–8, 10414–5), one from Sipora (JAM 10730), four from South Pagai (JAM 10535, 10547, 10558, 10678), and 12 from Enggano (JAM 4224–6, 4244–5, 4380–2, 4387–90).

Eutropis rudis (Boulenger, 1887)

Common name: Rough mabuya, brown mabuya.
Description: Like *E. multifasciata* this species of ground-dwelling skink has a robust build and strong limbs. The snout short and obtuse, and the lower eyelid is scaly. The postnasals are present. The body has 30–36 scales around the middle. The tail is almost twice the length of head and body. The limbs are strong, and the hind limb reaches the axilla or the shoulder. The digits are compressed, with keeled lamellae below (vs. smooth in *E. multifasciata*). The color above is olive-brown; with a dark brown light-edged lateral band beginning at the eye. The flanks are brown with light spots. Lower parts are brownish or greenish; sometimes black spots on the throat (deRooij 1915).
Occurrence & relative abundance: Siberut (rare).
Habits & collection: This species inhabit flat as well as hilly terrains, both in grassy, open areas as well as forest floor. We only collected one specimen from the island of Siberut (JAM 10392).

Eutropis rugifera (Stoliczka, 1870)

Common name: Nicobar Island skink.
Description: This species of ground-dwelling skink is similar in build to *E. rudis* and *E. multifasciata*, with a snout is short and obtuse and scaly lower eyelid. However, in *E. rugifera* the postnasal is absent, and the body has 20–26 scales around the middle. The frontonasal is more broad than long. The nuchal, dorsal and lateral scales have five strong keels. The tail is 1 2/3 times the length of head and body. The limbs are strong with keeled scales, and the hind limb reaches the elbow. The digits have smooth lamellae below. The color is olive brown above, uniform or with 5 or 7 light longitudinal lines. The lower parts are orange-red (deRooij 1915).
Occurrence & relative abundance: Nias (rare).
Habits & collection: This species inhabits lowland forests up to elevations of 1,000m above sea level. We collected one specimen from Nias (JAM 10262), in a patch of disturbed secondary growth forest adjacent to a stream.

Lipinia relicta Vinciguerra, 1892

Common name: Vinciguerra's lipinia.

Description: This small species of skink has a lower eyelid with a transparent disk. The ear opening is covered with scales, and its presence indicated instead by a depression. The body is long, with 20–22 smooth scales around the middle, and enlarged preanals. The tail is thick, longer than the head and body. The limbs are short, and the hind limbs do not reach the fore limbs when stretched. The digits are slender, with the fourth toe being the longest. The digits have 18 smooth lamellae below. The color is brown above, with four longitudinal black lines. There is a light vertebral stripe beginning between the eyes. The labials have a small median white spot. The lower parts are light brown (deRooij 1915).
Occurrence & relative abundance: Siberut (rare), Enggano (infrequent).
Habits & collection: We encountered this species on Siberut (JAM 10461) crawling on a pile of firewood outside of a house. It was also found on Enggano (JAM 4374–8), where it was collected under decomposing logs in selectively logged forest.

Lipinia vittigera Boulenger, 1894

Common name: Yellow-striped tree skink.
Description: This is a small species of skink with a slender body. The lower eyelid has a transparent disk. The tympanum is distinct, and the supranasals are absent. The rostral forms a suture with the frontonasal; frontal not broader than the supraocular region; enlarged nuchals present. The limbs are strong and pentadactylous. The hind limb is longer than the distance between the centre of the eye and the forelimb. The body has 28 smooth scales around the middle, with the two vertebral series being the largest. The laterals are small and the preanals are enlarged. The color is pale reddish-brown above, with a greenish white vertebral stripe that begins at the tip of the snout, bordered on each side by a broad black stripe. The flanks are pale olive color, with or without black dots. The limbs are black-spotted. Lower part of the body is greenish-white (deRooij 1915).
Occurrence & relative abundance: Nias (rare).
Habits & collection: This species is known to live in hills as well as flatland habitats up to 1,600m elevation, usually in forests. It is often encountered hiding under loose tree bark. We found one individual from Nias living in a disturbed secondary forest (JAM 10159).

Sphenomorphus cf. *modiglianii* (Boulenger, 1894)

Common name: Modigliani's forest skink.
Occurrence & relative abundance: Sipora (indeterminate), South Pagai (indeterminate).
Habits & collection: This is a forest-floor species of skink that inhabits primary and mature secondary forests. Since we did not utilize pitfall traps, it is difficult to determine the abundance of this species. My small collection was made primarily serendipitously from Sipora (JAM 10806, 10888), and South Pagai (JAM 10563).
Taxonomic comment: This genus is undergoing some revisions and recent data indicate that many species may consist of multiple lineages (C.W. Linkem, pers. comm.).

TYPICAL SNAKES – FAMILY COLUBRIDAE

Ahaetulla prasina (Boie, 1827)

Common name: Oriental whipsnake, Asian vine snake.

Description: This species of vine snake has a slender build and a sharply pointed snout, projecting more than twice as long as the eye. The internasals are usually in contact with the labials; one to four small loreals in a row between the prefrontal and the labials; frontal as long as or a little longer than its distance from the tip of the snout, longer than the parietals; a pre-ocular, in contact with the frontal; two postoculars; temporals 2 + 2 or 3 + 3 (1+2); nine upper labials, fourth to sixth entering the eye; four lower labials in contact with the anterior chin-shields; latter shorter than the posterior. Scales are in 15 rows, those of the sacral region usually keeled; ventrals 194–235; anal divided (rarely entire); subcaudals 151–207. The color is green, olive or greyish-brown; skin of the neck black and white. Lower parts are greenish or greyish; a yellow or white lateral stripe on each side (deRooij 1915).

Occurrence & relative abundance: Nias (rare).

Habits & collection: This species inhabits primary lowland and montane moist forests, secondary forests, dry and open forests, scrublands, plantations, gardens, monsoon forest, cultivated land, roadsides, and city gardens. The species of this genus are arboreal, diurnal snakes, living on shrubs and bushes, but foraging on the ground. We collected one specimen from Nias Island (JAM 10234).

Aplopeltura boa Boie, 1828

Common name: Blunt-headed slug snake.

Description: This species has a snout that is very short and deep; rostral is narrow, much more deep than broad; frontal not broader than the supraocular, almost twice as long as broad, longer than its distance from the tip of the snout, as long as or a little longer than the parietals; two or three enlarged occipitals; two or three superposed loreals, the lower sometimes entering the eye; 6–8 shields in addition to the supraocular round the eye; temporals 3 + 3 or 4; eight to ten upper labials; two pair of lower labials in contact behind the mental; three or four pairs of large chin-shields, the anterior sometimes fused or preceded by an azygous shield. The scales are arranged in 13 rows; ventrals 148–191; anal entire; subcaudals 88–127. Pale brown or yellowish above, usually with large, dark brown blotches, sometimes extending to the belly; a large, dark brown spot on the head; sides of head whitish, with dark streaks radiating from the eye. Lower surface is yellowish, mottled with dark brown (deRooij 1915).

Occurrence & relative abundance: Banyak Islands (infrequent), Nias (rare).

Habits & collection: This species is nocturnal and arboreal. We found our specimens curled around branches on low-lying vegetation. We obtained specimens on the Banyak Islands (JAM 11115, 11183) and Nias (JAM 10129).

Boiga cynodon (Boie, 1827)

Common name: Dog-toothed cat snake.

Description: This species of cat snake has a more robust build compared to other *Boiga* such as *B. drapiezii* or *B. nigriceps*. It has a snout that is longer than the eye; the rostral is more broad than deep, just visible from above; internasals shorter than the prefrontals;

frontal as long as or longer than its distance from the tip of the snout, shorter than the parietals; loreal as long as deep or more long; a preocular, extending to the upper surface of the head, narrowly separated from the frontal; two post-oculars; temporals 2 + 2, 2 + 3 or 3 + 3; eight to ten upper labials, third to fifth, fourth and fifth, fourth to sixth or fifth to seventh entering the eye; four or five lower labials in contact with the anterior chin-shields; latter smaller than the posterior; anterior palatine teeth strongly enlarged. Scales are in 23 or 25 rows, vertebrals strongly enlarged; ventrals 248–290; anal entire; subcaudals 114–159. The color is yellow or reddish-brown above, with dark brown or black transverse spots or bars, sometimes absent, or blackish above with lighter transverse bars and a series of white spots on the sides; a dark streak on each side of the head behind the eye; labials sometimes with dark vertical lines. Lower surface yellow, uniform or speckled with brown, or entirely black (deRooij 1915).

Occurrence & relative abundance: Nias (rare), South Pagai (rare).

Habits & collection: This species is arboreal and is typically encountered in lowland areas. We found our specimens actively foraging at night, usually high in the branches of medium- to large-sized trees. Two specimens were collected, one each from Nias (JAM 10237) and South Pagai (JAM 10633).

Boiga drapiezii (Boie, 1827)

Common name: White-spotted cat snake.

Description: In this species of cat snake, the eye is as long as the snout; the rostral is more broad than deep, just visible from above; the internasals are shorter than the prefrontals; frontal as long as its distance from the tip of the snout, shorter than the parietals; loreal small or absent; a preocular, in contact with the frontal or narrowly separated from it; two postoculars; temporals 2 + 2, 2 + 3 or 3 + 3; eight upper labials, third to fifth or fourth and fifth entering the eye; five or six lower labials in contact with the anterior chin-shields; latter as long as or longer than the posterior; anterior palatine teeth not much enlarged. Scales are in 19 rows, vertebrals enlarged; ventrals 250–276; anal entire; subcaudals 114–163. The color is light brown above with dark brown transverse spots or brown with yellow or red, dark-edged transverse bands, each band ending in a white spot. Lower surface is brownish-white, uniform or speckled with brown and with two brown longitudinal lines, sometimes indistinct (deRooij 1915).

Occurrence & relative abundance: Batu Islands (rare), South Pagai (infrequent).

Habits & collection: This species is commonly found in lowland areas up to 1,100m, in rainforests as well as freshwater swamp habitats (citation). Our specimens came from the Batu Islands (JAM 10956) and South Pagai Island (JAM 10634, 10676).

Boiga nigriceps (Günther, 1863)

Common name: Black-headed cat snake.

Description: Snout is longer than eye; rostral more broad than deep, visible from above; internasals shorter than the prefrontals; frontal as long as its distance from the tip of the snout, shorter than the parietals; loreal as long as deep or more long; a pre- ocular, in contact with the frontal or narrowly separated from it; two postoculars; temporals 1+ 2 or 2 + 3 or 3 + 3; eight upper labials, third to fifth entering the eye; four or five lower labials in contact with the anterior chin-shields; latter often much shorter than the posterior; anterior palatine teeth not much enlarged. Scales are arranged in 21 rows,

vertebrals much enlarged; ventrals 240–263; anal entire; subcaudals 140–154. The color is brownish or reddish-grey, uniform or speckled with dark brown, sometimes a series of black spots on the back; head dark gray or reddish; upper lip paler than surrounding skin. Lower surface grey, with dark spots (deRooij 1915).
Occurrence & relative abundance: Simeulue (rare), Siberut (rare), South Pagai (infrequent).
Habits & collection: This species is known to inhabit the forests but also occurs in abandoned man-made structures, at elevations up to 1,100 m above sea level (citation). We collected one specimen from Simeulue (JAM 10063), one from Siberut (JAM 10393), and two from South Pagai (JAM 10516, 10635).

Cerberus rynchops (Schneider, 1799)

Common name: Dog-faced water snake.
Description: The frontal in this snake is distinct or broken up into small shields; the nasal cleft extends to the first upper labial, sometimes to the second; loreal usually in contact with the three or four anterior labials and with the internasal; the eye is bordered by four or six shields, a supraocular, a preocular, one or two post- and one, two or three suboculars; nine or ten upper labials; four lower labials in contact with the anterior chin-shields; posterior chin-shields smaller, between the anterior and the labials. The scales are strongly keeled, in 23, 25, or 27 rows; ventrals 122–160; anal divided; subcaudals 49–72. Color is usually grey, olive or dark brown above, with black spots or transverse bands, sometimes indistinct; a light lateral band; a black streak on each side of the head, passing through the eye. Lower surface is whitish, spotted with black, or with black transverse bands or almost entirely black (deRooij 1915).
Occurrence & relative abundance: Batu Islands (infrequent), South Pagai (rare), Enggano (infrequent).
Habits & collection: This species is commonly found inhabiting mangroves and mudflats of coastal areas, but can also be observed occasionally in inland freshwater and is often abundant in rice fields. Our encounters were sporadic and infrequent, resulting in two specimens from the Batu Islands (JAM 10968–9), one specimen from South Pagai (JAM 10515), and four specimens from Enggano (JAM 4369–72).

Dendrelaphis caudolineatus (Gray, 1834)

Common name: Striped bronzeback.
Description: In this species, the eye is longer than its distance from the nostril. The rostral is more broad than deep, visible from above; internasals as long as or shorter than the prefrontals; frontal longer than its distance from the tip of the snout, shorter than the parietals; loreal long; one pre- and two postoculars; temporals 2 + 2; nine upper labials, fifth and sixth (fourth to sixth) entering the eye; five lower labials in contact with the anterior chin-shields; latter shorter than the posterior. Scales in 13 rows, vertebrals larger than adjacent dorsal scales; ventrals 171–189; anal divided; subcaudals 97–118. The color is brownish or greenish-yellow above, with black longitudinal lines that are formed by the edges of the scales. A yellow lateral streak is present between two black bands, with the lower band on the outer ends of the ventrals. The lips are yellow. The lower surface is yellow, with a black median line along the tail (after deRooij 1915).
Occurrence & relative abundance: Banyak Islands (rare), Nias (rare).

Habits & collection: The striped bronzeback inhabits a variety of habitats, ranging from closed forests and secondary growth, to scrubland, and is especially abundant along stream courses. It is a diurnal species, but can be found at night sleeping in overhanging branches. We collected two specimens: one from Banyak Islands (JAM11117) and one from Nias (JAM10134).

Dendrelaphis formosus (Boie, 1827)

Common name: Elegant bronzeback.
Description: This species is easy to distinguish from other bronzebacks from its exceptionally large eyes, which are as long as their distance from the rostral or the anterior border of the nostril. 28–31 maxillary teeth. The rostral is more broad than deep, visible from above; and the internasals are longer than the prefrontals. The frontal as long as its distance from the tip of the snout, as long as the parietals; loreal long; one pre- and two to four postoculars; temporals 2 + 2; nine upper labials, fifth and sixth, fourth to sixth or third to fifth entering the eye; five lower labials in contact with the anterior chin-shields; latter much shorter than the posterior. Scales are in 15 rows, with the vertebral scales larger than adjacent dorsal scales; ventrals 174–205; anal divided; subcaudals 132–158. The color is predominantly olive, bronze or yellowish-brown above, with black-edged scales and red and green tints. A black stripe is present on each side of the head, passing through the eye, and is widest on the nape. The neck is red-brown; sometimes two black lines along each side of the body posteriorly; upper lip greenish-yellow. Lower surface pale green (deRooij 1915).
Occurrence & relative abundance: Batu Islands (rare), South Pagai (rare).
Habits & collection: The elegant bronzeback is found in lowland rainforests. They live an arboreal lifestyle, and thus can be seen climbing on branches and vines. Our collection was made form the Batu Islands (JAM 11078) and South Pagai Island (JAM 10514).

Dryocalamus subannulatus Duméril, Bibron & Duméril, 1854

Common name: Malayan bridle snake.
Description: This species has a rostral that is visible from above. The nasal is divided or partly divided; the suture between the internasals is as long as or longer than that between the prefrontals; frontal longer than its distance from the tip of the snout, shorter than the parietals; loreal more long than deep, entering the eye; one pre- and two post-oculars; temporals 2 + 2; seven upper labials, third and fourth entering the eye; three or four lower labials in contact with the anterior chin-shields; latter longer than the posterior. Scales are in 15 rows; ventrals 225–244; anal entire; subcaudals 88–107. The color is light brown above, with large, brown, transverse spots across the back; on each side a series of small spots, alternating with the dorsals. There are two transverse brown streaks on the head: the anterior on the prefrontals, and the other between the eyes; with a brown spot on the parietals. The lower surface is yellowish (deRooij 1915).
Occurrence & relative abundance: Siberut (rare).
Habits & collection: The Malayan bridle snake is an inhabitant of flat primary and secondary rainforests. We found our only specimen (JAM 10460) actively foraging on the trunk of a large buttess tree at night on Siberut in a patch of mature secondary forest.

Dryophiops rubescens (Gray, 1835)

Common name: Keel-bellied whip snake, brown whip snake.
Description: This species has a rostral that is two times as broad as deep, just visible from above. The internasals are shorter than the prefrontals; the frontal is as long as its distance from the tip of the snout, shorter than the parietals; loreal long; one preocular, in contact with the frontal; two or three postoculars; temporals 2 + 2; nine upper labials, fourth to sixth entering the eye; four or five lower labials in contact with the anterior chin-shields, posterior larger. The scales are reddish-brown above, with small black spots; on the head wavy longitudinal markings are present, as well as a median streak on the occiput and neck. A dark streak is present on each side passing through the eye. The labials have black spots. The lower surface is yellow or greenish, reddish or brownish posteriorly, dotted with dark and with or without small dark spots (deRooij 1915).
Occurrence & relative abundance: Banyak Islands (rare).
Habits & collection: This slender, climbing snake is an inhabitant of lowland primary and secondary forest, although it will also wander into adjacent disturbed, open areas. We found our specimen climbing on the roof struts of a bamboo hut in an open, freshly logged field in the Banyak Islands (JAM 11198).

Gonyosoma oxycephalum (Boie, 1827)

Common name: Red-tailed green rat snake, red-tailed racer.
Description: This snake has a long, projecting snout. The rostral is about as broad as deep, visible from above; internasals shorter than the prefrontals, which are large; the frontal is as long as its distance from the rostral or the tip of the snout, shorter than the parietals; loreal long; preocular large, in contact with the frontal; two postoculars; temporals 2 + 3; nine to eleven upper labials, fifth and sixth or sixth and seventh entering the eye; six lower labials in contact with the anterior chin-shields; latter much longer than the posterior. The body compressed; scales in 23–27 rows, smooth or feebly keeled; ventrals 233–263, with a lateral angle; anal divided; subcaudals 122–157. The coloration is bright green above, usually with black edges on the scales. The head is olive-brown, with a black streak on each side passing through the eye. The tail is yellowish- or reddish-brown, sometimes with vermilion bands. The lower surface is yellow or greenish. Young specimens are olive-brown with narrow oblique light bars on the posterior part of the back; lower parts lighter, throat yellowish, each ventral bordered behind with yellow, ventral keels yellowish (deRooij 1915).
Occurrence & relative abundance: Banyak Islands (rare), Nias (rare), Sipora (rare).
Habits & collection: Red-tailed racers live in lowland areas up to about 750m above sea level. They can be found in jungle, agricultural land, as well as mangrove forests. An excellent climber, they spend most of their time in trees and bushes. Fitting their diurnal lifestyle, we found them resting atop strong branches ~6m above ground, or actively foraging during the day. We collected one specimen from the Banyak Islands (JAM 11167), one from Nias (JAM 10089), and one from Sipora (JAM 10850). The latter was discovered after it had been bitten by a large king cobra (*Ophiophagus hannah*) and became progressively paralyzed over the course of the following 1-2 hours.

Lepturophis albofuscus (Duméril, Bibron & Duméril, 1854)

Common name: Dark wolf snake.

Description: The snout of the dark wolf snake is depressed. The eyes are moderately sized. The rostral is just visible from above; internasals half as long as the prefrontals; frontal as long as the prefrontals or slightly longer, much shorter than the parietals; loreal more long than deep, not entering the eye; one pre- and two postoculars; temporals 2 + 2; eight upper labials, third to fifth entering the eye; five lower labials in contact with the anterior chin-shields; latter shorter than the posterior. The body is slender; scales in 17 rows, all strongly keeled; ventrals 238–256, with strong lateral angle; anal divided; subcaudals 155–208 pair. The coloration is a uniform dark brown above, and yellowish below. Young specimens have yellow transverse bands (deRooij 1915).
Occurrence & relative abundance: Banyak Islands (rare).
Habits & collection: The dark wolf snake is active at night and at dusk, and is an excellent climber despite being a ground dweller in primary and secondary forests. It is common near streams and creek banks, which is just the sort of habitat in which we found our only specimen from the Banyak Islands (JAM 11150).

Lycodon subcinctus (Reinwardt, 1827)

Common name: Banded wolf snake.
Description: This species has a broad snout that is strongly depressed, and eyes that are small. The rostral is just visible from above; internasals much shorter than the prefrontals; frontal shorter than its distance from the tip of the snout, much shorter than the parietals; loreal long, widely separated from the internasal, usually entering the eye; no preocular; two or three postoculars; temporals 1+2; eight upper labials, third to fifth or sixth entering the eye; four lower labials in contact with the anterior chin-shields; latter longer than the posterior. Scales in 17 rows, dorsals feebly keeled; ventrals 128–230, with a lateral angle; anal divided (rarely entire); subcaudals 61–90 pair. The color is dark brown or black above, with a white occipital region and widely separated rings on the body and tail, disappearing in the adult. Lower surface brown or yellowish-brown (deRooij 1915).
Occurrence & relative abundance: Sipora (rare).
Habits & collection: This relatively harmless snake mimics the color of the many-banded krait (*Bungarus multicinctus*), with which it shares the northern range of distribution. It lives in primary and secondary forests up to elevation of 1,200m above sea level. Our specimen from Sipora (SZL 073), a juvenile, was captured while actively crawling at night, on a dirt road adjacent to a forest patch.

Psammodynastes pulverulentus (Boie, 1827)

Common name: Common mock viper.
Description: This species has a short snout that is pointed or slightly turned up in the adult. The rostral is more broad than deep; internasals shorter than the prefrontals; frontal two times or two times and a half as long as broad, narrower than the supraocular, longer than its distance from the tip of the snout, shorter than the parietals; loreal as long as deep, sometimes vertically divided; one or two pre- and two to four postoculars; temporals 2 + 3 or 2 + 2; eight upper labials, third to fifth entering the eye; three or four lower labials in contact with the anterior chin-shields; two smaller pairs of chin-shields posteriorly. Scales in 17 or 19 rows; ventrals 146–175; anal entire; subcaudals 44–70. Color is dark brown or reddish-brown above, with small dark and light spots; a dark band

along each side; head with symmetrical longitudinal markings, a dark band on each side of the head, passing through the eye. Lower surface speckled with brown and with dark lines and spots (deRooij 1915).
Occurrence & relative abundance: Siberut (rare), Enggano (common).
Habits & collection: The common mock viper is known to occur in primary and secondary forests, although occasionally they are also found on farmlands and agricultural fields. They are active at night, and during they day hide under rocks and inside root hollows. On Enggano, we found several specimens actively foraging at night along the margin of a pond, where they appeared to be hunting frogs. We collected this species on Siberut (JAM 10459) and Enggano (JAM 4211, 4340–2, 4407–8).

Psammodynastes pictus Günther, 1858

Common name: Painted mock viper.
Description: This species has internasals that are as long as, or a little shorter than, the prefrontals. The frontal two and a half or three times as long as broad, narrower than the supraocular, as long as the parietals; loreal as long as deep; two or three pre- and three or four post- oculars; eight upper labials, third to fifth entering the eye; third lower labial very large, bordering the mental groove behind the anterior chin-shields. Scales in 17 rows; ventrals 152–171; anal entire; subcaudals 60–80. The color is yellowish, reddish or pale brown above, with dark transverse bands between two light stripes or a dark vertebral band; a dark streak on each side of the head, passing through the eye and across the rostral, edged above with white in young specimens. The lower surface is whitish, speckled with brown and with brown dots (deRooij 1915).
Occurrence & relative abundance: Banyak Islands (rare), Batu islands (infrequent).
Habits & collection: This species occurs along the margins of shallow streams, especially in marshy mangrove forests. We encountered ours at night in patches of mangrove forest on the Banyak Islands (JAM 11162) and the Batu Islands (JAM 11048–51). On both islands, the snakes were perched atop the small branches of low-lying vegetation.

Ptyas fuscus Günther, 1858

Common name: White-bellied rat snake.
Description: The white-bellied rat snake has a rostral that is more broad than deep, visible from above; internasals shorter than the prefrontals; frontal as long as its distance from the rostral or the tip of the snout, shorter than the parietals; three loreals; one preocular; one or two small sub-oculars; two postoculars; temporals 2 + 2; nine upper labials, fifth and sixth (fourth and fifth) entering the eye; five lower labials in contact with the anterior chin-shields; latter much than the posterior. The scales are in 16 rows, smooth; ventrals 153–198; anal divided; subcaudals 160–179. The color is olive or olive-brown above. Occasionally a red, black-edged vertebral line and dark oblique bars are present on the posterior part of the body. There is a black lateral band posteriorly, covering the outer ends of the ventrals and subcaudals. The lower surface is pale yellow (deRooij 1915).
Occurrence & relative abundance: Nias (rare).
Habits & collection: This rat snake lives in primary and secondary forests up to elevations of ~900m. It also occurs in disturbed habitats such as in oil palm plantations.

My specimen from Nias (JAM 10143) was obtained dead on the road presumably after being run over by a vehicle.

Rhabdophis chrysargos (Schlegel, 1837)

Common name: Speckle-bellied keelback.
Description: This species of keelback has large eyes, and the rostral is just visible from above. The internasals are broadly truncate in front, and as long as the prefrontals. The frontal is as long as its distance from the tip of the snout, shorter than the parietals. The loreal is about as deep as long; one or two preoculars and three postoculars; temporals 2 + 2 or 2 + 3. Eight or nine upper labials, fourth to sixth or third to fifth entering the eye; five or six lower labials in contact with the anterior chin-shields; latter shorter than the posterior. Scales are in 19 rows, all strongly keeled. Ventrals 140–176; anal divided; sub-caudals 56–94. The color is brown or olive-green above, usually with yellow spots or transverse bars on each side of the back; the skin between the scales sometimes red; upper labials yellow with black sutures, the yellow colour continued as an angular or crescentic band on the nape. Young specimens with black transverse bars or black-spotted. Lower surface is yellow, sometimes black-dotted and with black spots along each side (deRooij 1915).
Occurrence & relative abundance: Sipora (rare).
Habits & collection: The speckle-bellied keelback is a snake species known from lowland and hilly areas. It is nocturnal and occurs along streams and in forest. Our specimen was captured during night collection in a hilly secondary forest patch atop a small hill ridge on Sipora (JAM 10798).

Xenochrophis trianguligeris (Boie, 1827)

Common name: Triangle keelback.
Description: This snake has moderate-sized eye, and the rostral is scarcely visible from above. The inter-nasals are trapezoid in shape, as long as or longer than the prefrontals. The frontal is as long as its distance from the tip of the snout, and shorter than the parietals. The loreal is as long as deep or more deep; one (2) preocular and three or four postoculars. Temporals 2 + 2 or 2 + 3; nine upper labials, fourth to sixth entering the eye; five lower labials in contact with the anterior chin-shields; latter shorter than the posterior. Scales are in 19 rows, and strongly keeled, but those of the outer row are feebly keeled or smooth. Ventrals 134–150; anal divided; subcaudals 69–105. The color is dark olive above, with small black spots; a lateral series of large, triangular black spots, the points reaching the ventrals and sometimes forming bands across the belly, separated by red interspaces; on the posterior part of the body the spots are indistinct; upper labials yellow, with black sutures. Lower surface is yellow, uniform or the ventrals edged with black (deRooij 1915).
Occurrence & relative abundance: Nias (common), Batu Islands (infrequent), Sipora (rare).
Habits & collection: The triangle keelback is an inhabitant of lowland moist forests. Fitting its semi-aquatic lifestyle, my collection was made primarily near or in water (slow moving creeks or small streams, although it has been reported to occur in standing body of water as well). It is a diurnal species. We made small collections from Nias (JAM 10130–1, 10224–7), the Batu Islands (JAM 10957, 11069), and Sipora (JAM 10840).

PIT VIPERS – FAMILY CROTALIDAE

Trimeresurus hageni (Lidth de Jeude, 1886)

Common name: Hagen's pit viper
Description: This species of pit viper has a long head with a short snout and moderately sized eyes. The rostral is as broad as deep or a little more broad. The nasal is entire or divided; scales on the head large, smooth, largest on the snout; supraocular large; no scales or only one between the internasals; 4–9 scales between the supraoculars; two or three postoculars; a subocular, in contact with the third or third and fourth labials; nine to eleven upper labials, second bordering the loreal pit, third largest temporal scales smooth. Scales feebly keeled, in 21 rows ventrals 180–191; anal entire; subcaudals 58–82, in two rows tail prehensile. The color is bright green above, usually with black-edged scales, with or without black transverse bands. Sometimes two series of small, light spots are present on the back, also a yellowish streak on each side along the outer row of scales. Lower surface is yellowish or green, sometimes the ventrals black-edged; end of tail red (deRooij 1915).
Occurrence & relative abundance: Nias (rare), Sipora (rare).
Habits & collection: This pit viper species resides in flatland rainforests. It can be found at night, usually curled up in trees and bushes as well as on the ground, waiting for a prey item to pass by. Compared to other pit vipers, Hagen's viper is more docile and does not attack as readily. We collected one specimen from Nias (JAM 10132), and one specimen from Sipora (JAM 10854).

Tropidolaemus wagleri (Boie, 1827)

Common name: Wagler's pit viper.
Description: This species of pit viper has a distinctly broad, triangular head. The snout is short and broad, with rather distinct ridge. The eyes are very small. The rostral is as broad as deep, or slightly more broad. The scales on the head are small and keeled. The dorsal scales are keeled, in 19–27 rows; ventrals 127–154; anal entire; subcaudals 45–56, in two rows; tail prehensile. The color is primarily green above, with black edges around the scales. May have bright yellow, black-edged transverse bands, or black with yellow transverse bands, or green above with large red, black-edged spots. The head is black, yellow-spotted. The lower surface is yellow or greenish, the ventrals black-edged, or white with black spots and powdered with red; end of tail black or red. Young specimens green, with yellow or white transverse lines, edged with blue or purple posteriorly, or with two series of small spots on the back; a light line on each side of the head, passing through the eye and edged below with blue or purple. Lower parts white or green, uniform or with black borders to the scales; end of tail red or reddish-brown (deRooij 1915).
Occurrence & relative abundance: Banyak Islands (rare), South Pagai (rare).
Habits & collection: Wagler's pit viper is a nocturnal species that can be found in lowland primary and old secondary forests. We found our specimens in the Banyak Islands (JAM 11141) and on South Pagai (JAM 10671).

COBRAS, KRAITS & CORAL SNAKES – FAMILY ELAPIDAE

Calliophis bivirgata (Boie, 1827)

Common name: Blue Malayan coral snake.

Description: Rostral is slightly more broad than deep; frontal large, as long as or longer than its distance from the tip of the snout, as long as or shorter than the parietals; one pre- and two postoculars; temporals 1 + 1 or 1 + 2; six upper labials, third and fourth entering the eye; three or four lower labials in contact with the anterior chin-shields; latter a little longer than the posterior. The scales are arranged in 13 rows; ventrals 244–295; the anal is entire; subcaudals 34–53. The color is primarily black or dark purple above, with a fine white lateral line between the two outer rows of scales. Sometimes it has four white lines, with the outer ones broader and running along the two outer rows of scales, or with a pale blue lateral band along the two outer rows. The head and tail are red. The lower surface is red (deRooij 1915). Highly venomous.

Occurrence & relative abundance: Banyak Islands (rare)

Habits & collection: This species was observed but not collected during our fieldwork. We encountered one individual while night collecting in a disturbed secondary forest patch. It was actively foraging and only briefly visible, and we were consequently unable to capture the snake.

Ophiophagus hannah Cantor, 1836

Common name: King cobra.

Description: The king cobra—one of the world's longest venomous snakes—has a rostral that is more broad than deep, just visible from above. The large pair of occipitals is an easily distinguishable character of this snake. Scales are in 15 rows, 19–21 round the neck; ventrals 215–262; anal entire; subcaudals 80–120, the anterior usually single. The color is usually yellowish, brown, olive or black above, with or without dark or white transverse bars; sometimes with black edges to the scales. Lower surface whitish, the shields black-edged, or dark brown, chin and throat yellow. Young specimens are black, with yellow round spots in transverse series or with a yellow spot on each scale (deRooij 1915). Large sized—the animals we saw are all ~3–4m long—and highly venomous.

Occurrence & relative abundance: Simeulue (rare), Siberut (rare), Sipora (rare).

Habits & collection: Despite numerous sightings of this species, we were only able to make a collection from Simeulue (JAM 10038), where the animal was found dead on the road having been killed by locals. On Siberut, we caught a glimpse of one individual at night, before it disappeared into a large pile of branches on the ground in a cleared patch of forest not too far away from primary growth. On Sipora, J.A. McGuire saw a large individual (approximately 4 m in total length during the day in a patch of mature secondary forest, but was unable to capture it.

BLIND SNAKES – FAMILY TYPHLOPIDAE

Typhlops lineatus (Schlegel, 1839)

Common name: Striped blind snake.

Description: This species of blind snake has a rounded snout that is strongly projecting and with an inferiorly placed nostrils. The rostral is very large; the nasal incompletely divided, the cleft proceeding from the first labial; a single large ocular on each side behind the nasal. The eyes are not distinct. The prefrontal, supraoculars and parietals are enlarged and transverse. The body has 22 scales around the middle; its diameter 40 to 60 times in the total length. The tail is about as long as broad, ending in a spine. The color is blackish above, each scale spotted with yellow, or yellow or pale brown with dark brown longitudinal lines between the series of scales. The head and lower surface is yellowish (deRooij 1915).

Occurrence & relative abundance: Enggano (rare).

Habits & collection: The one individual that we obtained was on Enggano (JAM 4379). It was found beneath a decomposing log in selectively-logged forest.

SUNBEAM SNAKES – XENOPELTIDAE

Xenopeltis unicolor Reinwardt, 1827

Common name: Sunbeam snake.

Description: This monotypic species is easily identifiable from its uniformly brown, iridescent dorsal coloration. It has a head that is depressed with a rounded snout. The nostril is placed between two nasals; the frontal is as long as its distance from the rostral; the preocular is large; two postoculars, upper one largest; a small supraocular, smaller than the upper postocular; a large, azygous interparietal, in the middle of four parietals; eight upper labials, first in contact with the internasal, fourth and fifth entering the eye; a pair of small chin-shields, in contact with the three anterior lower labials. The scales are smooth and in 15 rows. 164–193 ventral scales. The anal is divided, and it has 26–31 subcaudals. Lower surface is white. In young specimens, the head is whitish with a white or yellow collar present (deRooij 1915).

Occurrence & relative abundance: Banyak Islands (rare), Siberut (rare).

Habits & collection: Banyak Islands JAM 11180, Siberut (JAM 10369).

REPTILIA, TESTUDINES

SOUTH AMERICAN AND ASIAN POND TURTLES – FAMILY GEOEMYDIDAE

Cuora amboinensis Daudin, 1802

Common name: Asian box turtle.

Description: The distinguishing features of this species are the yellow face and neck, with the dorsal surface of the head black, and three black stripes on side of face. The plastron is pale, usually with dark spot on the outer edge of each scute. The plastron is hinged, allowing the turtle to close up its shell like a box. The underside of the marginals are yellow with black spot along the border (Stuart et al. 2001, Asian Turtle Conservation Network).

Occurrence & relative abundance: Enggano (rare).

Habits & collection: This is a terrestrial and aquatic species that can often be found quite far away from water, but more typically they occur in streams and marshes in lowland forests, rice paddies, as well as creeks in mangrove habitats. J.A. McGuire collected this species from Enggano Island (JAM 4343).

Heosemys spinosa (Gray, 1830)

Common name: Spiny pond turtle.
Description: The head of this species is covered with smooth skin, undivided. The alveolar surfaces are narrow, without median ridge. The choanae are located between the eyes. The plastron is united to the carapace by suture. The tail is very short. The carapace is unicarinate, and the axillary and inguinal shields are present. The bony temporal arch is absent. The carapace is reddish-brown in color; the plastron is yellow and brown with radiating streaks on each shield. The soft parts are brown, with a yellow spot on each side of the nect near the ear. The head and limbs are scarlet-spotted in life (van Kampen 1923).
Occurrence & relative abundance: Siberut (rare).
Habits & collection: The spiny pond turtle inhabits lowland and hill rainforest, usually in the vicinity of small streams, typically in hilly areas up to elevations of 900 m above sea level (Asian Turtle Trade Working Group Data 2000). We encountered this species in a shallow stream situated in a pristine primary forest on the northern part of the island of Siberut. Because the locality was designated as a no-capture research station, we did not make a collection of the animal.

DISCUSSION

This list is by no means comprehensive. Considering that my stay at any given locality was limited and my sampling method did not include pitfall trapping, I am quite certain that my survey missed many forest-floor and less common species. Nevertheless, we were able to add considerably to our knowledge of the herpetofauna of the area, especially for islands that had received the least amount of scientific attention in the recent past. For example, the Banyak Islands had never been mentioned in older records and aside from another recent study (Tapley & Muurman 2011), all the species encountered by my team represent a new record for the island group.

It is quite clear from morphological evidence that Nias, Simeulue and Enggano seem to have many endemics. By contrast, the Mentawai, Batu and Banyak Islands seem to be inhabited by species that also occur on adjacent Sumatra, and molecular data are required to determine how isolated these populations are.

The time cannot be more fitting to study the biodiversity of Western Archipelago herpetofauna. Studies on the effect of Pleistocene glaciation in the Sunda Shelf indicated that the islands of Western Archipelago serve as forest refugia when the climate was drier (Gathorne-Hardy et al. 2002; Meijaard 2003), and that the landmasses of Sunda Shelf is currently in a refugial state (Cannon et al. 2009). This means that the diversity inhabiting Western Archipelago will have a significant role as source populations during the next glaciation cycle. Despite this importance, no conservation status has been granted to these islands except for the Siberut National Park on the northernmost island of the Mentawai group. My personal observation during fieldwork confirmed that forest logging and agricultural land conversion seem to run rampant on these islands. With the lack of protection, scientists must race against deforestation and habitat degradation to document the biodiversity and study these islands in greater details.

References

AmphibiaWeb: Information on amphibian biology and conservation. [web application]. 2011. Berkeley, California: AmphibiaWeb. Available: http://amphibiaweb.org/. (Accessed: Sep 17, 2011).

Asian Turtle Conservation Network. *Cuora amboinensis*. http://www.asianturtlenetwork.org/field_guide/Cuora_amboinensis.htm. Accessed: September 17, 2011.

Asian Turtle Trade Working Group 2000. *Heosemys spinosa*. In: IUCN 2011. IUCN Red List of Threatened Species. Version 2011.1. <www.iucnredlist.org>. Downloaded on 17 September 2011.

Boulenger, G.A. 1890. *The fauna of British India*: *Reptilia and Batrachia*. Taylor & Francis, London: 541pp.

Boulenger, G.A. 1894. A list of the reptiles and batrachians collected by Dr. E. Modigliani on Sereinu (Sipora), Mentawai Islands. *Annal. Mus.Civ. Stor. Nat. Genova* (2a)14: 613–618.

Brongersma, L.D. 1933. Herpetological notes: III Snakes from the Mentawei Islands. *Zoologische Mededeelingen*, Leiden 16:3–12.

Brongersma, L.D. 1934. Contribution to Indo-Australian Herpetology. *Zoologische Mededeelingen*, Leiden 17:161–251.

Cannon, C.H., R.J. Morley, A.B.G. Bush. 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.

Crump, M. L. and N. J. Scott Jr.. 1994. Visual encounter surveys. In Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L-A. C. Hayek, and M. S. Foster (Eds.). *Measuring and monitoring biological diversity: standard methods for amphibians.* Smithsonian Institution Press, Washington. Pp 84–92.

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.

Das, I. & K.K.P. Lim. 2005. New species of Dibamus (Squamata: Dibamidae) from Pulau Nias, Indonesia. *Journal of Herpetology* 39(1): 113–117.

deRooj, N. 1917. *The reptiles of the Indo-Australian Archipelago, Vol. I & II.* E.J. Brill, Ltd., Leiden.

Dring, J.C.M., C.J. McCarthy & A.J. Whitten. 1989. The terrestrial herpetofauna of the Mentawai Islands, Indonesia. *Indo-Malayan Zoology* 6: 119–132.

Emerson, S., and Ward, R. 1998. Male secondary sexual characteristics, sexual selection, and molecular divergence in fanged ranid frogs of Southeast Asia. *Zool. J. Linn. Soc.* 122: 537–553.

Emerson, S.B., R.F. Inger & D.T. Iskandar. 2000. Molecular systematics and biogeography of the fanged frogs of Southeast Asia. *Molecular Phylogenetis and Evolution* 16(1): 131–142.

Gathorne-Hardy, F.J., Syaukani, R.G. Davies, P. Eggleton & D.T. Jones. 2002. Quaternary rainforest refugia in south-east Asia: Using termites (Isoptera) as indicators. *Biol. J. Linn. Soc.* 75: 453–466. Hennig, W. 1936. Revision der Gattung Draco (Agamidae). *Temminckia* 1: 153–220.

Inger, R.F. 1966. The systematics and zoogeography of the amphibia of Borneo. *Fieldiana Zoology* 44(20): 151–159.

Inger, R.F. & R.B. Stuebing. 2005. *A field guide to the frogs of Borneo.* Natural History Publications, Kinabalu: 200pp.

Iskandar, D.T. & E. Colijn. 2001. *A checklist of Southeast Asian and New Guinean Reptiles part I: Serpentes*. Bina Mitra, Jakarta: 195 pp.

Ladage, S., W. Weinrebe, C. Gaedicke, U. Barckhausen, E.R. Flueh, I. Heyde, A. Krabbenhoeft, H. Kopp, S. Fajar & Y. Djajadiharja. 2006. Bathymetric survey images structure off Sumatra. *Eos* 87(17): 165–166.

Manthey, U. and Grossmann, W. (1997). *Amphibien & Reptilien Südostasiens.* Natur und Tier Verlag, Münster, Germany: 512 pp.

McLeod, D.S. 2010. Of Least Concern? Systematics of a cryptic species complex: *Limnonectes kuhlii* (Amphiba; Anura: Dicroglossidae). *Molecular Phylogenetics and Evolution*. 56: 991–1000.

Meijaard, E. 2003. Mammals of South-east Asian islands and their Pleistocene environments. *Journal of Biogeography* 30: 1245–1257.

Rödel, M.O. & R. Ernst. 2004. Measuring and monitoring amphibian diversity in tropical forests. I. An evaluation of methods with recommendations for standardization. *Ecotropica* 10:1–14.

Roos, C., T. Ziegler, J.K. Hodges, H. Zischler & C. Abegg. 2003. Molecular phylogeny of Mentawai macaques: taxonomic and biogeographic implications. *Molecular Phylogenetic & Evolution* 29(1): 139–150.

Sidik, I. 2008. An inventory of reptiles and amphibians in North-West of Siberut Island, West Sumatera. *Zoo Indonesia* 17(2): 35–48.

Smith, M.A. 1926. VIII- 'Spolia Mentawia': Reptiles and Amphibians. *Ann. Mag. Nat. Hist. London* (9)18:76-81.

Stuart, Bryan L., Peter Paul van Dijk, and Douglas B. Hendrie. 2001. *Photographic Guide to the Turtles of Thailand, Laos, Vietnam, and Cambodia*. Design Group, Cambodia.

Tapley, B. & M. Muurmans. 2011. The herpetofauna of Pulau Bangkaru. *Herpetology notes*. Accepted for publication.

Tilson, R.L. 1977. Social organization of simakobu monkeys (Nasalis concolor) in Siberut Island, Indonesia. *Journal of Mammalogy* 58(2): 202–212.

Peter Paul van Dijk, Djoko Iskandar, Robert Inger, Michael Wai Neng Lau, Yang Datong, Annemarie Ohler, Lu Shunqing, Saibal Sengupta, Sabitry Bordoloi 2004. Limnonectes kuhlii. In: IUCN 2011. *IUCN Red List of Threatened Species*. Version 2011.1. <www.iucnredlist.org>. Downloaded on 09 September 2011.

vanKampen, P.N. 1923. *The Amphibia of the Indo-Australian Archipelago*. E.J. Brill, Ltd., Leiden.

Voris, H.K. 2000. Maps of Pleistocene sea levels in Southeast Asia: Shorelines, river systems and time durations. *Journal of Biogeography* 27(5): 1153–1167.

Whittaker, D.J. 2005. New population estimates for the endemic Kloss's gibbon *Hylobates klossii* on the Mentawai Islands, Indonesia. *Oryx* 39: 458–461.

Whittaker, D. J. 2009. Phylogeography of Kloss's gibbon (Hylobates klossii) populations and implications for conservation planning in the Mentawai Islands. In *The Gibbons: New Perspectives on Small Ape Socioecology and Population Biology*, ed. S. Lappan and D. J. Whittaker. New York: Springer, pp. 73-89.

Whitten, T., S.J. Damanik, J. Anwar & N. Hisyam. 2000. *The ecology of Sumatra*. Periplus Editions, Hong Kong: xxxiii + 478 pp.

Table 1. Sampling localities from each island/island group in the Western Archipelago. The coordinates given are from the general vicinities of the trailhead or the start of transect.

Island name	**Location name, verbatim**	**Coordinate**	**Habitat type**
Simeulue	Desa Busung, Kecamatan Simeulue Timur, Kabupaten Simeulue, propinsi Nanggroe Aceh Darussalam	N 02.39037 E 96.33588	Coconut grove along coastline
	Desa Lantik, Kecamatan Teupah Barat, Kabupaten Simeulue, propinsi Nanggroe Aceh Darussalam	N 02.43314 E 96.25847	Coconut grove along coastline
	Tanjung Raya Waterfall, Kecamatan Teluk Dalam, Kabupaten Simeulue, propinsi Nanggroe Aceh Darussalam	N 02.61857 E 96.21865	Gallery forest along a creek
	Lasia island, Kecamatan Teupah Selatan, Kabupaten Simeulue, Propinsi Nanggroe Aceh Darussalam	N 02.17047 E 96.64958	Coconut grove along coastline
	Putra Jaya Waterfall, Kecamatan Simeulue Tengah, Kabupaten Simeulue, Propinsi Nanggroe Aceh Darussalam	N 02.58555 E 96.03952	Primary growth forest on karst soil
Banyak Islands	Desa Haloban, Pulau Tuangku, Kecamatan Pulau Banyak, Kabupaten Aceh Singkil, Propinsi Aceh Nanggroe Darussalam	N 02.22698 E 97.23334	Disturbed secondary forest near *ladang*
Nias	Desa Madula, Kecamatan Gunung Sitoli, Kabupaten Nias, Propinsi Sumatra Utara	N 01.23382 E 97.62055	Secondary growth near settlements
	Desa Afia, Kecamatan Gunung Sitoli Utara, Kabupaten Nias, Propinsi Sumatra Utara	N 01.38176 E 97.54481	Trees along roadside.
	Desa Maliwa'o, Kecamatan Ida Nogawo, Kabupaten Nias, Propinsi Sumatra Utara	N 01.05210 E 97.79224	Trees along roadside.
	Desa Lili'uso, Kecamatan Lolofitumoi, Kabupaten Nias, Propinsi Sumatra Utara	N 01.13282 E 97.58228	Secondary growth along a river
	Air Terjun Moawo, Kecamatan Gunung Sitoli, Kabupaten Nias, Propinsi Sumatra Utara	N 01.30079 E 97.57737	Secondary growth along dried river bed
Batu Islands	Desa Labuhan Bajau, Pulau Pini, Kecamatan Pulau Batu Timur, Kabupaten Nias Selatan, Propinsi Sumatra Utara	N 00.08523 E 98.83968	Logged secondary forest
		N 00.10071 E 98.85307	Brackish swamp forest near coast
		N 00.08853 E 98.83625	Logged secondary forest
Siberut	Dusun Pokhai, Desa Muara Sikabaluan, Kecamatan Siberut Utara, Kabupaten Kepulauan Mentawai, Propinsi Sumatra Barat	S 01. 08845 E 98.96507	Coconut grove along coastline
		S 01.12692 E 98.93879	Disturbed primary dipterocarp stand
	Desa Mongan Poula, Kecamatan Siberut Utara, Kabupaten Kepulauan Mentawai, Propinsi Sumatra Barat	S 01.15264 E 98.95486	Agricultural fields of fruit trees
Sipora	Desa Tua Pejat, Kecamatan Sipora Utara, Kabupaten Kepulauan Mentawai, Propinsi Sumatra Barat	S 02.02934 E 99.58842	Beach coastline
		S 02.10622 E 99.62143	Hilly gallery forest along hill ridge.
	Desa Goiso Oinan, Jl. Raya Tua Pejat KM 18, Kecamatan Sipora Utara, Kabupaten Kepulauan Mentawai, Propinsi Sumatra Barat	N/A	Irrigation ditches along dirt rural road
	Desa Sioban, Kecamatan Sipora Selatan, Kabupaten Kepulauan Mentawai, Propinsi Sumatra Barat	S 02.19077 E 99.72191	Coconut trees in yards
North Pagai	Desa Sikakap, Kecamatan Pagai Utara, Kabupaten Kepulauan Mentawai, Propinsi Sumatra Barat	S 02.77834 E 100.21338	Human settlements
South Pagai	Desa Bulasat, Kecamatan Pagai Selatan, Kabupaten Kepulauan Mentawai, Propinsi Sumatra Barat	S 03.07747 E 100.28314	Coconut trees on the beach
		S 03.08012 E 100.29369	Secondary forest along coast line
Enggano	Vicinity of village of Malakoni, Pulau Enggano, Kecamatan Enggano, Kabupaten Bengkulu, Propinsi Bengkulu	S 05.34878 E 102.27369	

Table 2. Consolidated records of reptile and amphibian species from the Western Archipelago. Sim = Simeulue, Ban = Banyak Islands, Bat = Batu Islands, Sib = Siberut, Sip = Sipora, N.P. = North Pagai, S.P. = South Pagai, Eng = Enggano.

Species	**Sources of records**								
	Sim	**Ban**	**Nias**	**Bat**	**Sib**	**Sip**	**N. P.**	**S. P.**	**Eng**
CAECILIANS									
ICHTHYOPHIDAE									
Ichthyophis glutinosus						3			
Ichthyophis paucisulcus					9	1	6		
FROGS									
BUFONIDAE									
Duttaphrynus melanostictus	13				13	13			
Ingerophrynus biporcatus		13							
Ingerophrynus claviger			3, 13						
Nectophryne guentheri			3,10						
Pelophryne signata					9, 13	1, 13		13	
MICROHYLIDAE									
Kaloula baleata					1, 5				
Kalophrynus punctatus				13	9	1, 13		13	
Microhyla achatina	3								
Microhyla heymonsi			13						
Microhyla palmipes								13	
Phrynella pulchra			13		4, 9, 13			13	
RANIDAE									
Fejervarya limnocharis			13						
Hylarana chalconota			13			13		13	
Hylarana erythraea	3				11				
Hylarana nicobariensis	3		13		9, 13	13		13	13
Hylarana parvaccola		13		13		13		13	
Hylarana siberu					9, 13	13		13	
Limnonectes blythii	3	13	3						3
Limnonectes kuhlii					4, 9	1, 13		13	
Limnonectes macrodon	3				4, 9, 13	1			
Limnonectes microdiscus	3		13	13	9	1, 13			
Limnonectes paramacrodon		12							
Limnonectes shompenorum	13	13	13	13	13	13		13	13
Occidozyga laevis	3				9	1			
Occidozyga sumatrana				13		13			
Odorrana hosii	3				9	13		13	
Pulchrana glandulosa				13					
Rana chalconota sensu Schlegel	3				4, 9	1			6
RHACOPHORIDAE									
Nyctixalus pictus			13		4, 13	13		13	
Polypedates leucomystax	3		13		6, 13	13	6	13	
Polypedates macrotis			3		4, 13				
Rhacophorus appendiculatus					9, 13	1, 13		13	
Rhacophorus pardalis		12	13	13	9, 13	1, 13			
LIZARDS									

Species	Sources of records								
	Sim	Ban	Nias	Bat	Sib	Sip	N. P.	S. P.	Eng
AGAMIDAE									
Aphaniotis acutirostris		12, 13	13	13	9, 13	13		13	
Aphaniotis sp. nov. Simeulue	13								
Bronchocela cristatella		12, 13	13		11, 13	1, 13	6	13	
Draco cristatellus		13		13	4, 13	13		13	
Draco melanopogon		13		13					
Draco modiglianii									2, 13
Draco obscurus		13		13	4, 11, 13	13	13	7, 13	
Draco quinquefasciatus		13		13					
Draco sumatranus		13	13	13	13	1, 13	13	13	
Draco sp. nov. Simeulue	13								
Gonocephalus chamaeleontinus		12, 13			9	1		13	
Gonocephalus grandis		13	13		9	1			
GEKKONIDAE									
Cnemaspis dezwaani[1]			13						
Cnemaspis kandiana sensu Kelaart[1]					9	1			
Cnemaspis modiglianii[1]									13
Cnemaspis whittenorum[1]					13			13	
Cyrtodactylus consobrinus		13							
Cyrtodactylus cf. *lateralis*		13							
Cyrtodactylus marmoratus									13
Cyrtodactylus cf. *quadrivirgatus*			13	13	9, 13	1, 13			
Gehyra mutilata					11, 13				
Gekko monarchus	13		13	13					
Gekko smithi		13	13		13				
Hemidactylus craspedotus		13							
Hemidactylus frenatus		12			2, 9		13		13
Hemidactylus platyurus			13			13	13		
Hemiphyllodactylus typus		13							13
Lepidodactylus lugubris									13
Ptychozoon kuhlii	13	13			2, 13				13
SCINCIDAE									
Dasia olivacea	13	13	13		4, 9, 13	13			
Emoia atrocostata					4				
Eutropis multifasciatus			13	13	9, 11, 13	1, 13		13	
Eutropis rudis					11, 13				
Eutropis rugifera			13		4, 9, 11	1			
Lipinia relicta					9, 13	1			1, 13
Lipinia vittigera			13		9, 11	1			
Sphenomorphus cf. *modigliani*						1, 13		13	
VARANIDAE									
Varanus salvator					9,11	4			
SNAKES									
BOIDAE									
Python curtus					9				
Python reticulatus	2, 5				9	1			
COLUBRIDAE									

Species	Sources of records								
	Sim	**Ban**	**Nias**	**Bat**	**Sib**	**Sip**	**N. P.**	**S. P.**	**Eng**
Ahaetulla prasina	2		13						
Aplopeltura boa		13	13						
Boiga cynodon			13		9	1		13	
Boiga dendrophila			2	2					
Boiga drapiezii					5, 9			13	
Boiga jaspidea					5				
Boiga nigriceps	2, 5, 13				2, 4, 5, 9, 13	4		13	
Calamaria elegans	2								
Calamaria klossi					9				
Calamaria lumbricoidea					2,9				
Calliophis melanurus	2								
Cerberus rynchops	2			13	2, 9, 11, 13	1		13	13
Chrysopelea paradisi		12				1			
Chrysopelea pelias					5				
Dendrelaphis caudolineatus		12, 13	13		9	1		6	
Dendrelaphis formosus				13	4, 5	4			
Dendrelaphis pictus		12			2			13	
Dryocalamus subannulatus		12			9, 13				
Dryophiops rubescens		13							
Elaphe flavolineata			2		2, 5	9			
Enhydris albomaculata	2								
Gonyosoma oxycephalum		13	13			13		6	
Lepturophis albofuscus		13							
Lycodon subcinctus	2				2, 5	13			
Oligodon purpurascens						1			
Pareas laevis					2, 9				
Psammodynastes pulverulentus		12			13				13
Psammodynastes pictus	2	13		13					
Pseudorabdion eiselti					9				
Ptyas fuscus			13						
Rhabdophis chrysargos	2				5, 9	1, 13			
Sibynophis geminatus					4, 9				
Xenochrophis trianguligeris		12	13	13		1, 13			
CROTALIDAE									
Trimeresurus hageni	5		5, 13			9, 13			
Trimeresurs puniceus	2								
Trimeresurus sumatranus	2								
Tropidolaemus wagleri		13						9, 13	
ELAPIDAE									
Maticora bivirgata		13			4				
Caliophis intestinalis					4				
Ophiophagus hannah	2, 13				13	13			
TYPHLOPIDAE									
Ramphotyphlops braminus					2				
Ramphotyphlops lineatus					2				
Typhlops lineatus									13
Typhlops muelleri					2				
XENOPELTIDAE									

Species	Sources of records								
	Sim	Ban	Nias	Bat	Sib	Sip	N. P.	S. P.	Eng
Xenopeltis unicolor	2	13			4, 13				
CROCODYLIDAE									
Crocodylus porosus		12							
TURTLES									
GEOEMYDIDAE									
Cuora amboinensis					11				13
Cyclemys dentata					9	1			
Heosemys spinosa					13				
DERMOCHELYDAE									
Dermochelys coriacea		12							
CHELONIDAE									
Caretta caretta		12							
Chelonia mydas		12							
Eretmochelys imbricata		12							

References: 1. Boulenger 1894; 2. deRooij 1915; 3. vanKampen 1923; 4. Smith 1926; 5. Brongersma 1933; 6. Brongersma 1934; 7. Hennig 1936; 8. Regenass & Kramer 1981; 9. Dring et al. 1989; 10. Iskandar & Colijn 2000; 11. Sidik 2008; 12. Tapley & Muurmans 2011; 13. This study.

Note:

1—Das (2005) designated the name *Cnemaspis kandiana* to only apply to Sri Lankan animals, whereas specimens from the Western Archipelago islands are to be broken up into several island-specific species: *C. jacobsoni* from Simeulue, *C. dezwaani* from Nias, *C. whittenorum* from Mentawai Islands, and *C. modiglianii* from Enggano.

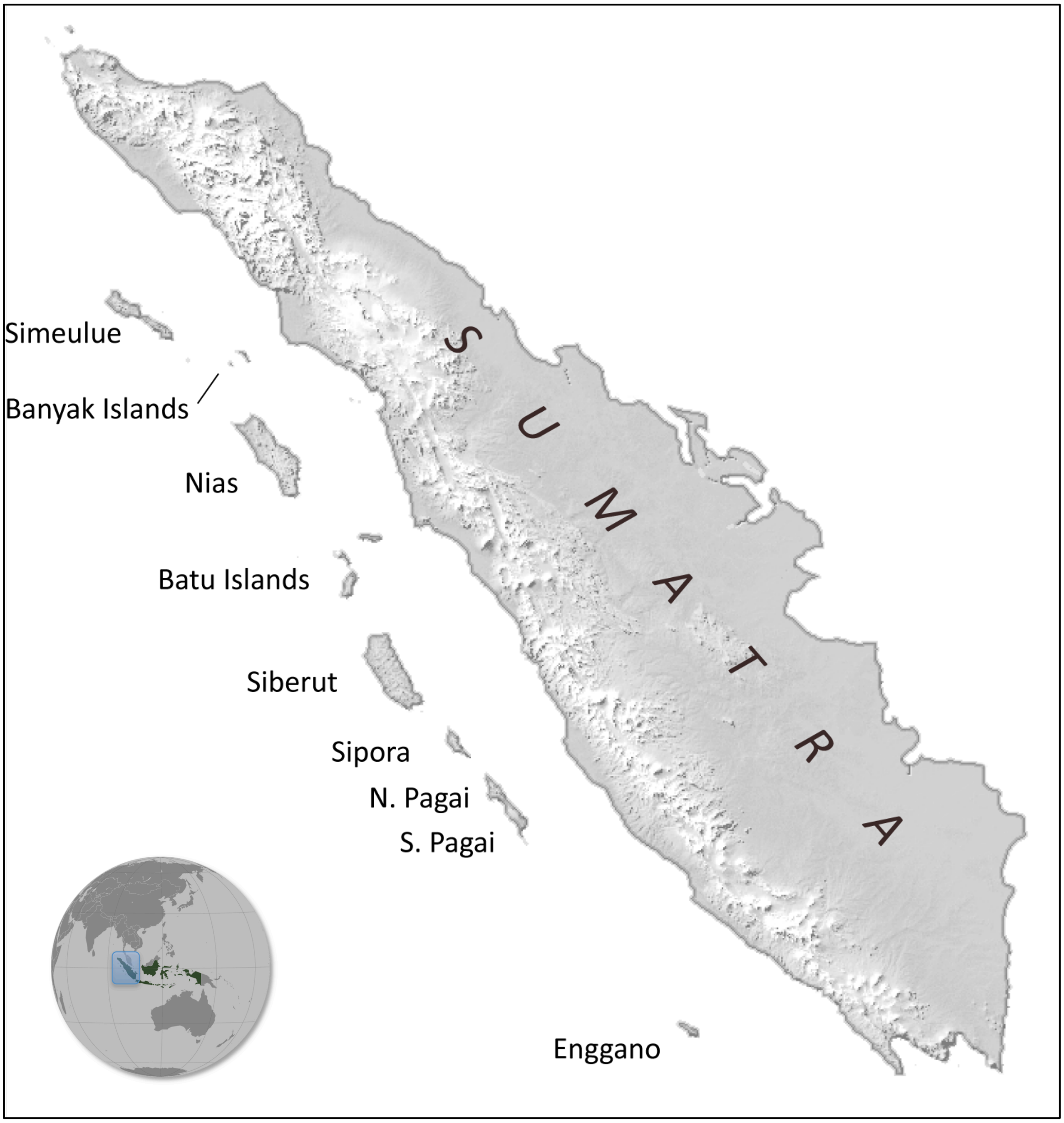


Figure 1. Map showing the location of the islands of the Western Archipelago.

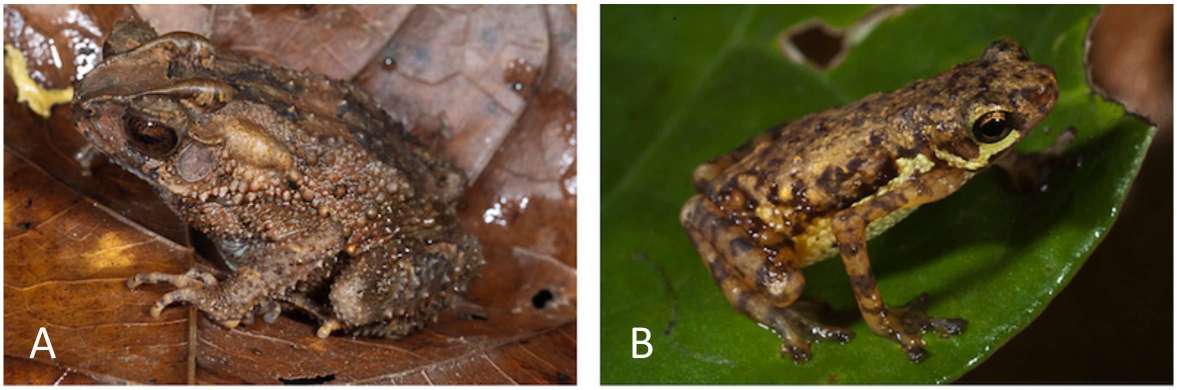


Figure 2. Some bufonids encountered in Western Archipelago. (A) *Ingerophrynus claviger* from Nias, and (B) *Pelophryne signata* from Siberut. Photos by J.A. McGuire.

Figure 3. Some microhylids encountered in the Western Archipelago. (A) *Kalophrynus punctatus* from South Pagai; (B) *Microhyla heymonsi* from Nias; (C) *Microhyla palmipes* from South Pagai; (D) *Phrynella pulchra* from Siberut. Photos by J.A. McGuire.


A
B
C
D
E
F
G

Figure 4.1. Some Ranidae frogs from the Western Archipelago: (A) *Pulchrana glandulosa* from Batu Islands; (B) *Hylarana nicobariensis* from Nias; (C) *Hylarana siberu* from Siberut; (D) *Odorrana hosii* from Sipora; (E) *Limnonectes macrodon* from Siberut; (F) *Limnonectes microdiscus* from Sipora; and (G) *Occidozyga sumatrana* from Batu Islands. Photos by the author (A,C,G) and J.A. McGuire (B,D,E,F).

Figure 5. Some rhacophorid frogs from the Western Archipelago. (A) *Nyctixalus pictus* from Siberut, (B) *Polypedates leucomystax* from Nias; (C) *Rhacophorus appendiculatus* from Siberut; (D) *R. pardalis* from Siberut. Photos by J.A. McGuire.

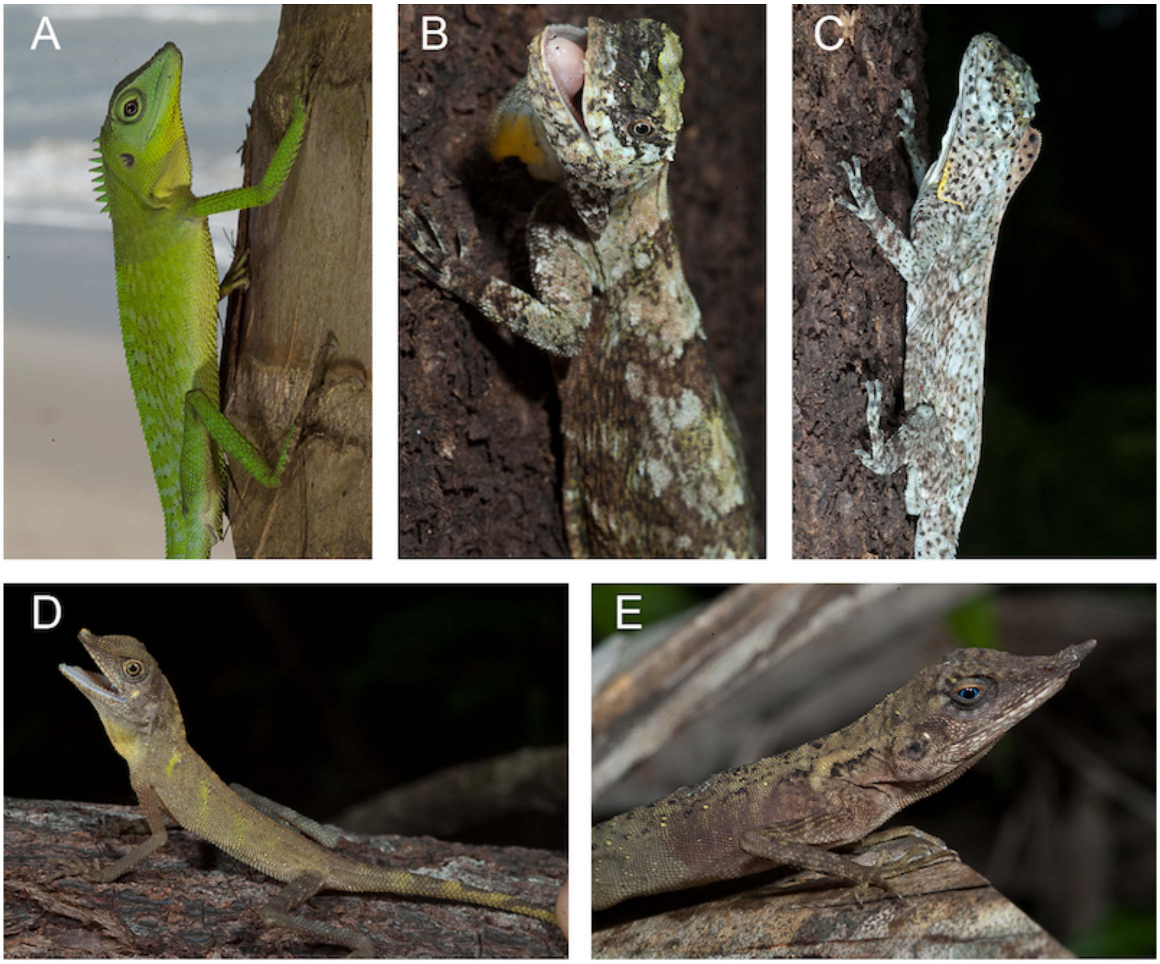


Figure 5.1. Some agamid lizards from Western Archipelago: (A) *Bronchocela cristatella* from Siberut; (B) a female *Draco cristatellus* from South Pagai; (C) a male *D. cristatellus* from South Pagai; (D) a female *Aphaniotis acutirostris* from South Pagai; (E) a male *Aphaniotis* sp. nov. from Simeulue. Photos by J.A. McGuire.

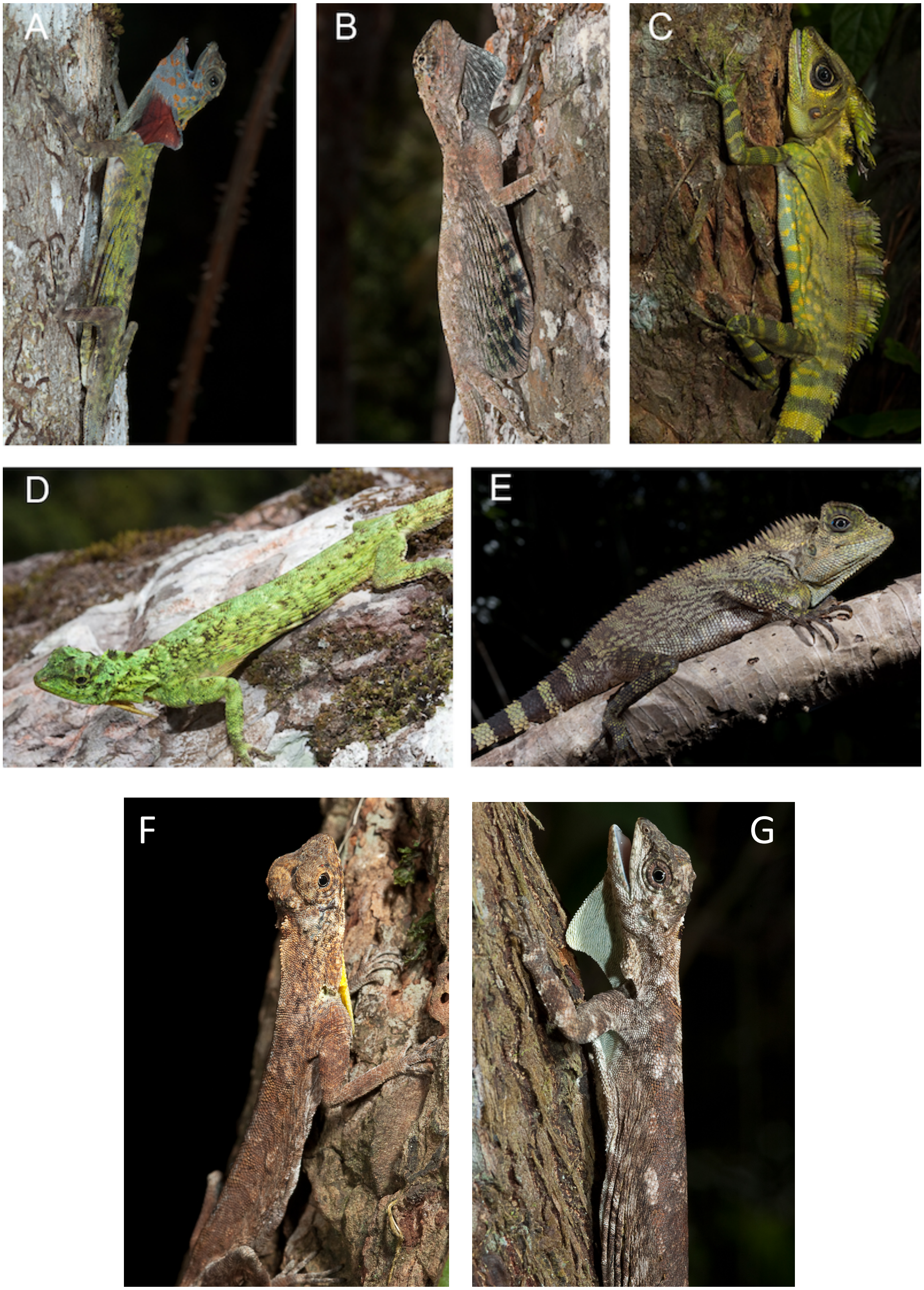

A
B
C
D
E
F
G

Figure 5.2. (A) a male *Draco obscurus* from South Pagai; (B) a female *Draco* sp. nov. Simeulue; (C) a male *Gonocephalus grandis* from Nias; (D) a male *D.* sp. nov. Simeulue; (E) a male *Gonocephalus chamaeleontinus* from South Pagai; (F) and (G), a more typical coloration for *D. sumatranus* male (F) and female (G). Photos by the author (B,D) and J.A. McGuire (A,C,E,F,G).

Figure 5.3. A male *Draco modiglianii* from Enggano. Photos by J.A.McGuire.

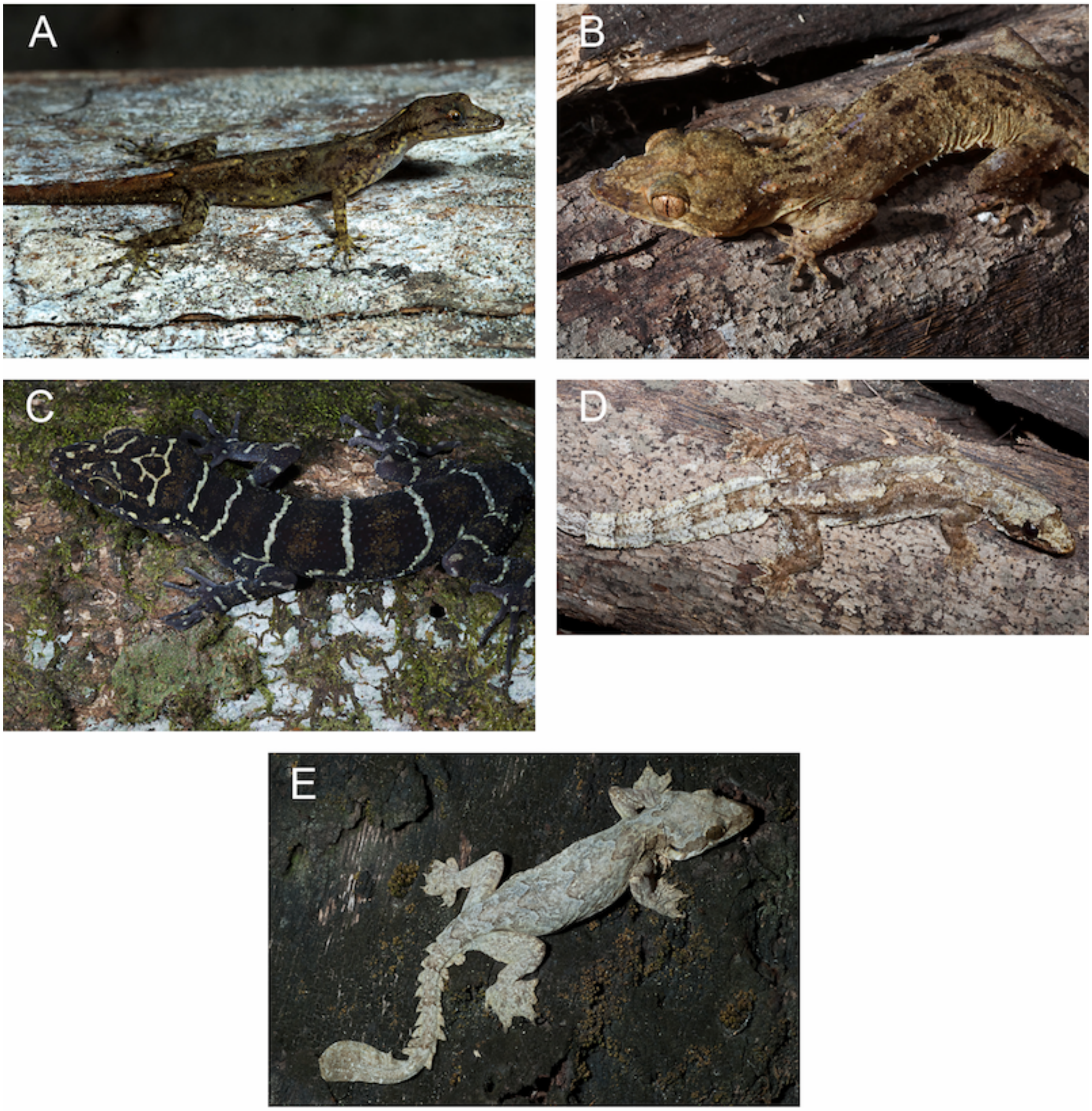


Figure 6. Some geckos that we encountered in Western Archipelago: (A) *Cnemaspis* cf. *whittenorum* from Siberut; (B) *Cyrtodactylus* cf. *lateralis* from Banyak Islands; (C) *Cyrtodactylus consobrinus* from Banyak Islands; (D) *Hemidactylus craspedotus* from Banyak Islands; (E) *Ptychozoon kuhlii* from Nias. Photos by the author (B,C,D) and J.A. McGuire (A,E).

Figure 7. Some skinks from Western Archipelago: (A) *Eutropis multifasciatus* from Siberut; (B) *Lipinia relicta* from Siberut. Photos by J.A. McGuire.

Figure 8.1. Some colubrid snakes that can be found in Western Archipelago. (A) *Ahaetulla prasina* from Nias; (B) *Psammodynastes pictus* from Banyak Islands; (C) *Psammodynastes pulverulentus* from Siberut; (D) *Boiga cynodon* from South Pagai; (E) *Boiga drapiezii* from South Pagai; (F) *Boiga nigriceps* from South Pagai; and (G) *Cerberus rynchops* from South Pagai. Photos by the author (B) and J.A. McGuire (the rest).

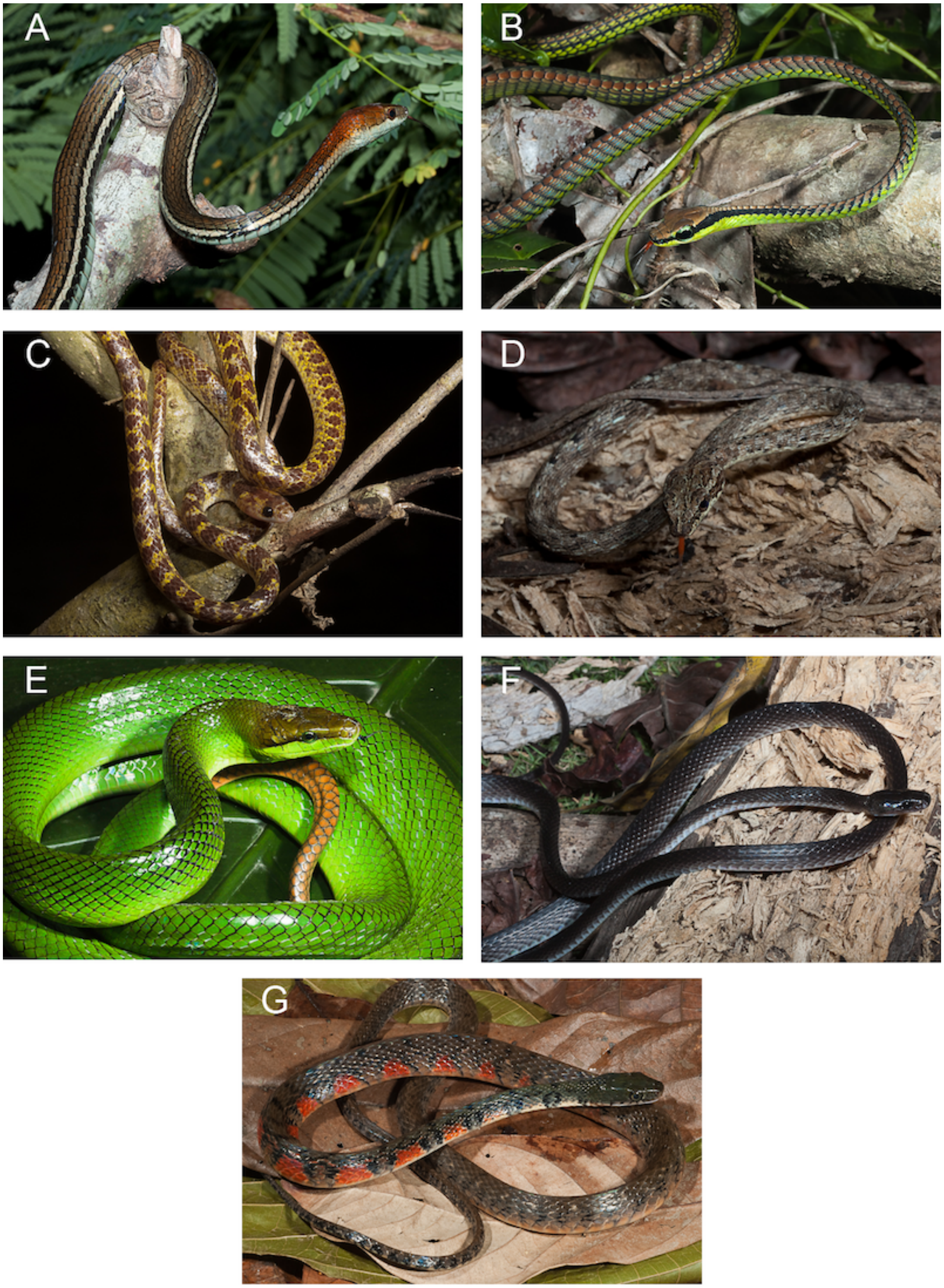

A
B
C
D
E
F
G

Figure 8.2. A few more colubrid snakes from the Western Archipelago. (A) *Dendrelaphis caudolineatus*, (B) *Dendrelaphis formosus* from South Pagai; (C) *Dryocalamus subannulatus* from Siberut; (D) *Dryophiops rubescens* from Banyak Islands; (E) *Gonyosoma oxycephalum*; (F) *Lepturophis albofuscus* from the Banyak Islands; (G) *Xenochrophis trianguligerus* from Nias. Photos by the author (A,D,F) and J.A. McGuire (B,C,E,G).

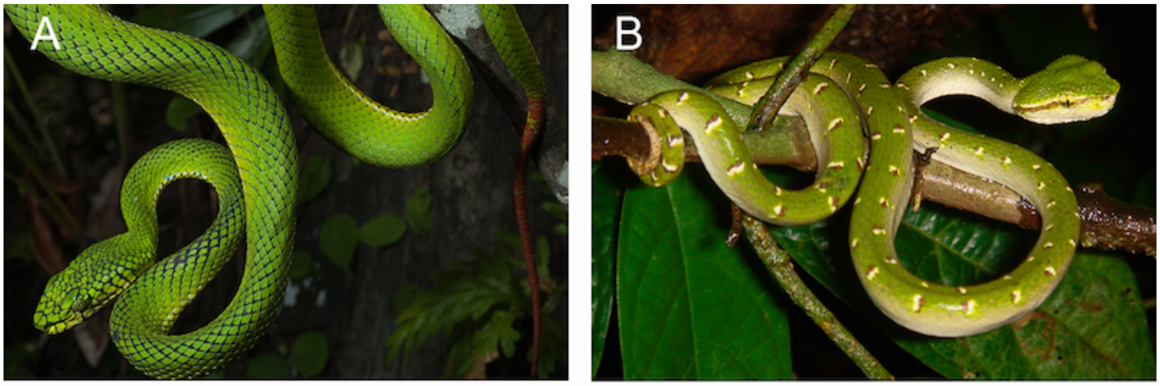


Figure 9. Two pit vipers from Western Archipelago: (A) *Trimeresurus hageni* from Nias, and (B) a male *Tropidolaemus wagleri* from South Pagai. Photos by J.A. McGuire.

CHAPTER 2

PHYLOGENETIC RELATIONSHIPS OF FLYING LIZARDS GENUS *DRACO* (IGUANIA: AGAMIDAE) BASED ON MULTILOCUS DNA SEQUENCE DATA

INTRODUCTION

The members of the genus *Draco,* known informally as 'flying lizards,' occur throughout Southeast Asia with one species occurring disjunctly in southwestern India. They exhibit a remarkable gliding ability enabled by an active mechanism that involves expansion of membrane-like patagial "wings" supported by modified, elongate, free thoracic ribs (Colbert 1967), as well as enlarged throat lappets supported by the hyoid apparatus. Together, the patagial membranes and throat lappets increase surface area and corresponding lift forces during gliding (McGuire, 2003, McGuire & Dudley 2005, 2011).

Lizards of the genus *Draco* have several characteristics that make them an ideal system with which one can study numerous biological questions. The genus includes approximately 40 species, providing ample opportunities for statistically powerful comparative studies. The group's distribution includes species that are widespread, some that are local endemics, and species that are found on large, continental landmasses as well as those found on oceanic and volcanic islands, thus setting the stage for biogeographic, phylogeographic, and diversification studies. At the interspecific level, the group exhibits a substantial degree of morphological disparity, with species typically being easily diagnosable based on the shape, pattern, and coloration of their patagial membranes and dewlap, which makes them an ideal system for studying the evolution of morphological characters. As many as seven species can be found in sympatry, providing opportunities to study ecological questions related to resource partitioning. This high level of sympatry, coupled with their highly territorial nature, allows one to answer behavioral questions on male–male as well as inter-specific competition.

Despite these advantageous characteristics, certain aspects of the group's taxonomy have not been fully resolved, especially regarding the *Draco fimbriatus* and *D. boschmai/timoriensis* groups. Much of this confusion stems from the fact that many older publications are based only on: (1) accounts of previous explorers and naturalists without the author's first-hand observation of live specimens, (2) examination of preserved museum specimens that may have lost their coloration, or (3) accounts of live observation without consulting established museum collections. To add to this uncertainty, many type specimens are accompanied by erroneous or non-specific locality information (Boulenger 1885; deRooij 1915; Hennig 1936; Inger 1983; and Musters 1983 – actually my taxonomic revision papers would be appropriate to cite here since I have identified some of the most taxonomically confusing examples of this). Equipped with numerous field observation hours, thorough examination of museum specimens, and advances in molecular approaches to phylogenetics, between the year 2000 and 2007, J.A. McGuire published a series of taxonomic revisions on *Draco* (McGuire & Alcala, 2000; McGuire et al. 2007), including mitochondrial DNA phylogenetics to infer the evolutionary relationships among the numerous lineages and species (McGuire & Kiew 2001).

Taxonomic Sampling & the Current State of Draco *systematics*

The first paper in the revisional series of *Draco* taxonomy was McGuire & Alcala (2000). In this paper, the authors recommended the following revisions to the taxonomy of Philippine *Draco*: (1) recognition of *D. palawanensis* as a new species distinct from *D. volans sumatranus*, (2) recognition of *D. bimaculatus* as a full species and not a subspecies of *D. lineatus*, (3) recognition of *D. cyanopterus* as a species, with *D. everetti* as its junior synonym, (4) recognition of *D. spilopterus* as the senior synonym of *D. rostratus*, (5) recognition of *D. guentheri* as the senior synonym of *D. rizali*, and (7) recognition of *D. ornatus*, *D. quadrasi, D. mindanensis*, and *D. jareckii*. My taxonomic sampling for Philippine *Draco* follow these recommendations, and while recognizing that there are data suggesting that it may be composed of several distinct lineages, I here treat *D. spilopterus* as a single species but include representation from several islands as a safeguard.

McGuire & Kiew (2001) co-authored the second paper in the aforementioned series of *Draco* taxonomic revisions. They utilized mitochondrial DNA sequence data to explain the evolutionary relationships of 53 species and/or populations of *Draco*, and the published results remain the most comprehensive molecular-based systematic treatment of the genus to date. My taxonomic sampling once again followed their recommendations in the following manner: (1) recognition of *D. indochinensis* as a diagnosably distinct species from *D. blanfordii*, (2) treatment of *D. formosus* and *D. obscurus* as distinct species, (3) recognition of *D. beccarii*, *D. bourouniensis*, *D. rhytisma* and *D. spilonotus* as full species instead of subspecies of *D. lineatus*, and (4) elevation of *D. sumatranus*, *D. timoriensis* and *D. boschmai* as full species distinct from *D. volans*. It is worth noting that there are significant morphological differences among island populations of *D. boschmai* and *D. timoriensis,* suggesting that these two species are composed of several lineages. McGuire & Kiew (2001) did not include *D. modiglianii* in their analysis but maintained that they should be regarded as a species distinct from *D. lineatus*. In this study, I include this and treat it as a distinct species.

The last paper in the taxonomic revision series, McGuire et al. (2007) recommended a number of changes in the taxonomy of *Draco lineatus* group. As with the Philippine group, the confusion in *D. lineatus* taxonomy stemmed from the lack of past workers' field experience with these lizards, insufficient consultation of comparative material, and type specimens with erroneous associated locality information. McGuire et al. (2007) had amassed an extensive collection of flying lizards from Sulawesi and several other Wallacean islands, and discovered that they can easily be divided into species by their remarkably distinct coloration in life and largely allopatric distributions. Supported by an unpublished phylogenetic analysis, they recommended the following modifications of the *D. lineatus* group: (1) recognition of *D. iskandari* and *D. supriatnai* as a new species, (2) elevation of *D. beccarii*, *D. rhytisma*, and *D. spilonotus* as full species instead of subspecies of *D. lineatus*, (3) recognition of *D. biaro* and *D. caerhulians* as distinct species, (4) recognition of *D. lineatus*, subsuming previous names including *D. ochropterus*, *D. bourouniensis* and *D. amboinensis* as junior synonyms, and (5) establishment of *D. walkeri* as a distinct species native to Sulawesi and not Timor, as indicated in its original description. Notably, populations that had been referred to *D. lineatus beccarii* in the recent literature were shown to be more properly referred to *Draco walkeri*, while the name *D. beccarii* should in fact be applied only to those *Draco* lizards from the eastern half of Sulawesi. The authors also established the exclusion of *D. modiglianii* from the *D. lineatus* complex, citing their unpublished phylogenetic analysis that placed *D. modiglianii* as a member of the *D. volans* species group instead.

Study objectives

The McGuire & Kiew (2001) study remains the most comprehensive molecular-based systematic treatment of the genus *Draco* to date. Since the time of its publication, however, much awareness has been raised cautioning against relying on single-locus inferences (e.g. Brito & Edwards 2009). Various processes such as lateral gene transfer, incomplete lineage sorting, and gene duplication can work together or independently to cause gene trees to deviate from the true underlying species tree (Maddison 1997; Carstens & Knowles 2007). Equipped with expanded sampling that has been accumulated by J.A. McGuire and myself, and taking advantage of the advances in the analytical methods of molecular phylogenetics, in this chapter I incorporate three nuclear markers to conduct a multi-locus phylogenetic analysis of *Draco* to corroborate the results of the McGuire and Kiew (2001) study, to estimate the phylogenetic position of taxa not available to McGuire and Kiew (2001), and to resolve nodes that were weakly supported with mtDNA data alone.

Some of these unresolved nodes have been alluded to above, i.e. the species identity and composition of *D. spilopterus*, *D. boschma*i, and *D. timoriensis* group. Further confusion comes from the phylogenetic placement of *D. bimaculatus*. Traditionally *D. bimaculatus* has been placed as a member of *D. lineatus* group—indeed, as a subspecies of *D. lineatus* (Hennig 1936; Musters 1983). In their mtDNA study, McGuire & Kiew (2001) recovered conflicting placements of *D. bimaculatus*: the most parsimonious tree placed *D. bimaculatus* as sister to *D. lineatus* group, albeit with low bootstrap support, while the Maximum Likelihood tree placed *D. bimaculatus* as the sister taxon of a large assemblage of *Draco* species comprising the *D. lineatus* and *D. volans* groups.

There are also unresolved issues in the taxonomy of *D. fimbriatus* and *D. cristatellus*. Musters (1983) examined the holotype specimen of *D. cristatellus* (terra typica: Sarawak, Borneo) and concluded it to be synonymous with the *D. fimbriatus fimbriatus* populations occurring on the Malay Peninsula, Borneo, and Sumatra (as opposed to *D. fimbriatus hennigi*, which he described from Java and Bali, apparently unaware that the type locality for *D. fimbriatus* also is on Java). Inger (1983), however, recognized the two as distinct species based on earlier accounts of different dewlap coloration in live animals (coral pink in *fimbriatus* versus bright yellow in *cristatellus*; Grandison 1972), on the basis of different adult body sizes (with *D. cristatellus* achieving much smaller adult body size), and on the basis of morphometric differences. However, examination of my own and J.A. McGuire's field collections, we have noted the presence of morphologically divergent specimens that likely represent distinct lineages within the *fimbriatus/cristatellus* group. In this study, I have included representatives of these putative lineages: (1) a *D.* cf. *cristatellus* specimen from Sarawak, Borneo—small, with no coloration on the gular sac; (2) a *D.* cf. *fimbriatus* specimen from Java—small, with yellow tinge on the gular sac and nuchal membranes; (3) several *D.* cf. *cristatellus* individuals from a diversity of localities across Sumatra, the Mentawai Archipelago, and one site on the Malay Peninsula—these lizards are characterized by a larger build with yellow gular sac and throat lappets; and (4) several specimens of *D. fimbriatus* from the Malay Peninsula—larger in size, with salmon-colored gular sac—and a smaller specimen from Sumatra with similar coloration.

MATERIALS & METHODS

Outgroup Selection

In his unpublished dissertation on the phylogeny of the family Agamidae, Moody (1980) suggested *Aphaniotis fuscus* and *Bronchocela cristatella* to be closely related to *Draco*. In this study, I included sequence data from *Aphaniotis fuscus* as an outgroup to *Draco*. OK – you need to cite the Macey et al. (2000) paper here – it is a much better reference than Moody and it also places Aphaniotis and Bronchocela in the Draconiine clade.

DNA Sequencing & Alignment

DNA was extracted from tissue samples using a standard salt extraction protocol (Sambrook et al. 2001). I collected DNA sequence data from the coding region of one mitochondrial locus (*NADH2* or *ND2*), as well as three nuclear coding genes (*CMOS, BDNF, PNN*; Saint et al. 1998, Townsend *et al.* 2008), comprising a total of 2864 base pairs. Primer sequences and PCR conditions are listed in Table 1. PCR products were purified using ExoSAP-IT, cycle sequenced using BigDye 3.1 terminator sequencing chemistry, and sequenced on ABI3730 automated sequencer. Sequences were cleaned and edited using Geneious Pro (Biomatter, New Zealand). Sequences from the same gene were aligned using the MUSCLE (Edgar 2004) plug-in as implemented in Geneious.

Model Selection & Phylogenetic Analyses

Geneious was used to detect the codon frame in each sequence alignment. A Perl script (MK Fujita, pers. comm.) was then used to separate the first, second and third codon positions of each gene into individual alignments. MrModeltest v.2.3 (Nylander 2008) was used to choose the most appropriate model of evolution for each partition of the various strategies explored (see below). To do this, each alignment under was analyzed in PAUP* (Swofford 2003) with the mrmodelblock provided in the MrModeltest package. The best model was selected according to the Akaike Information Criterion (AIC). Phylogenetic analyses were performed using both Maximum Likelihood (ML) and Bayesian methods. ML analyses were carried out using two versions of RAxML (Stamatakis 2006): Under version 7.0.4, the analyses were run using GTRGAMMA model for both bootstrapping and tree search, while under version 7.2.8, the bootstrap process was done under GTRCAT and the tree search was performed under GTRGAMMA. In both versions, analyses were run with 1,000 bootstrap replications each, employing the `-fa` option to make the program perform rapid bootstrapping and search for the best-scoring ML tree in a single run. Bayesian analyses were performed using MrBayes version 3.1.2 (Huelsenbeck & Ronquist 2001). All Bayesian analyses consisted of two independent runs starting at a random tree for 2 x 10^7 generations, each with one cold chain and three heated chains. Because of their computationally intensive nature, some of the analyses were run on TeraGrid—at the time of writing, the world's largest and most comprehensive cyber-infrastructure for open scientific research—through San Diego Supercomputer Center's CIPRES (Cyber Infrastructure for Phylogenetic Research; Miller et al. 2010) Science Gateway. After each MrBayes run, stationarity of the MCMC process was assessed using the online version of Are We There Yet (AWTY; Wilgenbusch et al. 2004) by uploading the two resulting .t files from each analysis and plotting the cumulative posterior probabilities of 20 of the most variable splits.

Comparing Alternative Partitioning Strategies

When dealing with complex, multi-locus data, it is desirable to partition the sequence alignment in order to model the data more accurately. However, because partitioning reduces the data into segments with fewer constituent nucleotides, this introduces random error to the parameter estimates for each partition, and it is thus possible to overpartition phylogenetic data sets (Brandley et al. 2005; McGuire et al. 2007; Brown & Lemmon 2007). The goal of selecting the best partitioning strategy, therefore, is to achieve a balance between accurate modeling and accumulating introduced error.

For both Maximum Likelihood and Bayesian analyses, I evaluated three different partitioning schemes that I deemed to be biologically meaningful: (1) Concatenated without partitioning ("unpartitioned"; 1 total partition); (2) Partitioned by gene ("gene"; 4 total partitions); (3) Partitioned by codon positions within gene ("codon"; 12 total partitions); and (4) Separating the 3rd codon position sites into their own partition while grouping the 1st and 2nd codon into a single partition ("$n_{12}n_3$"; 8 total partitions).

For Maximum Likelihood analyses, I compared alternative strategies using Likelihood Ratio Tests (LRT; Huelsenbeck & Crandall 1997, Huelsenbeck & Rannala 1997). The LRT statistics used to compare two competing hypotheses is given as:

$$\Lambda = \frac{\max[L(\text{null hypothesis} \mid \text{data})]}{\max[L(\text{alternative hypothesis} \mid \text{data})]}$$

When $\Lambda > 1$, the data are more probable under the null hypothesis and it is therefore favored, whereas when $\Lambda < 1$, the alternative hypothesis is favored. Competing partitioning strategies can be considered as a nested scenario where the strategy with fewer partitions is viewed as the more generalized case of the more heavily partitioned strategy. When two nested hypotheses are considered in LRT, Λ will always be <1 and $2 \log \Lambda$ is approximately χ^2-distributed with q degrees of freedom, where q is the difference in the number of free parameters between the two hypotheses (citation). This enables a chi-square test between the likelihood ratio of the two hypotheses:

$$\text{LR} = 2\ (\ln L_0 - \ln L_1)$$

For Bayesian analyses, I compared competing partitioning strategies using Bayes Factors (BF). Bayes Factors measure the relative predictive success of two hypotheses (Kass & Raftery 1995), computed by the following formula:

$$B_{01} = \frac{\Pr(D \mid H_0)}{\Pr(D \mid H_1)}$$

B_{01} is the Bayes factors score of the comparison between the marginal likelihood of the null hypothesis (H_0) and that of the alternative hypothesis (H_1). Because the marginal likelihood—i.e. the probability of the data after all the model parameters have been integrated out—is difficult to compute directly, it can be calculated using the harmonic mean of likelihood values sampled from the posterior distribution of the two hypotheses (Brandley et al. 2005, Brown & Lemmon 2007). The Bayes factors score is then given as:

$$B_{01} = \frac{\text{Harmonic Mean } L_0}{\text{Harmonic Mean } L_1}$$

For convenience, Bayes Factors can be ln-transformed, and the statistic then becomes 2lnBF, which is given as:

$$2\ln BF_{01} = 2[\ln(\text{HarmonicMean}_0) - \ln(\text{HarmonicMean}_1)]$$

The harmonic mean of each analysis was calculated using the `sump` command in MrBayes version 3.1.2 after the run reached stationarity and with burn-in samples discarded (see above). The Bayes Factors statistics is interpreted using a somewhat arbitrary cutoff value provided by Jeffreys (1935, 1961), which was later modified by Raftery (1996). This practice is essentially equivalent to choosing an arbitrary value of *P* as is typical in frequentist statistics (Brandley 2005). Kass & Raftery (1995) provided a sliding scale of 2lnBF values to determine level of support for H_1, where $2\ln BF<0$ is evidence for H_0, $0<2\ln BF<2$ is an evidence for H_1 that is "barely worth mentioning", $2<2\ln BF<6$ is "positive" evidence for H_1, $6<2\ln BF<10$ is "strong" evidence for H_1, and $2\ln BF>10$ is "very strong" evidence for H_1. In this study, I used the conservative value of $2\ln BF>10$ to choose between partitioning strategies.

RESULTS

DNA Sequencing & Alignment

The nucleotide alignment for *ND2*, *PNN*, *CMOS* and *BDNF* are 1,032, 698, 419, and 715 bases long, respectively. Once concatenated, the final sequence alignment of all four markers comprises 2,864 base pairs. Of these, 1,294 are variable and 1,083 are parsimony-informative. In total, I aligned sequence data from 465 individuals representing 40 species/lineages of *Draco*—of 465 individuals, 396 are represented completely by all four markers. The complete list of sample names and the markers for which they are sequenced are given in Appendix X.

Model Selection

The complete list of models selected for each gene and partition is given in Table 2. The most general model of GTR + I + Γ was appropriate for the majority of the partitions, even for partitions that are relatively short.

Comparing Alternative Partitioning Strategies

Likelihood Ratio Test and Bayes Factors scores are given in Table 2. For both analyses, the inferred tree topologies are generally similar across partitioning strategies. Not surprisingly, adding partitions to the analyses invariably resulted in improved likelihood scores, although the improvement is not always statistically significant. Under the Maximum Likelihood method, partitioning the data set by gene significantly improved the performance of the analysis compared to the unpartitioned run ($P = 0.0$), but further partitioning of the data by Gene + Codon and Gene + $N_{12}N_3$ did not ($P = 1.0$ for both comparisons). For further discussions of Maximum Likelihood results, therefore, I will be using the tree inferred under the gene partitioning strategy.

For Bayesian analysis, Bayes Factor calculations indicated that partitioning the data by gene significantly improves the likelihood of the data compared to the unpartitioned analysis (2lnBF = 4748.98). Differentiating the third codon from the first two (Gene + $N_{12}N_3$) does not further improve the likelihood score (2lnBF = −1191.86), but partitioning the data into first, second and third codon (Gene + Codon) does (2lnBF = 528.02). Therefore, in further discussion of my Bayesian results, I will be referring to the tree that was inferred under the Gene + Codon partitioning strategy.

Phylogenetic Analyses

Inferred trees from Maximum Likelihood and Bayesian methods are presented in Figures 1 and 2, respectively. Furthermore, I have presented Maximum Likelihood results based on mtDNA only (Figure 3A) and contrasted them against the nuclear DNA results (Figure 3B & C).

My results show that *Draco spilopterus* is a polyphyletic group, consisting of several clades that appear to be geographically structured. The first of these is made up of samples from the southern part of the distribution range of *D. spilopterus*: Panay, Cebu, Siquijor and Negros (100% bootstrap/1.0 posterior probability). Although with a weak support (32% bootstrap/0.68 PP), this clade is placed as the sister group to *D. quadrasi*. The second *D. spilopterus* clade is composed of individuals from the Bicol Peninsula of Luzon island (100% bootstrap/1.0 PP), which are placed as sister to *D. cyanopterus* and *D. reticulatus* (33% bootstrap/0.69 PP). This clade is then sister to the third well-supported *D. spilopterus* group, which is composed of individuals from the 'mainland' part of Luzon island (Zambales & Maragondon) and nearby island of Polillo (100% bootstrap/1.0 PP). The last *D. spilopterus* clade consisted of individuals from the northernmost satellite islands of Babuyan Claro (99% bootstrap, 1.0 PP). This clade is placed as the sister taxon to *D. jareckii*.

Both ML and Bayesian methods agree on the position of *D. bimaculatus* as the sister taxon to the rest of the *lineatus* group (80% Bootstrap value/1.0 posterior probability), thus lending further support to this hypothesis.

My ML and Bayesian results uncovered the presence of highly divergent lineages within *D. fimbriatus* and *D. cristatellus*. The small Bornean *D. cristatellus* is shown to be the most basal lineage in the group (100% bootstrap/1.0 PP), which is then sister to the rest of the clade. The second distinct lineage is made up of *D. cristatellus* from Borneo, Sumatra, the Mentawai Archipelago, and the Malay Peninsula, which are found to be a monophyletic assemblage (99% bootstrap/1.0 PP). The last divergence in this group occurred between the Javan and Sumatran+Malay Peninsula *D. fimbriatus* (100% bootstrap/1.0 PP). With the exception of the latter divergence, these clades are discovered in both mtDNA and nuDNA results (Figure 3A, B).

My results confirm the finding of McGuire et al. (2007) that *Draco modigliani* is not a member of the *Draco lineatus* group and is instead nested within the *D. volans* group, and is most closely related to *D. sumatranus*.

Lastly, my results find *D. dussumieri*, previously not included in the mtDNA study, to be the most basal lineage of *Draco*, and sister to all SE Asia *Draco*. The fact that *D. dussumieri* occurs only in the Western Ghats region of southern India implies that the flying lizards originated in this area and radiated into Indochina and insular Southeast Asia.

DISCUSSION

Both Maximum Likelihood and Bayesian analyses produced trees that are well resolved and with strong support for the major clades (Figure 1 and 2). The two methods also resulted in trees that are remarkably congruent in topology, with few disagreements that occurred, not surprisingly, in nodes that have lower bootstrap support values and/or posterior probabilities (i.e. less than 75% bootstrap or 0.85 posterior probability). These nodes tend to be relatively short internal branches connecting longer, more terminal branches.

One source of discord between the Maximum Likelihood and Bayesian results is the placement of *D. quinquefasciatus* within the dorsal nostril group. While neither finding is well supported, the Maximum Likelihood method placed *D. quinquefasciatus* as sister taxon to the clade that contains *D. blanfordi*, *D. taeniopterus*, *D. formosus*, *D. obscurus*, *D. melanopogon*, *D. indochinensis* and *D. haematopogon* (56% bootstrap support), while the Bayesian method placed *D. quinquefasciatus* in a smaller clade and sister to *D. maximus* and *D. mindanensis* (0.51 PP). Previous results from McGuire & Kiew (2001) support the Maximum Likelihood placement, but this placement is also not well supported (60% bootstrap). Without further evidence it is difficult to confidently resolve the placement of *D. quinquefasciatus* within the dorsal nostril group.

Comparing my results to those from the previous study (McGuire & Kiew 2001), all seven major clades of *Draco* (i.e. "*fimbriatus*", "dorsal nostril", "lacrimal bone", "*lineatus*", and a "*volans*" group that can be further divided into "Lesser Sunda *volans*" and "Philippine *volans*") are present and well supported in the current results (Figure 3). In addition to these clades, my results found that the main Sunda Shelf *volans* species (*D. volans*, *D. sumatranus*, *D. modiglianii*, and *D.* sp. nov. "Simeulue") form their own monophyletic clade, although with weak support (46% bootstrap support and 0.75 posterior probability) and shorter terminal branches compared to the Lesser Sunda and Philippine *volans* clades.

The results from this study also confirm the affinity of *D. modiglianii* to the *volans* instead of *lineatus* group. Both ML and Bayesian trees suggest that *D. modiglianii* forms a paraphyletic assemblage with *D. sumatranus* and *D.* sp. "Simeulue". While this may present a challenge to the integrity of their species status under a strict Phylogenetic Species Concept, I hypothesize that they are perfectly good species in the context of the General Lineage Species Concept (de Queiroz 1998, 1999, 2007), especially given the fact that both *D. modiglianii* and *D.* sp. "Simeulue" represent distinct evolutionary lineages and occur in allopatry with respect to *D. sumatranus* (*D. modiglianii* occur only on the island of Enggano, and *D.* sp. "Simeulue" on the island of Simeulue). Both species are also easily diagnosable from *D. sumatranus* based on morphology alone. I therefore hypothesize that the phylogenetic results reflect incomplete lineage sorting and conclude that the two should be regarded as a full species and not a subspecies of *D. sumatranus*. It should be mentioned that there is evidence that the paraphyletic relationship of *D. modiglianii* with respect to *D. sumatranus* does not hold up when more nuclear loci are added into the analysis (see Chapter 3), although *D.* sp. "Simeulue" remains nested deep within the Western Archipelago *D. sumatranus* assemblage. I also find that *D. sumatranus* exhibits a great degree of population structuring, and that Sumatran populations are highly divergent from one another and form clades with the Western Archipelago, Malay Peninsula, and Bornean populations that reflect unexpected relationships. This finding is explored in greater details in Chapter 3, where I investigate the population genetics of *Draco sumatranus*.

My findings of polyphyly within *D. spilopterus* is concordant with McGuire & Kiew's (2001) results. Comparing the current mitochondrial vs. nuclear DNA results, it appears that the nuDNA largely agrees with the strongly supported polyphyly shown in the mtDNA results, although the low support and near-polytomy in the nuDNA tree suggest the presence of incomplete lineage sorting. Regarding the *Draco spilopterus* complex, though the three subclades do not form a monophyletic assemblage, each is biogeographically cohesive. One subclade is comprised of individuals from Panay, Negros, Cebu, and Siquijor. Panay, Negros, and Cebu merge during sea level lowstands associated with glacial maxima, and have consequently been identified as the Visayan Philippine Aggregate Island Complex (PAIC; see Heaney (1986) and Rafe Brown refs). Siquijor, though separated by a deep-water channel from the Visayan PAIC, sits immediately off of its western coast. The second *D. spilopterus* subclade occurs on the Bicol Peninsula, which was a separate paleo-island that only recently merged with the main block of Luzon. The third *D. spilopterus* subclade occurs on the main block of Luzon and on satellite islands that extend off of Luzon's north coast.

One source of discord with the McGuire & Kiew's mtDNA results (2001) is my finding that the two species in the Philippine *volans* group that do not occur in the Philippines are sister to the rest of the group. *D. palawanensis*, occurring on the island of Palawan north of Borneo, is found to be the oldest divergence in the clade (99% bootstrap/1.0 PP), and with significantly less support (50% bootstrap/0.85 PP), *D. cornutus* (occurring on the island of Borneo) is found to be sister to the remainder of the Philippine *volans* species. This basal placement of *D. palawanensis* is in discord with the results of McGuire & Kiew (2001). Both their Maximum Likelihood and Maximum Parsimony results placed *D. palawanensis* nestled deep within the Philippine *volans* group. However, given its strong support, I believe the basal placement is more likely to reflect the true relationship of *D. palawanensis* to the rest of the Philippine group.

Perhaps surprisingly, the addition of nuclear markers has not resulted in a phylogenetic estimate that provides much in the way of well-supported additional resolution of the Philippine *volans* group, lending additional support to McGuire and Kiew's (2001) hypothesis that this assemblage radiated rapidly soon after reaching the Philippines.

The presence of four distinct lineages within *D. fimbriatus/cristatellus*—both in mtDNA and nuclear results—supports our notion that the current two-species taxonomy does not adequately reflect the diversity within this group. While it is not the purpose of this study to make formal taxonomic recommendations, based on my phylogenetic findings I would encourage a revision of the taxonomy of *D. fimbriatus* and *D. cristatellus* to reflect the four distinct lineages. This particular task would benefit greatly from better sampling from Borneo and Java, for which my coverage was limited.

The taxonomic recommendations of the *D. lineatus* group made by McGuire et al. in 2007 are well supported by the monophyly of each of the recommended species in both ML and Bayesian analyses. The phylogenetic relationships among them, however, remain ambiguous and exhibit quite a few disagreements.

Caveats of Concatenation Methods

Based on the improved resolution and support for some of the nodes in the analyses presented here compared to the mtDNA-based phylogeny, it is apparent that the multi-locus approach provides a better way of addressing evolutionary relationships among species. However, recent research has raised concerns regarding the practice of concatenating multi-locus data sets (e.g. Kubatko & Degnan 2007). The many occurrence of short internal branches leading to longer, more terminal branches in my phylogenies indicate that there may be extensive incomplete lineage sorting, which has been proven to cause species tree estimation using concatenation to misleadingly result in high support for an incorrect topology (Kubatko & Degnan 2007). This inconsistency can be somewhat improved by sampling more individuals per species (Maddison & Knowles 2006), but when such branches occur deep in the tree, increased sampling is not expected to improve the accuracy of phylogenetic estimates. Recent advances on the computational front of phylogeny estimation have resulted in a number of probabilistic methods of inferring species trees by explicitly taking into account the coalescent processes that affect individual genes stochastically, such as Bayesian Estimation of Species Tree (BEST; Liu & Pearl 2007, Liu 2008) or STEM (Species tree estimation using Maximum Likelihood; Kubatko et al. 2009). These methods are expected to more accurately infer the true species tree when incomplete lineage sorting is likely. In this light, I would caution against accepting the current findings as the true relationships among *Draco* species until they can be corroborated with results from coalescent-based analyses.

CONCLUSION

The addition of three nuclear markers to the phylogenetic analysis of *Draco* largely upholds the results from McGuire & Kiew's 2001 mtDNA study. However, this study includes much more comprehensive intraspecific sampling, as well as the addition of species unavailable to McGuire and Kiew such as *Draco dussumieri*, *D. modigliani*, *D.* sp. "Simulue", *D. walkeri*, *D. supriatnai*, and *D. jareckii* and thus provides a more comprehensive estimate of *Draco* phylogeny. The *D. cristatellus/fimbriatus* group is found to more deeply divergent lineages than is captured by the current taxonomy, and clearly is in need of taxonomic revision. *Draco* can be grouped into eight major clades, all with strong support except for the greater Sunda Shelf *volans* group. Results from Maximum Likelihood and Bayesian analyses are largely concordant with one another, with a few disagreements regarding the placement of *D. quinquefasciatus* within the dorsal nostril group. My phylogenetic trees are well supported, but there is reason to accept the results with a grain of salt, pending further exploration with coalescent-based methods of analysis.

REFERENCES

Avise, J.C. 2000. *Phylogeography: The History and Formation of Species*. Harvard University Press, Cambridge MA.

Brandley, M.C., A. Schmitz & T.W. Reeder. 2005. Partitioned Bayesian Analyses, Partition Choice, and the Phylogenetic Relationships of Scincid Lizards. *Syst. Biol.* 54(3): 373–390.

Brito, P.H. & S.V. Edwards. 2009. Multilocus phylogeography and phylogenetics using sequence-based markers. *Genetica* 135(3): 439–455.

Brown, J.M. & A.R. Lemmon. 2007. The Importance of Data Partitioning and the Utility of Bayes Factors in Bayesian Phylogenetics. *Syst. Biol.* 56(4): 643–655.

Carstens BC, Knowles LL (2007a) Estimating species phylogeny from gene-tree probabilities despite incomplete lineage sorting: an example from Melanoplus grasshoppers. *Syst. Biol.* 56:400– 411.

Colbert, E.H. 1967. Adaptations for gliding in the lizard *Draco*. Amer. Mus. Nov. 2283: 1–20.

de Queiroz K. 1998. The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations. In: Howard DJ, Berlocher SH (eds.) *Endless Forms: Species and Speciation*. Oxford: Oxford University Press, 57–75.

de Queiroz K. 1999. The general lineage concept of species and the defining properties of the species category. In: Wilson RA, (ed). *Species: New Interdisciplinary Essays*. Cambridge: The MIT Press, 49–89.

DeQueiroz, K. 2007. Species concepts and species delimitation. *Syst. Biol.* 56 (6): 879–886.

Edwards, S.V. 2009. Natural selection and phylogenetics. *Proceedings of the National Academy of Sciences* 106(22): 8799–8800.

Grandison, A.G.C. 1972. The Gunong Benom Expedition 1967. 5. Reptiles and amphibians of Gunong Benom with a description of a new spedes of *Macrocalamus*. *Bull. Br. Mus. (Nat. Hist.) Zool.*, 23: 45–101.

Heaney, L.R. 1986. Biogeography of mammals in SE Asia: Estimates of rates of colonization, extinction and speciation. *Biol. J. Linn. Soc.* 28: 127–165.

Huelsenbeck, J.P. & K.A. Crandall. 1997. Phylogeny estimation and Hypothesis testing using maximum likelihood. *Annu. Rev. Ecol. Syst.* 28: 437–466.

Huelsenbeck, J.P. & B. Rannala. 1997. Phylogenetic methods come of age: Testing hypotheses in an evolutionary context. *Science* 276(5310): 227–232.

Huelsenbeck, J. P. and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17:754–755.

Inger, R.F. 1983. Morphological and ecological variation in the flying lizards (genus *Draco*). *Fieldiana Zool., New Ser.* 18: 1–35.

Jeffreys, H. 1935. Some tests of significance, treated by the theory of probability. *P. Camb. Philos. Soc.* 31:203–222.

Jeffreys, H. 1961. Theory of probability. Oxford University Press, Oxford.

Kass, R.E. & A.E. Raftery. 1995. Bayes factors. *Journal of the American Statistical Association*. 90(430): 773–795.

Kubatko, L.S. & J.H. Degnan. 2007. Inconsistency of phylogenetic estimates from concatenated data under coalescence. *Syst. Biol.* 56(1): 17–24.

Kubatko, L.S., B.C. Carstens & L.L. Knowles. 2009. STEM: species tree estimation using maximum likelihood for gene trees under coalescence. *Bioinformatics* 25: 971–973.

Liu, L. & D.K. Pearl. 2007. Species tree from gene trees: Reconstructing Bayesian posterior distributions of a species phylogeny using estimated gene tree distributions. *Syst. Biol.* 56: 504–514.

Liu, L. 2008. BEST: Bayesian estimation of species trees under the coalescent model. *Bioinformatics* 24: 2542–2543.

Macey, J.R., Schulte, J.A., Larson, A., Ananjeva, N.B., Wang, Y., Pethiyagoda, R., Rastegar-Pouyani, N., Papenfuss, T.J. 2000. Evaluating trans-tethys migration: an example using acrodont lizard phylogenetics. *Syst. Biol.* 49 (2): 233–256.

Maddison, W. P. 1997. Gene trees in species trees. *Syst. Biol*. 46:523-53.

Maddison, W.P. & L.L. Knowles. 2006. Inferring phylogeny despite incomplete lineage sorting. *Syst. Biol.* 55(1): 21-30.

McGuire, J.A. & A.C. Alcala. 2000. A taxonomic revision of the flying lizards (Iguania: Agamidae: *Draco*) of the Philippine Islands, with a description of a new species. *Herpetological monographs* 14(2000): 81–138.

McGuire, J.A. & B.H. Kiew. 2001. Phylogenetic systematics of Southeast Asian flying lizards (Iguania: Agamidae: *Draco*) as inferred from mitochondrial DNA sequence data. *Biological Journal of the Linnean Society* 72: 203–229.

McGuire, J.A., R.M. Brown, Mumpuni, A. Riyanto & N. Andayani. 2007. The flying lizards of the *Draco lineatus* group (Squamata: Iguania: Agamidae): A taxonomic revision with descriptions of two new species. *Herpetological Monographs* 21: 179–212.

McGuire, J.A. & R. Dudley. 2011. The evolution of gliding performance in flying lizards (*Draco*). Integrative and Comparative Biology. 51: E90.

Miller, M.A., W. Pfeiffer, & T. Schwartz. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010, New Orleans, LA: 1–8.

Moody, S. M. 1980. Phylogenetic and historical biogeographical relationships ofthe genera in the family Agamidae (Reptilia: Lacertilia). Unpublished Ph.D. dissertation, University of Michigan, Ann Arbor, 373 pp.

Moyle, R.G., M. Schilthuizen, M.A. Rahman & F.H. Sheldon. 2005. Molecular phylogenetics analysis of the white-crowned forktail *Enicurus leschenaulti* in Borneo. *Journal of Avian Biology* 36: 96–101.

Musters, C.J.M. 1983. Taxonomy of the genus *Draco* L. (Agamidae, Lacertilia, Reptilia). *Zool. Verhandelingen* 199: 1–120.

Nylander, J. A. A. 2004. MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Raftery, A. 1996. Hypothesis testing and model selection. In: Gilks, W.R., S. Richardson, & D. J. Spiegelhalter. (eds.) *Markov Chain Monte Carlo in Practice*. Chapman and Hall, New York, USA: pp 163–187.

Sambrook, J., and D.W. Russell. 2001. Molecular Cloning: A Laboratory Manua;, third ed. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, New York.

Saint, K. M., C. C. Austin, S. C. Donnellan, & M. N. Hutchinson. 1998. *C-mos*, a nuclear marker useful for squamate phylogenetic analysis. *Molecular Phylogenetics and Evolution* 10: 259-263.

Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, **22**: 2688–2690.

Swofford, D. L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Townsend, T.M., R.E. Alegre, S.T. Kelly, J.J. Wiens & T.W. Reeder. Rapid development of multiple nuclear loci for phylogenetic analysis using genomic resources: An example from squamate reptiles. *Molecular Phylogenetics & Evolution*, **47**(1): 129–142.

Wilgenbusch J.C., Warren D.L., Swofford D.L. 2004. AWTY: A system for graphical exploration of MCMC convergence in Bayesian phylogenetic inference. http://ceb.csit.fsu.edu/awty/

Table 1. A list of primer names, sequences and annealing temperatures for the loci used in this study.

Locus Name	**Primer name**	**Sequence (5′ → 3′)**	**Annealing Temp. (°C)**	**Reference**
NADH-2 (ND2)	MetF1 (PCR-External)	AAGCAGTTGGGCCCATRCC	50-48-45 (stepdown)	Modified from Macey et al. 1997
	AlaR2 (PCR-External)	AAAGTGTCTGAGTTGCATTCRG		
	ND2F5 (Sequencing-internal)	AACCAAACCCAACTACGAAAAAT	N/A	
	ND2R6 (Sequencing-internal)	ATTTTTCGTAGTTGGGTTTGRTT	N/A	
CMOS	G73	GCGGTAAAGCAGGTGAAGAAA	54	Saint et al. 1998
	G74	TGAGCATCCAAAGTCTCCAATC		
BDNF	BDNF-F	GACCATCCTTTTCCTKACTATG	50	Townsend et al. 2008
	BDNF-R	CTATCTTCCCCTTTTAATGGTC		
PNN	PNN-L	TGCCAGCAGATGGTGAACAG	57	Townsend et al. 2008
	PNN-R	TATCCCTTCGCTTCCGATCC		

Table 2. List of models selected for all partitions used in the Bayesian analyses.

Partitioning Method	Model Selected	No. of characters in partition
All Genes Concatenated	GTR + I + Γ	2864
ND2	GTR + I + Γ	1032
ND2 1st Codon	GTR + I + Γ	344
ND2 2nd Codon	GTR + I + Γ	344
ND2 3rd Codon	GTR + I + Γ	344
ND2 1st + 2nd Codon	GTR + I + Γ	688
CMOS	SYM + I + Γ	419
CMOS 1st Codon	HKY + Γ	140
CMOS 2nd Codon	K80 + Γ	139
CMOS 3rd Codon	SYM + Γ	140
CMOS 1st + 2nd Codon	HKY + I + Γ	279
PNN	GTR + I + Γ	698
PNN 1st Codon	GTR + Γ	233
PNN 2nd Codon	GTR + Γ	233
PNN 3rd Codon	SYM + Γ	232
PNN 1st + 2nd Codon	GTR + I + Γ	466
BDNF	GTR + I + Γ	715
BDNF 1st Codon	GTR + I	239
BDNF 2nd Codon	K80	238
BDNF 3rd Codon	HKY + Γ	238
BDNF 1st + 2nd Codon	HKY + I	477

Table 3. Scores from Likelihood Ratio Test (LR; below diagonal) and Bayes Factor comparison (2lnBF; above diagonal) of different partitioning schemes. The Likelihood score (-lnL) from the best Maximum Likelihood tree and the harmonic mean of Likelihood score (HM) from the summarized Bayesian tree is given under each strategy in the first column.

Strategy	Unpartitioned	Gene	Gene + $N_{12}N_3$	Gene + Codon
Unpartitioned (-lnL=51024.41) (HM=-52326.45)		2lnBF = 4748.98		
By Gene (-lnL=49878.01) (HM=-49951.96)	LR = 2292.41 D.F. = 1416 *P* = 0.00		2lnBF=-1191.86	2lnBF=528.02
By Gene + $N_{12}N_3$ (-lnL=49115.77) (HM=-50547.89)	LR = 3817.28 D.F. = 3304 *P* = 0.00	LR = 1524.48 D.F. = 1888 *P* = 1.00		
By Gene + Codon (-lnL=48943.93) (HM=-49687.95)	LR = 4160.96 D.F. = 5192 *P* = 1.00	LR = 1868.16 D.F. = 3776 *P* = 1.00	LR = 343.68 D.F. = 1888 *P* = 1.00	

Figure 1. Maximum Likelihood tree of the 4-genes data set partitioned by gene, inferred under GTR + I + Γ model in RAxML (-lnL = 49,878.01). Nodes are labeled with their bootstrap values based on 1,000 replicates. Scores under 75% are marked in red.

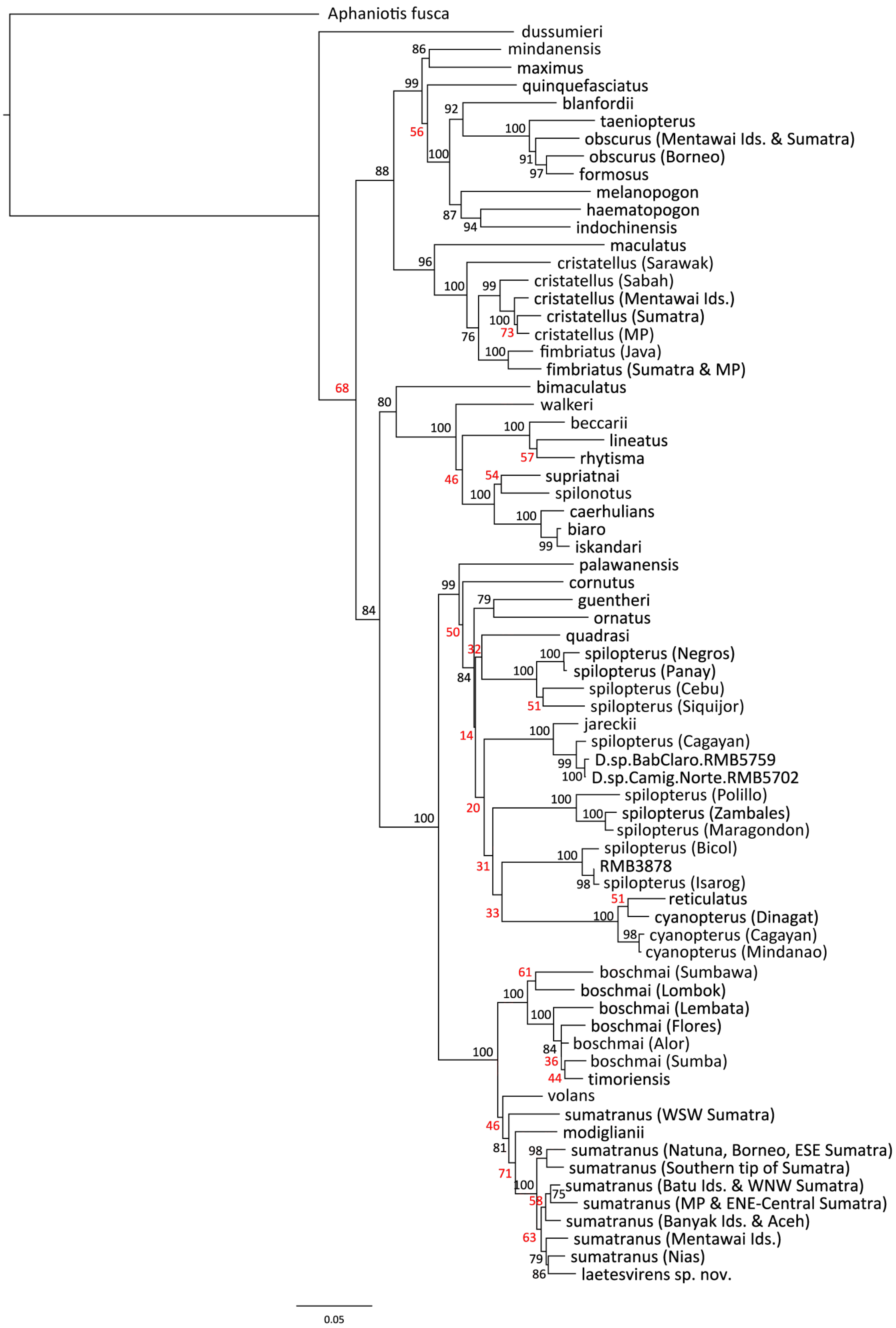

Aphaniotis fusca
dussumieri
86
mindanensis
maximus
99
quinquefasciatus
92
blanfordii
56
100
taeniopterus
obscurus (Mentawai Ids. & Sumatra)
91
obscurus (Borneo)
100
97
formosus
88
melanopogon
haematopogon
87
94
indochinensis
maculatus
96
cristatellus (Sarawak)
99
cristatellus (Sabah)
100
cristatellus (Mentawai Ids.)
cristatellus (Sumatra)
100
73
cristatellus (MP)
76
100
fimbriatus (Java)
fimbriatus (Sumatra & MP)
bimaculatus
68
80
walkeri
100
100
beccarii
lineatus
rhytisma
57
54
supriatnai
46
spilonotus
100
caerhulians
100
biaro
99
iskandari
palawanensis
cornutus
99
79
guentheri
84
ornatus
50
quadrasi
32
100
spilopterus (Negros)
100
spilopterus (Panay)
84
spilopterus (Cebu)
51
spilopterus (Siquijor)
jareckii
100
14
spilopterus (Cagayan)
D.sp.BabClaro.RMB5759
99
100
D.sp.Camig.Norte.RMB5702
spilopterus (Polillo)
100
20
100
spilopterus (Zambales)
100
spilopterus (Maragondon)
spilopterus (Bicol)
100
31
RMB3878
98
spilopterus (Isarog)
51
reticulatus
33
100
cyanopterus (Dinagat)
98
cyanopterus (Cagayan)
cyanopterus (Mindanao)
61
boschmai (Sumbawa)
boschmai (Lombok)
100
100
boschmai (Lembata)
boschmai (Flores)
84
boschmai (Alor)
100
36
boschmai (Sumba)
44
timoriensis
volans
sumatranus (WSW Sumatra)
46
modiglianii
81
98
sumatranus (Natuna, Borneo, ESE Sumatra)
sumatranus (Southern tip of Sumatra)
71
100
75
sumatranus (Batu Ids. & WNW Sumatra)
58
sumatranus (MP & ENE-Central Sumatra)
sumatranus (Banyak Ids. & Aceh)
63
sumatranus (Mentawai Ids.)
79
sumatranus (Nias)
86
laetesvirens sp. nov.
0.05

Figure 2. Bayesian tree of the 4-genes data set, partitioned by codon. Numbers indicate the posterior probability for each node, with low supported nodes (PP<0.85) marked in red. MP = Malay Peninsula.

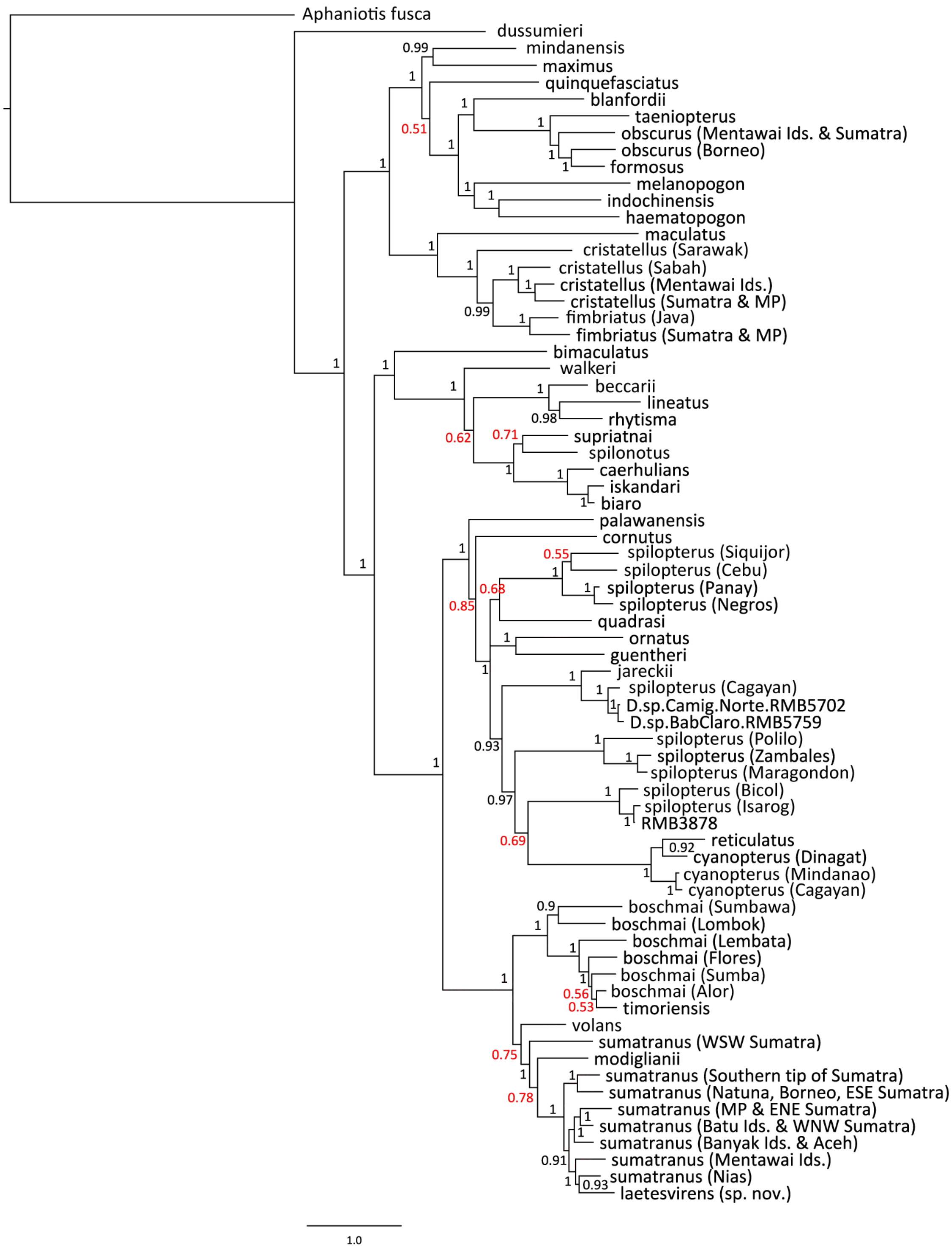

Aphaniotis fusca
dussumieri
0.99
mindanensis
maximus
1
quinquefasciatus
1
blanfordii
taeniopterus
1
obscurus (Mentawai Ids. & Sumatra)
0.51
1
1
obscurus (Borneo)
1
formosus
1
melanopogon
1
1
indochinensis
haematopogon
maculatus
1
cristatellus (Sarawak)
1
1
cristatellus (Sabah)
1
cristatellus (Mentawai Ids.)
cristatellus (Sumatra & MP)
0.99
fimbriatus (Java)
1
fimbriatus (Sumatra & MP)
1
bimaculatus
1
walkeri
1
beccarii
1
lineatus
0.98
rhytisma
0.62
0.71
supriatnai
spilonotus
1
caerhulians
1
iskandari
1
biaro
palawanensis
1
cornutus
1
spilopterus (Siquijor)
0.55
spilopterus (Cebu)
1
0.68
spilopterus (Panay)
1
0.85
spilopterus (Negros)
quadrasi
1
ornatus
guentheri
1
jareckii
1
spilopterus (Cagayan)
1
D.sp.Camig.Norte.RMB5702
1
D.sp.BabClaro.RMB5759
0.93
spilopterus (Polilo)
1
spilopterus (Zambales)
1
1
spilopterus (Maragondon)
spilopterus (Bicol)
0.97
1
spilopterus (Isarog)
1
RMB3878
0.69
reticulatus
0.92
cyanopterus (Dinagat)
1
cyanopterus (Mindanao)
1
cyanopterus (Cagayan)
0.9
boschmai (Sumbawa)
1
boschmai (Lombok)
boschmai (Lembata)
1
boschmai (Flores)
1
1
boschmai (Sumba)
0.56
boschmai (Alor)
0.53
timoriensis
volans
sumatranus (WSW Sumatra)
0.75
modiglianii
1
sumatranus (Southern tip of Sumatra)
1
0.78
sumatranus (Natuna, Borneo, ESE Sumatra)
1
sumatranus (MP & ENE Sumatra)
1
sumatranus (Batu Ids. & WNW Sumatra)
1
sumatranus (Banyak Ids. & Aceh)
0.91
sumatranus (Mentawai Ids.)
1
sumatranus (Nias)
0.93
laetesvirens (sp. nov.)
1.0

Figure 3. Maximum Likelihood tree inferred from the mitochondrial gene *NADH-2*, partitioned by 1^{st}, 2^{nd} and 3^{rd} codon (A); and from three concatenated nuclear loci *CMOS*, *BDNF*, and *PNN* partitioned by gene and codon position (B). Bootstrap values (based on 1,000 replicates) are given for each major node where the value is greater than 75%. The Sunda Shelf *volans* group has been truncated, but is presented in greater details in Figure 3 (C).

Aphaniotis fusca
75
mindanensis
maximus
86
quinquefasciatus
blanfordii
78
taeniopterus
obscurus (Mentawai Ids. & Sumatra)
99
formosus
90
obscurus (Borneo)
88
94
melanopogon
haematopogon
96
indochinensis
maculatus
cristatellus (Sarawak)
92
cristatellus (Sabah)
88
cristatellus (Mentawai)
99
cristatellus (Sumatra)
94
cristatellus (Malay Peninsula)
79
fimbriatus (Java)
96
fimbriatus (Sumatra & MP)
dussumieri
bimaculatus
walkeri
100
rhytisma
lineatus
100
beccarii
100
supriatnai
spilonotus
100
caerhulians
biaro
92
97
iskandari
quadrasi
palawanensis
ornatus
100
spilopterus (Bicol)
RMB3878
96
spilopterus (Isarog)
100
cyanopterus (Mindanao)
cyanopterus (Cagayan)
99
cyanopterus (Dinagat)
reticulatus
91
guentheri
guentheri
79
jareckii
100
98
spilopterus (Cagayan)
D.sp.Camig.Norte.RMB5702
99
D.sp.BabClaro.RMB5759
spilopterus (Polillo)
100
spilopterus (Maragondon)
99
spilopterus (Zambales)
99
spilopterus (Siquijor)
100
spilopterus (Cebu)
spilopterus (Panay)
100
spilopterus (Negros)
volans
81
boschmai (Sumbawa)
100
100
boschmai (Lombok)
boschmai (Lembata)
boschmai (Flores)
100
boschmai (Alor)
79
boschmai (Sumba)
timoriensis
sumatranus (SW Sumatra)
75
modiglianii
92
sumatranus (Banyak Ids. & NW Sumatra)
95
sumatranus (NE Sumatra & Malay Peninsula)
sumatranus (Central & Western Sumatra)
99
sumatranus (SE Sumatra, Natuna Ids. & Borneo)
sumatranus (Mentawai Ids.)
98
sp. nov. Simeulue
sumatranus (Nias)
A
0.2
Aphaniotis fusca
dussumieri
maculatus
98
97
fimbriatus (Sumatra, Java & MP)
cristatellus (Sarawak)
88
cristatellus (Mentawai Ids., Sumatra, MP, Sabah)
quinquefasciatus
84
mindanensis
maximus
taeniopterus
77
obscurus (Mentawai & Malay Peninsula)
obscurus (Borneo)
formosus (Malay Peninsula)
formosus (Malay Peninsula)
94
formosus (Malay Peninsula)
formosus (Malay Peninsula)
blanfordii
melanopogon
haematopogon
indochinensis
melanopogon
bimaculatus
90
94
beccarii
lineatus
79
rhytisma
98
supriatnai
walkeri
spilonotus
caerhulians
99
caerhulians
iskandari
iskandari
biaro
palawanensis
cornutus
quadrasi
D.sp.Camig.Norte.RMB5702
D.sp.BabClaro.RMB5759
spilopterus (Cagayan)
jareckii
spilopterus (Zambales)
spilopterus (Zambales)
spilopterus (Maragondon)
spilopterus (Zambales)
spilopterus (Polillo)
spilopterus (Bicol)
spilopterus (Isarog)
RMB3878
reticulatus
cyanopterus (Dinagat)
cyanopterus (Dinagat)
cyanopterus (Dinagat)
cyanopterus (Cagayan)
cyanopterus (Mindanao)
spilopterus (Cebu)
spilopterus (Siquijor)
spilopterus (Negros & Panay)
ornatus (Bohol)
ornatus (Samar)
guentheri
Sundashelf volans group
B
0.06

Figure 3.C. The Sunda Shelf *volans* section of the Maximum Likelihood tree inferred from three concatenated nuclear loci (*CMOS*, *BDNF*, and *PNN*), partitioned by gene and codon position. In the insert is the same section as inferred from mtDNA results (See Figure 3(A) for the rest of the tree).


modiglianii
sumatranus (Mentawai)
sum.Banyak.JAM11166
sumatranus (Batu, Banyak & NW Sumatra)
sum.Kutablang.JAM9931
sum.Nias.JAM10082
sum.LabuhanHaji.JAM9934
sum.Pandan.JAM10303
sum.Kutablang.JAM9930
sum.Banyak.JAM11191
sum.Sitahuis.JAM10288
sum.MadiNa.JAM10316
sum.MadiNa.JAM10318
sum.MadiNa.JAM10319
sum.MadiNa.JAM10317
sumatranus (Nias), sp. nov. Simeulue
sum.Sibolangit.JAM9758
sum.Sibolangit.JAM9759
sum.Sibolangit.JAM9757
sum.Sibolangit.JAM9760
sum.Banyak.JAM11092
sum.MadiNa.JAM10315
sum.Kutablang.JAM9929
sum.LabuhanHaji.JAM9933
sum.Nias.JAM10080
sum.Nias.JAM10085
sum.Sibolangit.JAM9761
sum.BatuRaja.JAM9126
sumatranus.ID7221
sum.Serasan.BJE167
sum.Borneo.JAM1195
sum.Subi.BJE133
sum.Serasan.BJE165
sum.Serasan.BJE166
sum.Serasan.BJE168
sum.Tioman.4007
sum.Mersing.JAM3994
sum.Natuna.BJE101
sum.Natuna.BJE100
sum.Tioman.4031
sum.Panti.JAM9676
sum.BatuKuning.JAM9127
sum.Pasaman.JAM10325
sum.Tinggi.LSUHC4714
sum.Tinggi.LSUHC4715
sum.Mersing.JAM3995
sum.Panti.JAM9678
sum.Solok.JAM9297
sum.Harau.JAM9417
sum.Gombak.JAM1362
sum.Solok.JAM9295
sum.Solok.JAM9294
sum.Solok.JAM9296
sum.Tioman.4038
sum.Batu.JAM11005
sum.Natuna.BJE099
sum.Pandan.JAM10301
timoriensis
sum.Pandan.JAM10302
sum.Batu.JAM11004
sum.TelukBetung.JAM9076
sum.TelukBetung.JAM9073
sum.TelukBetung.JAM9074
sum.Kalianda.JAM9123
sum.TelukBetung.JAM9075
sum.Anai.JAM9338
sum.Kalianda.JAM9124
sum.Kalianda.JAM9122
sum.BatuRaja.JAM9125
sum.TelukBetung.JAM9078
sum.Panti.JAM9652
sum.Pandan.JAM10300
sum.Pandan.JAM10306
sum.Banyak.JAM11091
sum.KarangPauh.JAM9390
sum.KarangPauh.JAM9389
sum.Bengkulu.JAM4114
sum.LubukKumpai.JAM9395
sum.PesSelatan.JAM11208
sum.PesSelatan.JAM11207
sum.UAndalas.JAM9240
sum.KarangPauh.JAM9388
sum.KarangPauh.JAM9391
sum.KarangPauh.JAM9387
sum.Panti.JAM9677
sum.PesSelatan.JAM11206
sum.UAndalas.JAM9242
sum.Bengkulu.JAM4113
sum.Kemumu.JAM9138
sum.UAndalas.JAM9243
sum.UAndalas.JAM9244
sum.PesSelatan.JAM11204
sum.PesSelatan.JAM11205
sum.UAndalas.JAM9241
sumatranus (Mentawai Ids.)
boschmai (Sumba)
boschmai (Lembata)
boschmai (Lembata)
boschmai (Flores)
boschmai (Flores)
boschmai (Lombok)
timoriensis
volans
volans
81
boschmai (Sumbawa)
100
boschmai (Lombok)
boschmai (Lembata)
100
boschmai (Flores)
boschmai (Alor)
79
boschmai (Sumba)
timoriensis
sumatranus (SW Sumatra)
75
modiglianii
92
sumatranus (Banyak Ids. & NW Sumatra)
95
sumatranus (NE Sumatra & Malay Peninsula)
sumatranus (Batu Ids, Central-Western Sumatra)
99
sumatranus (SE Sumatra, Natuna Ids. & Borneo)
sumatranus (Mentawai Ids.)
98
sp. nov. Simeulue
sumatranus (Nias)
0.06

Figure 4. The major clades within *Draco*. Support values for the nodes are given in parentheses, the first number indicate bootstrap percentage and the latter posterior probabilities. A = dorsal nostril group, B = lacrimal bone group, C = *fimbriatus* group, D = *lineatus* group, E = Philippine *volans* group, F = *volans* group, G = Lesser Sunda *volans* group, and H = Greater Sunda Shelf *volans* group.

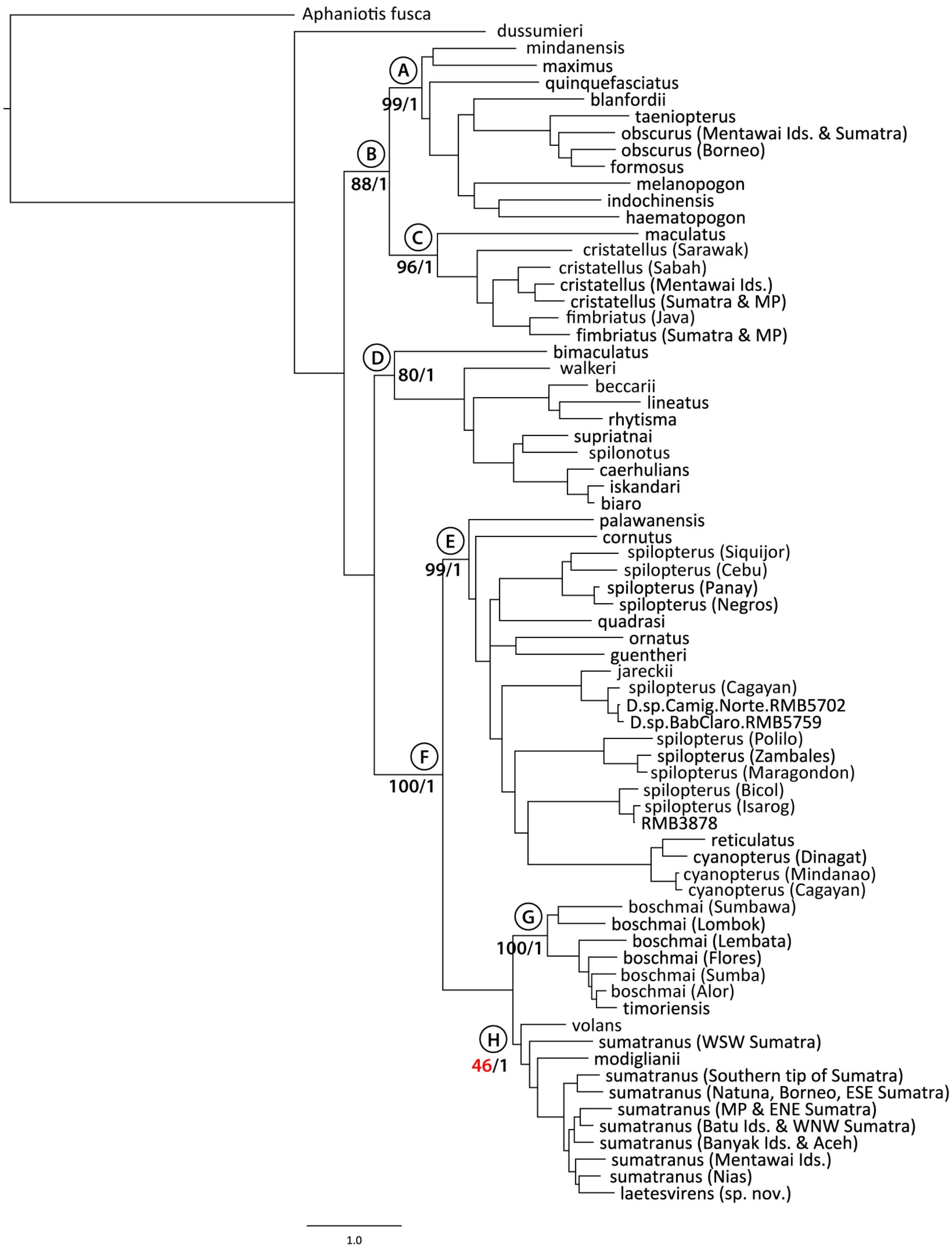
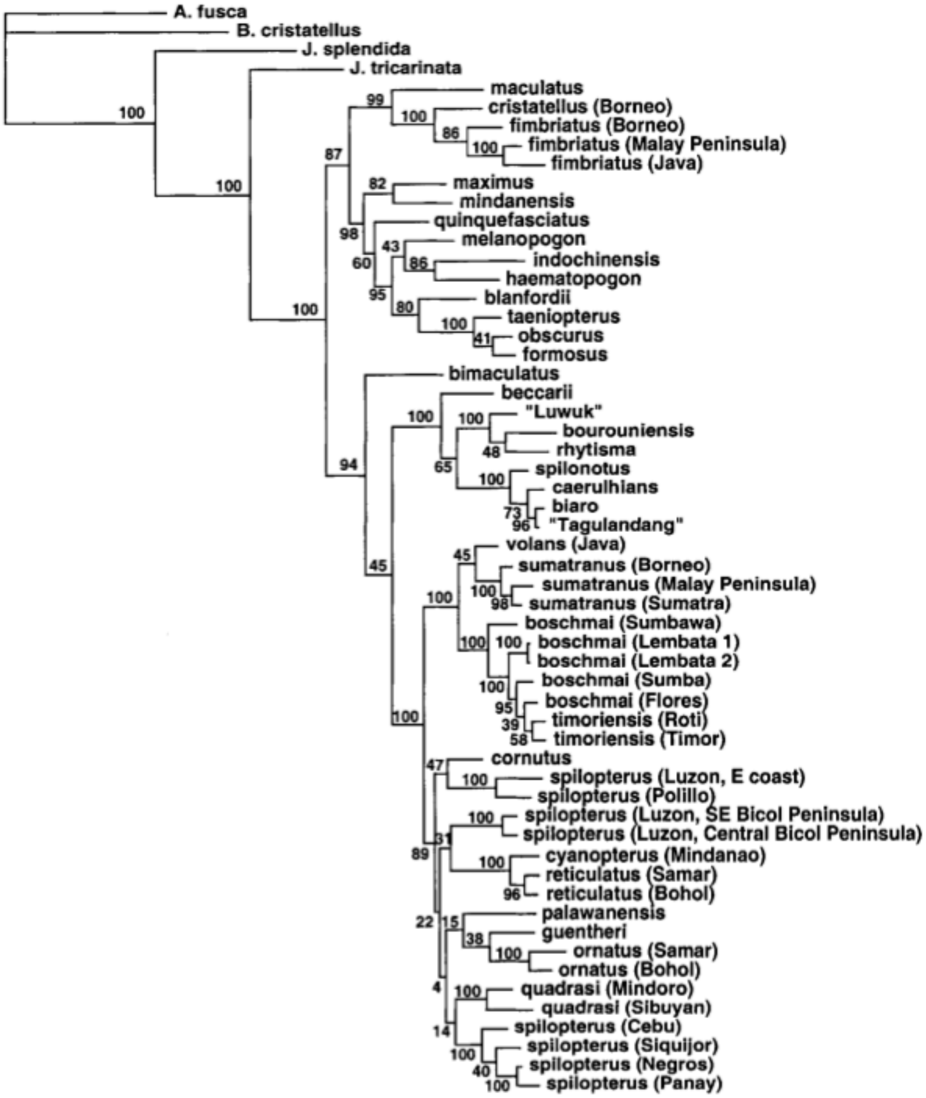

Aphaniotis fusca
dussumieri
mindanensis
maximus
A
quinquefasciatus
99/1
blanfordii
taeniopterus
B
obscurus (Mentawai Ids. & Sumatra)
obscurus (Borneo)
88/1
formosus
melanopogon
indochinensis
haematopogon
C
maculatus
cristatellus (Sarawak)
96/1
cristatellus (Sabah)
cristatellus (Mentawai Ids.)
cristatellus (Sumatra & MP)
fimbriatus (Java)
fimbriatus (Sumatra & MP)
D
bimaculatus
80/1
walkeri
beccarii
lineatus
rhytisma
supriatnai
spilonotus
caerhulians
iskandari
biaro
palawanensis
E
cornutus
spilopterus (Siquijor)
99/1
spilopterus (Cebu)
spilopterus (Panay)
spilopterus (Negros)
quadrasi
ornatus
guentheri
jareckii
spilopterus (Cagayan)
D.sp.Camig.Norte.RMB5702
D.sp.BabClaro.RMB5759
spilopterus (Polilo)
F
spilopterus (Zambales)
spilopterus (Maragondon)
100/1
spilopterus (Bicol)
spilopterus (Isarog)
RMB3878
reticulatus
cyanopterus (Dinagat)
cyanopterus (Mindanao)
cyanopterus (Cagayan)
boschmai (Sumbawa)
G
boschmai (Lombok)
boschmai (Lembata)
100/1
boschmai (Flores)
boschmai (Sumba)
boschmai (Alor)
timoriensis
volans
H
sumatranus (WSW Sumatra)
46/1
modiglianii
sumatranus (Southern tip of Sumatra)
sumatranus (Natuna, Borneo, ESE Sumatra)
sumatranus (MP & ENE Sumatra)
sumatranus (Batu Ids. & WNW Sumatra)
sumatranus (Banyak Ids. & Aceh)
sumatranus (Mentawai Ids.)
sumatranus (Nias)
laetesvirens (sp. nov.)
1.0

Figure 5. Maximum Likelihood results from McGuire & Kiew (2001). Values indicate bootstrap score (100 replicates).


A. fusca
B. cristatellus
J. splendida
J. tricarinata
100
100
100
87
99
maculatus
100
cristatellus (Borneo)
86
fimbriatus (Borneo)
100
fimbriatus (Malay Peninsula)
fimbriatus (Java)
82
maximus
mindanensis
98
quinquefasciatus
43
melanopogon
60
86
indochinensis
haematopogon
95
80
blanfordii
100
taeniopterus
41
obscurus
formosus
94
bimaculatus
100
beccarii
100
"Luwuk"
bourouniensis
48
rhytisma
65
100
spilonotus
caerulhians
73
biaro
96
"Tagulandang"
45
45
volans (Java)
100
sumatranus (Borneo)
100
sumatranus (Malay Peninsula)
98
sumatranus (Sumatra)
boschmai (Sumbawa)
100
100
boschmai (Lembata 1)
boschmai (Lembata 2)
100
boschmai (Sumba)
95
boschmai (Flores)
39
timoriensis (Roti)
58
timoriensis (Timor)
100
47
cornutus
100
spilopterus (Luzon, E coast)
spilopterus (Polillo)
100
spilopterus (Luzon, SE Bicol Peninsula)
spilopterus (Luzon, Central Bicol Peninsula)
89
31
100
cyanopterus (Mindanao)
reticulatus (Samar)
96
reticulatus (Bohol)
22
15
palawanensis
38
guentheri
100
ornatus (Samar)
ornatus (Bohol)
4
100
quadrasi (Mindoro)
quadrasi (Sibuyan)
14
spilopterus (Cebu)
100
spilopterus (Siquijor)
40
spilopterus (Negros)
100
spilopterus (Panay)

Sample Name	**Species**	**ND2**	**PNN**	**CMOS**	**BDNF**
Aphan.fuscus.JAM1141	*Aphaniotis fusca*	✓	✓	✓	✓
biaro.JAM2361	*Draco biaro*	✓	✓	✓	✓
biaro.JAM2362	*Draco biaro*	✓	✓	✓	✓
bimac.Bohol.JAM1564	*Draco bimaculatus*	✓	✓	✓	✓
bimac.Bohol.JAM1565	*Draco bimaculatus*	✓	✓	✓	✓
bimac.Bohol.JAM1568	*Draco bimaculatus*	✓	✓	✓	✓
bimac.Mindanao.JAM1249	*Draco bimaculatus*	✓	✓	✓	✓
bimac.Mindanao.JAM1250	*Draco bimaculatus*	✓	✓	✓	✓
bimac.Mindanao.JAM1259	*Draco bimaculatus*	✓	✓	✓	✓
bimac.Samar.JAM791	*Draco bimaculatus*	✓	✓	✓	✓
bimac.Samar.JAM792	*Draco bimaculatus*	✓	✓	✓	✗
bimac.Samar.JAM834	*Draco bimaculatus*	✓	✓	✓	✓
blan.Bago1.CAS221153	*Draco blanfordii*	✓	✓	✓	✓
blan.Kachin.CAS228480	*Draco blanfordii*	✓	✓	✓	✓
blan.Sagaing.CAS228466	*Draco blanfordii*	✓	✓	✓	✓
blan.Taninth1.CAS228467	*Draco blanfordii*	✓	✓	✓	✓
blan.Taninth1.CAS228470	*Draco blanfordii*	✓	✓	✓	✓
blan.Taninth2.CAS228476	*Draco blanfordii*	✓	✓	✓	✓
blan.Taninth2.CAS228478	*Draco blanfordii*	✓	✓	✓	✓
blan.Taninth2.CAS228479	*Draco blanfordii*	✓	✓	✓	✓
blanfordii.Perlis.JAM1077	*Draco blanfordii*	✓	✓	✓	✓
boschmai.Alor.WAM107583	*Draco boschmai*	✓	✗	✗	✗
boschmai.bje034.Lombok	*Draco boschmai*	✓	✓	✓	✓
boschmai.Flores.bje077	*Draco boschmai*	✓	✓	✓	✓
boschmai.Flores.WAM104530	*Draco boschmai*	✓	✓	✓	✓
boschmai.Lembata.WAM105107	*Draco boschmai*	✓	✗	✓	✗
boschmai.Lembata.WAM105108	*Draco boschmai*	✓	✓	✓	✓
boschmai.Lombok.JAM3149	*Draco boschmai*	✓	✓	✓	✓
boschmai.Sumba.WAM101714	*Draco boschmai*	✓	✓	✓	✓
boschmai.Sumbawa.WAM98623	*Draco boschmai*	✓	✗	✓	✗
caerhulians.JAM2304	*Draco caerhulians*	✓	✓	✓	✓
caerhulians.JAM2305	*Draco caerhulians*	✓	✓	✓	✓
CC.walk.Puncak.j6728	*Draco walkeri*	✓	✓	✓	✓
corn.Sabah.JAM1206	*Draco cornutus*	✓	✓	✓	✓
corn.Sabah.JAM1224	*Draco cornutus*	✓	✓	✓	✓
corn.SarawakBako.DAS	*Draco cornutus*	✓	✗	✓	✗
cri.Banyak.JAM11194	*Draco cristatellus*	✓	✓	✓	✓
cri.Banyak.JAM11195	*Draco cristatellus*	✓	✓	✗	✓
cri.Banyak.JAM11203	*Draco cristatellus*	✓	✓	✓	✓
cri.Batu.JAM11076	*Draco cristatellus*	✓	✓	✓	✓
cri.MaDiNa.JAM10320	*Draco cristatellus*	✓	✓	✓	✓
cri.MP.LSUHC5617	*Draco cristatellus*	✓	✓	✓	✓
cri.Pagai.JAM10533	*Draco cristatellus*	✓	✓	✓	✓
cri.Pagai.JAM10534	*Draco cristatellus*	✓	✓	✓	✓
cri.Pandan.JAM10312	*Draco cristatellus*	✓	✓	✓	✓
cri.Pandan.JAM10313	*Draco cristatellus*	✓	✓	✓	✓
cri.Panti.JAM9604	*Draco cristatellus*	✓	✓	✓	✓
cri.Panti.JAM9679	*Draco cristatellus*	✓	✓	✓	✓

Sample Name	Species	ND2	PNN	CMOS	BDNF
cri.Poring.JAM1216	*Draco cristatellus*	✓	✓	✓	✓
cri.Sarawak.JAM1203	*Draco cristatellus*	✓	✓	✓	✓
cri.Siberut.SZL1	*Draco cristatellus*	✓	✗	✓	✗
cri.Siberut.SZL47	*Draco cristatellus*	✓	✗	✓	✓
cri.Sibolangit.JAM9820	*Draco cristatellus*	✓	✗	✓	✗
cri.Sipirok.JAM9688	*Draco cristatellus*	✓	✓	✓	✓
cri.Sipirok.JAM9689	*Draco cristatellus*	✓	✓	✓	✓
cri.Sipirok.JAM9690	*Draco cristatellus*	✓	✗	✗	✓
cri.Sipirok.JAM9691	*Draco cristatellus*	✓	✗	✗	✓
cri.Sipirok.JAM9692	*Draco cristatellus*	✓	✗	✗	✓
cri.Sipora.SZL17	*Draco cristatellus*	✓	✓	✓	✓
cri.Sitahuis.JAM10298	*Draco cristatellus*	✓	✓	✓	✓
cri.Sitahuis.JAM10299	*Draco cristatellus*	✓	✓	✓	✓
cri.TelukBetung.JAM9082	*Draco cristatellus*	✓	✓	✓	✓
cyanopt.Cagayan.JAM1309	*Draco cyanopterus*	✓	✓	✓	✓
cyanopt.Dinagat.cwl277	*Draco cyanopterus*	✓	✓	✓	✓
cyanopt.Dinagat.cwl278	*Draco cyanopterus*	✓	✓	✓	✓
cyanopt.Dinagat.cwl279	*Draco cyanopterus*	✓	✓	✓	✓
cyanopt.Mindanao.JAM1300	*Draco cyanopterus*	✓	✓	✓	✓
D.sp.BabClaro.RMB5759	*Draco spilopterus* (?)	✓	✓	✓	✓
D.sp.Camig.Norte.RMB5702	*Draco spilopterus* (?)	✓	✓	✓	✓
dussumieri.167	*Draco dussumieri*	✓	✓	✓	✓
ECC.becc.Betelme.jam5053	*Draco beccarii*	✓	✓	✓	✓
fim.Java.JAM2065	*Draco fimbriatus*	✓	✓	✓	✓
fim.Larut.JAM1414	*Draco fimbriatus*	✓	✓	✓	✓
fim.LSUHC4601	*Draco fimbriatus*	✓	✓	✓	✓
fim.Panti.JAM9643	*Draco fimbriatus*	✓	✓	✓	✓
fim.Sumatra.LSUHC4101	*Draco fimbriatus*	✓	✓	✓	✓
fim.Tioman.4001	*Draco fimbriatus*	✓	✓	✓	✓
fim.Tioman.4002	*Draco fimbriatus*	✓	✓	✓	✓
formosus.Gombok.JAM1016	*Draco formosus*	✓	✓	✓	✓
formosus.Pekan.lsuhc4874	*Draco formosus*	✓	✓	✓	✓
formosus.Tinggi.lsuhc4802	*Draco formosus*	✓	✓	✓	✓
formosus.Tinggi.lsuhc4804	*Draco formosus*	✓	✓	✓	✓
guentheri.JAM1252	*Draco guentheri*	✓	✓	✓	✓
guentheri.JAM1268	*Draco guentheri*	✓	✓	✓	✓
hae.AirBusuk.JAM9298	*Draco haematopogon*	✓	✓	✗	✓
hae.AirBusuk.JAM9299	*Draco haematopogon*	✓	✓	✗	✓
hae.AirBusuk.JAM9300	*Draco haematopogon*	✓	✓	✗	✓
hae.AirBusuk.JAM9301	*Draco haematopogon*	✓	✓	✓	✓
hae.AirBusuk.JAM9302	*Draco haematopogon*	✓	✓	✓	✓
hae.Borneo.id7200	*Draco haematopogon*	✓	✓	✓	✓
hae.Borneo.RMBR00838	*Draco haematopogon*	✓	✗	✓	✗
hae.Java.JAM3072	*Draco haematopogon*	✓	✓	✓	✓
hae.Kalianda.JAM9116	*Draco haematopogon*	✓	✓	✓	✓
hae.Kalianda.JAM9117	*Draco haematopogon*	✓	✓	✓	✓
hae.Kalianda.JAM9118	*Draco haematopogon*	✓	✓	✓	✓
hae.Kalianda.JAM9119	*Draco haematopogon*	✓	✓	✓	✓
hae.Kalianda.JAM9120	*Draco haematopogon*	✓	✓	✓	✓

Sample Name	**Species**	**ND2**	**PNN**	**CMOS**	**BDNF**
hae.Larut.JAM1381	*Draco haematopogon*	✓	✓	✓	✓
hae.MaDiNa.JAM10323	*Draco haematopogon*	✓	✓	✓	✓
hae.Sipolha.JAM9713	*Draco haematopogon*	✓	✗	✗	✗
hae.Sumatra.JAM4109	*Draco haematopogon*	✓	✗	✓	✗
hae.Sumatra.JAM4110	*Draco haematopogon*	✓	✓	✓	✓
hae.Sumatra.JAM4111	*Draco haematopogon*	✓	✓	✓	✓
hae.TalangEmpat.JAM9129	*Draco haematopogon*	✓	✓	✓	✓
hae.TalangEmpat.JAM9130	*Draco haematopogon*	✓	✓	✓	✓
hae.TalangEmpat.JAM9131	*Draco haematopogon*	✓	✓	✓	✓
hae.TalangEmpat.JAM9132	*Draco haematopogon*	✓	✓	✓	✓
hae.TalangEmpat.JAM9133	*Draco haematopogon*	✓	✓	✓	✓
hae.TelukBetung.JAM9083	*Draco haematopogon*	✓	✓	✓	✓
hae.TelukBetung.JAM9103	*Draco haematopogon*	✓	✓	✓	✓
hae.TelukBetung.JAM9105	*Draco haematopogon*	✓	✓	✓	✓
hae.TelukBetung.JAM9106	*Draco haematopogon*	✓	✓	✓	✓
hae.TelukBetung.JAM9107	*Draco haematopogon*	✓	✓	✓	✓
indochin.ROM31987	*Draco indochinensis*	✓	✓	✓	✓
indochin.ROM31991	*Draco indochinensis*	✓	✓	✓	✓
iskandari.JAM2331	*Draco iskandari*	✓	✓	✓	✓
iskandari.JAM2333	*Draco iskandari*	✓	✓	✓	✓
jareckii.rmb7601	*Draco jareckii*	✓	✓	✓	✓
laetv.Lasia.JAM9988	*Draco* sp. nov. “Simeulue”	✓	✓	✓	✓
laetv.Lasia.JAM9989	*Draco* sp. nov. “Simeulue”	✓	✓	✓	✓
laetv.Lasia.JAM9990	*Draco* sp. nov. “Simeulue”	✓	✓	✓	✓
laetv.Lasia.JAM9991	*Draco* sp. nov. “Simeulue”	✓	✓	✓	✓
laetv.Lasia.JAM9992	*Draco* sp. nov. “Simeulue”	✓	✓	✓	✓
laetv.Simeulue.JAM10061	*Draco* sp. nov. “Simeulue”	✓	✓	✓	✓
laetv.Simeulue.JAM10062	*Draco* sp. nov. “Simeulue”	✓	✓	✓	✓
laetv.Simeulue.JAM9957	*Draco* sp. nov. “Simeulue”	✓	✓	✓	✓
laetv.Simeulue.JAM9958	*Draco* sp. nov. “Simeulue”	✓	✓	✓	✓
laetv.Simeulue.JAM9959	*Draco* sp. nov. “Simeulue”	✓	✓	✓	✓
laetv.Simeulue.JAM9960	*Draco* sp. nov. “Simeulue”	✓	✓	✓	✓
laetv.Simeulue.JAM9961	*Draco* sp. nov. “Simeulue”	✓	✓	✓	✓
lineatus.Ambon.JAM2146	*Draco lineatus*	✓	✓	✓	✗
lineatus.Ambon.JAM2148	*Draco lineatus*	✓	✓	✓	✓
lineatus.Buru.JAM2217	*Draco lineatus*	✓	✗	✓	✓
lineatus.Buru.JAM2221	*Draco lineatus*	✓	✓	✓	✓
lineatus.Seram.JAM2189	*Draco lineatus*	✓	✓	✓	✓
lineatus.Seram.JAM2194	*Draco lineatus*	✓	✓	✓	✓
mac.Bago2.CAS222144	*Draco maculatus*	✓	✓	✓	✓
mac.Chin.CAS220002	*Draco maculatus*	✓	✓	✓	✓
mac.Chin.CAS220005	*Draco maculatus*	✓	✓	✓	✓
mac.Chin.CAS220006	*Draco maculatus*	✓	✓	✓	✓
mac.Chin.CAS220007	*Draco maculatus*	✓	✓	✓	✓
mac.Chin.CAS220018	*Draco maculatus*	✓	✓	✓	✓
mac.Chin.CAS220019	*Draco maculatus*	✓	✓	✓	✓
mac.Chin.CAS220050	*Draco maculatus*	✓	✓	✓	✓
mac.China.KUFS326	*Draco maculatus*	✓	✓	✓	✓
mac.China.KUFS340	*Draco maculatus*	✓	✓	✓	✓

Sample Name	**Species**	**ND2**	**PNN**	**CMOS**	**BDNF**
mac.fmnh263343.Cambodia	*Draco maculatus*	✓	✗	✗	✗
mac.Hainan.tp26348	*Draco maculatus*	✓	✓	✓	✓
mac.Mandalay.CAS214083	*Draco maculatus*	✓	✓	✓	✓
mac.Perlis.JAM1084	*Draco maculatus*	✓	✓	✓	✓
mac.Rakhine1.CAS220057	*Draco maculatus*	✓	✓	✓	✓
mac.Rakhine2.CAS221127	*Draco maculatus*	✓	✓	✓	✓
mac.Sagaing2.CAS210160	*Draco maculatus*	✓	✓	✓	✓
mac.Sagaing2.CAS210245	*Draco maculatus*	✓	✓	✓	✓
mac.Sagaing2.CAS210502	*Draco maculatus*	✓	✓	✓	✓
mac.Sagaing3.CAS215538	*Draco maculatus*	✓	✓	✓	✓
mac.Sagaing3.CAS215634	*Draco maculatus*	✓	✓	✓	✓
mac.Sagaing3.CAS215637	*Draco maculatus*	✓	✓	✓	✓
mac.Shan1.CAS228463	*Draco maculatus*	✓	✓	✓	✓
mac.Shan2.CAS215259	*Draco maculatus*	✓	✓	✓	✓
mac.Shan3.CAS228473	*Draco maculatus*	✓	✓	✓	✓
mac.Shan4.CAS228474	*Draco maculatus*	✓	✓	✓	✓
mac.Taninth2.CAS228472	*Draco maculatus*	✓	✓	✓	✓
mac.Taninth3.CAS228475	*Draco maculatus*	✓	✓	✓	✓
max.Anai.JAM9340	*Draco maximus*	✓	✗	✗	✓
max.Anai.JAM9341	*Draco maximus*	✓	✓	✗	✓
max.Bengkulu.RMBR00683	*Draco maximus*	✓	✗	✓	✓
max.Bengkulu.RMBR00837	*Draco maximus*	✓	✗	✓	✓
max.Gombok.JAM1043	*Draco maximus*	✓	✓	✓	✓
max.Lembing.LSUHC4951	*Draco maximus*	✓	✓	✓	✓
max.Panti.JAM9631	*Draco maximus*	✓	✗	✓	✓
max.Panti.JAM9644	*Draco maximus*	✓	✗	✗	✗
max.RMBR01002	*Draco maximus*	✓	✗	✓	✓
max.Sabah.JAM1221	*Draco maximus*	✓	✓	✓	✓
mel.Anai.JAM9327	*Draco melanopogon*	✓	✓	✓	✓
mel.Anai.JAM9328	*Draco melanopogon*	✓	✓	✓	✓
mel.Anai.JAM9329	*Draco melanopogon*	✓	✗	✓	✓
mel.Anai.JAM9330	*Draco melanopogon*	✓	✓	✓	✓
mel.Anai.JAM9331	*Draco melanopogon*	✓	✓	✓	✓
mel.Banyak.JAM11090	*Draco melanopogon*	✓	✓	✓	✓
mel.Banyak.JAM11118	*Draco melanopogon*	✓	✓	✓	✓
mel.Banyak.JAM11119	*Draco melanopogon*	✓	✓	✓	✓
mel.Banyak.JAM11120	*Draco melanopogon*	✓	✓	✓	✓
mel.Banyak.JAM11122	*Draco melanopogon*	✓	✓	✓	✓
mel.Batu.JAM10964	*Draco melanopogon*	✓	✓	✓	✓
mel.Batu.JAM10965	*Draco melanopogon*	✓	✓	✓	✓
mel.Batu.JAM11007	*Draco melanopogon*	✓	✓	✓	✓
mel.Batu.JAM11008	*Draco melanopogon*	✓	✓	✓	✓
mel.Batu.JAM11009	*Draco melanopogon*	✓	✓	✓	✓
mel.Gombak.JAM1015	*Draco melanopogon*	✓	✓	✓	✓
mel.Harau.JAM9413	*Draco melanopogon*	✓	✓	✓	✓
mel.Harau.JAM9414	*Draco melanopogon*	✓	✗	✓	✗
mel.Harau.JAM9415	*Draco melanopogon*	✓	✗	✓	✓
mel.Harau.JAM9416	*Draco melanopogon*	✓	✓	✓	✓
mel.Kemumu.JAM9140	*Draco melanopogon*	✓	✓	✓	✓

Sample Name	**Species**	**ND2**	**PNN**	**CMOS**	**BDNF**
mel.Lembeng.LSUHC4985	*Draco melanopogon*	✓	✓	✓	✓
mel.Mersing.JAM3996	*Draco melanopogon*	✓	✓	✓	✓
mel.Mersing.JAM3997	*Draco melanopogon*	✓	✓	✓	✓
mel.Mersing.JAM3999	*Draco melanopogon*	✓	✓	✓	✓
mel.Panti.JAM9605	*Draco melanopogon*	✓	✓	✓	✓
mel.Panti.JAM9606	*Draco melanopogon*	✓	✓	✓	✓
mel.Panti.JAM9607	*Draco melanopogon*	✓	✓	✓	✓
mel.Panti.JAM9611	*Draco melanopogon*	✓	✓	✓	✓
mel.Panti.JAM9612	*Draco melanopogon*	✓	✓	✓	✓
mel.PesSelatan.JAM11218	*Draco melanopogon*	✓	✓	✓	✓
mel.PesSelatan.JAM11219	*Draco melanopogon*	✓	✓	✗	✓
mel.RMBR01038	*Draco melanopogon*	✓	✗	✓	✓
mel.RMBR01039	*Draco melanopogon*	✓	✓	✓	✓
mel.RMBR01040	*Draco melanopogon*	✓	✓	✓	✓
mel.Sibolangit.JAM9772	*Draco melanopogon*	✓	✓	✓	✓
mel.Sibolangit.JAM9814	*Draco melanopogon*	✓	✓	✓	✓
mel.Sibolangit.JAM9815	*Draco melanopogon*	✓	✓	✓	✓
mel.Sibolangit.JAM9816	*Draco melanopogon*	✓	✓	✓	✓
mel.Sibolangit.JAM9817	*Draco melanopogon*	✓	✓	✓	✓
mel.Sibulanbulan.JAM9696	*Draco melanopogon*	✓	✓	✓	✓
mel.Sibulanbulan.JAM9697	*Draco melanopogon*	✓	✓	✓	✓
mel.Sibulanbulan.JAM9698	*Draco melanopogon*	✓	✓	✓	✓
mel.Sipirok.JAM9684	*Draco melanopogon*	✓	✓	✓	✓
mel.Sitahuis.JAM10289	*Draco melanopogon*	✓	✓	✓	✓
mel.Sitahuis.JAM10290	*Draco melanopogon*	✓	✓	✓	✓
mel.Sitahuis.JAM10291	*Draco melanopogon*	✓	✓	✓	✓
mel.Sitahuis.JAM10292	*Draco melanopogon*	✓	✓	✓	✓
mel.Sumatra.JAM4014	*Draco melanopogon*	✓	✗	✗	✓
mel.Sumatra.JAM4102	*Draco melanopogon*	✓	✗	✓	✗
mel.Taba.JAM4105	*Draco melanopogon*	✓	✗	✓	✗
mel.TaHuRa.JAM9250	*Draco melanopogon*	✓	✓	✓	✓
mel.TaHuRa.JAM9251	*Draco melanopogon*	✓	✗	✓	✓
mel.TaHuRa.JAM9252	*Draco melanopogon*	✓	✓	✓	✓
mel.TaHuRa.JAM9253	*Draco melanopogon*	✓	✓	✓	✓
mel.TaHuRa.JAM9254	*Draco melanopogon*	✓	✓	✗	✓
mel.TelukBetung.JAM9098	*Draco melanopogon*	✓	✗	✓	✓
mel.TelukBetung.JAM9112	*Draco melanopogon*	✓	✓	✓	✓
mel.TelukBetung.JAM9113	*Draco melanopogon*	✓	✓	✓	✓
mel.Tioman.JAM4000	*Draco melanopogon*	✓	✓	✓	✓
mel.Tioman.JAM4018	*Draco melanopogon*	✓	✓	✓	✓
mel.Tioman.JAM4023	*Draco melanopogon*	✓	✓	✓	✓
mindanensis.JAM1269	*Draco mindanensis*	✓	✓	✓	✓
mod.Enggano.JAM4265	*Draco modiglianii*	✓	✗	✓	✓
mod.Enggano.JAM4280	*Draco modiglianii*	✓	✓	✓	✓
mod.Enggano.JAM4281	*Draco modiglianii*	✓	✓	✓	✓
mod.Enggano.JAM4285	*Draco modiglianii*	✓	✓	✓	✓
mod.Enggano.JAM4361	*Draco modiglianii*	✓	✓	✓	✓
obs.Anai.JAM9339	*Draco obscurus*	✓	✗	✗	✓
obs.Banyak.JAM11080	*Draco obscurus*	✓	✓	✓	✓

Sample Name	**Species**	**ND2**	**PNN**	**CMOS**	**BDNF**
obs.Banyak.JAM11081	*Draco obscurus*	✓	✓	✓	✓
obs.Banyak.JAM11082	*Draco obscurus*	✓	✓	✓	✓
obs.Banyak.JAM11083	*Draco obscurus*	✓	✓	✓	✓
obs.Banyak.JAM11084	*Draco obscurus*	✓	✓	✓	✓
obs.Batu.JAM11017	*Draco obscurus*	✓	✓	✓	✓
obs.Batu.JAM11018	*Draco obscurus*	✓	✓	✓	✓
obs.Batu.JAM11075	*Draco obscurus*	✓	✓	✓	✗
obs.Borneo.RMBR00797	*Draco obscurus*	✓	✗	✓	✓
obs.Kemumu.JAM9141	*Draco obscurus*	✓	✗	✗	✓
obs.Pagai.SZL81	*Draco obscurus*	✓	✓	✓	✗
obs.Pagai.SZL82	*Draco obscurus*	✓	✓	✓	✓
obs.Pagai.SZL83	*Draco obscurus*	✓	✓	✓	✓
obs.Pagai.SZL84	*Draco obscurus*	✓	✓	✓	✓
obs.Pagai.SZL85	*Draco obscurus*	✓	✓	✓	✓
obs.Panti.JAM9618	*Draco obscurus*	✓	✗	✗	✗
obs.Panti.JAM9639	*Draco obscurus*	✓	✗	✗	✗
obs.Panti.JAM9640	*Draco obscurus*	✓	✓	✓	✓
obs.Panti.JAM9641	*Draco obscurus*	✓	✓	✗	✓
obs.Panti.JAM9642	*Draco obscurus*	✓	✗	✓	✓
obs.Sabah.JAM1220	*Draco obscurus*	✓	✓	✓	✓
obs.Sabah.JAM1484	*Draco obscurus*	✓	✓	✓	✓
obs.Siberut.JAM10335	*Draco obscurus*	✓	✓	✓	✓
obs.Siberut.JAM10336	*Draco obscurus*	✓	✓	✓	✓
obs.Siberut.JAM10337	*Draco obscurus*	✓	✓	✓	✓
obs.Siberut.JAM10338	*Draco obscurus*	✓	✓	✓	✓
obs.Siberut.JAM10339	*Draco obscurus*	✓	✓	✓	✓
obs.Sibolangit.JAM9765	*Draco obscurus*	✓	✓	✓	✓
obs.Sibolangit.JAM9766	*Draco obscurus*	✓	✓	✓	✓
obs.Sibolangit.JAM9821	*Draco obscurus*	✓	✗	✗	✓
obs.Sipora.JAM10732	*Draco obscurus*	✓	✓	✗	✗
obs.Sipora.JAM10733	*Draco obscurus*	✓	✓	✓	✓
obs.Sipora.JAM10734	*Draco obscurus*	✓	✓	✓	✓
obs.Sipora.JAM10841	*Draco obscurus*	✓	✓	✓	✓
obs.Sipora.JAM10844	*Draco obscurus*	✓	✓	✓	✓
obs.Sitahuis.JAM10295	*Draco obscurus*	✓	✓	✓	✓
obs.Sitahuis.JAM10296	*Draco obscurus*	✓	✓	✓	✓
obs.Sitahuis.JAM10297	*Draco obscurus*	✓	✓	✓	✓
obs.TaHuRa.JAM9257	*Draco obscurus*	✓	✓	✓	✓
obs.TaHuRa.JAM9258	*Draco obscurus*	✓	✓	✓	✓
obs.TaHuRa.JAM9259	*Draco obscurus*	✓	✓	✓	✓
ornatus.Bohol.JAM1562	*Draco ornatus*	✓	✓	✓	✓
ornatus.Samar.JAM862	*Draco ornatus*	✓	✓	✓	✓
palawan.BP.RMB3085	*Draco palawanensis*	✓	✓	✓	✓
palawan.Irawan.RMB3098	*Draco palawanensis*	✓	✗	✓	✗
palawan.Quezon.JAM1336	*Draco palawanensis*	✓	✓	✓	✓
quad.Mindoro.JAM888	*Draco quadrasi*	✓	✓	✓	✓
quad.Sibuyan.FMNH236070	*Draco quadrasi*	✓	✓	✓	✓
qui.Banyak.JAM11086	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Banyak.JAM11087	*Draco quinquefasciatus*	✓	✓	✓	✓

Sample Name	**Species**	**ND2**	**PNN**	**CMOS**	**BDNF**
qui.Banyak.JAM11088	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Banyak.JAM11089	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Banyak.JAM11124	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Batu.JAM10962	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Batu.JAM10963	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Batu.JAM11010	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Batu.JAM11015	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Batu.JAM11016	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Borneo.1201	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Gombak.JAM1029	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Pekan.4875	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Pekan.4877	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Pekan.4881	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Pekan.LSUHC4852	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.RMBR01041	*Draco quinquefasciatus*	✓	✗	✓	✗
qui.Sitahuis.JAM10293	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.Sitahuis.JAM10294	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.TalangEmpat.JAM9136	*Draco quinquefasciatus*	✓	✓	✓	✓
qui.TalangEmpat.JAM9137	*Draco quinquefasciatus*	✓	✓	✓	✓
reticulatus.Bohol.JAM1549	*Draco reticulatus*	✓	✓	✓	✓
reticulatus.Samar.JAM869	*Draco reticulatus*	✓	✓	✓	✓
rhytisma.JAM2477	*Draco rhytisma*	✓	✓	✓	✓
rhytisma.JAM2478	*Draco rhytisma*	✓	✓	✓	✓
RMB3255		✓	✗	✗	✗
RMB3878		✓	✓	✓	✗
spilopt.Bicol.JAM768	*Draco spilopterus*	✓	✓	✓	✓
spilopt.Cagayan.RMB6098	*Draco spilopterus*	✓	✓	✓	✓
spilopt.Cebu.JAM1530	*Draco spilopterus*	✓	✓	✓	✓
spilopt.Isarog.RMB141	*Draco spilopterus*	✓	✓	✓	✓
spilopt.Maragondon.JAM992	*Draco spilopterus*	✓	✓	✓	✓
spilopt.Negros.ROM773	*Draco spilopterus*	✓	✓	✓	✓
spilopt.Negros.ROM774	*Draco spilopterus*	✓	✗	✗	✓
spilopt.Panay.JAM1504	*Draco spilopterus*	✓	✓	✓	✓
spilopt.Panay.JAM1505	*Draco spilopterus*	✓	✓	✓	✓
spilopt.Panay.JAM1508	*Draco spilopterus*	✓	✓	✓	✓
spilopt.Polillo.JAM1005	*Draco spilopterus*	✓	✓	✓	✓
spilopt.Siquijor.JAM1592	*Draco spilopterus*	✓	✓	✓	✓
spilopt.Zambales.RMB4617	*Draco spilopterus*	✓	✗	✓	✓
spilopt.Zambales.RMB4620	*Draco spilopterus*	✓	✓	✓	✓
spilopt.Zambales.RMB4626	*Draco spilopterus*	✓	✗	✓	✓
sum.Anai.JAM9338	*Draco sumatranus*	✓	✓	✓	✓
sum.Banyak.JAM11091	*Draco sumatranus*	✓	✓	✓	✓
sum.Banyak.JAM11092	*Draco sumatranus*	✓	✓	✓	✓
sum.Banyak.JAM11165	*Draco sumatranus*	✓	✓	✓	✓
sum.Banyak.JAM11166	*Draco sumatranus*	✓	✓	✓	✓
sum.Banyak.JAM11191	*Draco sumatranus*	✓	✓	✓	✓
sum.Batu.JAM10966	*Draco sumatranus*	✓	✓	✓	✓
sum.Batu.JAM11003	*Draco sumatranus*	✓	✓	✓	✓
sum.Batu.JAM11004	*Draco sumatranus*	✓	✓	✓	✓

Sample Name	Species	ND2	PNN	CMOS	BDNF
sum.Batu.JAM11005	*Draco sumatranus*	✓	✓	✓	✗
sum.Batu.JAM11006	*Draco sumatranus*	✓	✓	✓	✓
sum.BatuKuning.JAM9127	*Draco sumatranus*	✓	✓	✓	✓
sum.BatuRaja.JAM9125	*Draco sumatranus*	✓	✓	✓	✓
sum.BatuRaja.JAM9126	*Draco sumatranus*	✓	✓	✓	✓
sum.Bengkulu.JAM4113	*Draco sumatranus*	✓	✓	✓	✓
sum.Bengkulu.JAM4114	*Draco sumatranus*	✓	✗	✓	✗
sum.Borneo.JAM1195	*Draco sumatranus*	✓	✓	✓	✓
sum.Gombak.JAM1362	*Draco sumatranus*	✓	✓	✓	✓
sum.Harau.JAM9417	*Draco sumatranus*	✓	✓	✓	✓
sum.Kalianda.JAM9122	*Draco sumatranus*	✓	✓	✓	✓
sum.Kalianda.JAM9123	*Draco sumatranus*	✓	✓	✓	✓
sum.Kalianda.JAM9124	*Draco sumatranus*	✓	✓	✓	✓
sum.KarangPauh.JAM9387	*Draco sumatranus*	✓	✓	✓	✓
sum.KarangPauh.JAM9388	*Draco sumatranus*	✓	✓	✓	✓
sum.KarangPauh.JAM9389	*Draco sumatranus*	✓	✓	✓	✓
sum.KarangPauh.JAM9390	*Draco sumatranus*	✓	✓	✓	✓
sum.KarangPauh.JAM9391	*Draco sumatranus*	✓	✓	✓	✓
sum.Kemumu.JAM9138	*Draco sumatranus*	✓	✓	✓	✓
sum.Kutablang.JAM9929	*Draco sumatranus*	✓	✓	✓	✓
sum.Kutablang.JAM9930	*Draco sumatranus*	✓	✓	✓	✓
sum.Kutablang.JAM9931	*Draco sumatranus*	✓	✓	✓	✓
sum.LabuhanHaji.JAM9933	*Draco sumatranus*	✓	✓	✓	✓
sum.LabuhanHaji.JAM9934	*Draco sumatranus*	✓	✓	✓	✓
sum.LubukKumpai.JAM9395	*Draco sumatranus*	✓	✓	✓	✓
sum.MadiNa.JAM10315	*Draco sumatranus*	✓	✓	✓	✓
sum.MadiNa.JAM10316	*Draco sumatranus*	✓	✓	✓	✓
sum.MadiNa.JAM10317	*Draco sumatranus*	✓	✓	✓	✓
sum.MadiNa.JAM10318	*Draco sumatranus*	✓	✓	✓	✓
sum.MadiNa.JAM10319	*Draco sumatranus*	✓	✓	✓	✓
sum.Mersing.JAM3994	*Draco sumatranus*	✓	✓	✓	✓
sum.Mersing.JAM3995	*Draco sumatranus*	✓	✓	✓	✓
sum.Natuna.BJE099	*Draco sumatranus*	✓	✓	✓	✓
sum.Natuna.BJE100	*Draco sumatranus*	✓	✓	✓	✓
sum.Natuna.BJE101	*Draco sumatranus*	✓	✓	✓	✓
sum.Nias.JAM10080	*Draco sumatranus*	✓	✓	✓	✓
sum.Nias.JAM10082	*Draco sumatranus*	✓	✓	✓	✓
sum.Nias.JAM10083	*Draco sumatranus*	✓	✓	✓	✓
sum.Nias.JAM10084	*Draco sumatranus*	✓	✓	✓	✓
sum.Nias.JAM10085	*Draco sumatranus*	✓	✓	✓	✓
sum.Pagai.JAM10463	*Draco sumatranus*	✓	✓	✓	✓
sum.Pagai.JAM10464	*Draco sumatranus*	✓	✓	✓	✓
sum.Pagai.JAM10465	*Draco sumatranus*	✓	✓	✓	✓
sum.Pagai.JAM10466	*Draco sumatranus*	✓	✓	✓	✓
sum.Pagai.JAM10467	*Draco sumatranus*	✓	✓	✓	✓
sum.Pandan.JAM10300	*Draco sumatranus*	✓	✓	✓	✓
sum.Pandan.JAM10301	*Draco sumatranus*	✓	✓	✓	✓
sum.Pandan.JAM10302	*Draco sumatranus*	✓	✓	✓	✓
sum.Pandan.JAM10303	*Draco sumatranus*	✓	✓	✓	✓

Sample Name	**Species**	**ND2**	**PNN**	**CMOS**	**BDNF**
sum.Pandan.JAM10306	*Draco sumatranus*	✓	✓	✓	✓
sum.Panti.JAM9652	*Draco sumatranus*	✓	✓	✓	✓
sum.Panti.JAM9676	*Draco sumatranus*	✓	✓	✓	✓
sum.Panti.JAM9677	*Draco sumatranus*	✓	✓	✓	✓
sum.Panti.JAM9678	*Draco sumatranus*	✓	✓	✓	✓
sum.Pasaman.JAM10325	*Draco sumatranus*	✓	✓	✓	✓
sum.PesSelatan.JAM11204	*Draco sumatranus*	✓	✓	✓	✓
sum.PesSelatan.JAM11205	*Draco sumatranus*	✓	✓	✓	✓
sum.PesSelatan.JAM11206	*Draco sumatranus*	✓	✓	✓	✓
sum.PesSelatan.JAM11207	*Draco sumatranus*	✓	✓	✓	✓
sum.PesSelatan.JAM11208	*Draco sumatranus*	✓	✓	✓	✓
sum.PesSelatan.JAM11209	*Draco sumatranus*	✓	✗	✗	✗
sum.Serasan.BJE165	*Draco sumatranus*	✓	✓	✓	✓
sum.Serasan.BJE166	*Draco sumatranus*	✓	✓	✓	✓
sum.Serasan.BJE167	*Draco sumatranus*	✓	✓	✓	✓
sum.Serasan.BJE168	*Draco sumatranus*	✓	✓	✓	✓
sum.Siberut.SZL3	*Draco sumatranus*	✓	✓	✓	✓
sum.Siberut.SZL4	*Draco sumatranus*	✓	✓	✓	✓
sum.Siberut.SZL5	*Draco sumatranus*	✓	✓	✓	✓
sum.Siberut.SZL7	*Draco sumatranus*	✓	✓	✓	✓
sum.Sibolangit.JAM9757	*Draco sumatranus*	✓	✓	✓	✓
sum.Sibolangit.JAM9758	*Draco sumatranus*	✓	✓	✓	✓
sum.Sibolangit.JAM9759	*Draco sumatranus*	✓	✓	✓	✓
sum.Sibolangit.JAM9760	*Draco sumatranus*	✓	✓	✓	✓
sum.Sibolangit.JAM9761	*Draco sumatranus*	✓	✓	✓	✓
sum.Singkil.JAM9923	*Draco sumatranus*	✓	✓	✓	✓
sum.Singkil.JAM9924	*Draco sumatranus*	✓	✓	✓	✓
sum.Sipirok.JAM9693	*Draco sumatranus*	✓	✓	✓	✓
sum.Sipirok.JAM9694	*Draco sumatranus*	✓	✓	✓	✓
sum.Sipora.SZL19	*Draco sumatranus*	✓	✓	✓	✓
sum.Sipora.SZL56	*Draco sumatranus*	✓	✓	✓	✓
sum.Sipora.SZL57	*Draco sumatranus*	✓	✓	✓	✓
sum.Sipora.SZL58	*Draco sumatranus*	✓	✓	✓	✓
sum.Sipora.SZL59	*Draco sumatranus*	✓	✓	✓	✗
sum.Sitahuis.JAM10288	*Draco sumatranus*	✓	✓	✓	✓
sum.Solok.JAM9294	*Draco sumatranus*	✓	✓	✓	✓
sum.Solok.JAM9295	*Draco sumatranus*	✓	✓	✓	✓
sum.Solok.JAM9296	*Draco sumatranus*	✓	✓	✓	✓
sum.Solok.JAM9297	*Draco sumatranus*	✓	✓	✓	✓
sum.Subi.BJE133	*Draco sumatranus*	✓	✓	✓	✓
sum.Sumatra.Aceh	*Draco sumatranus*	✓	✗	✗	✗
sum.TelukBetung.JAM9073	*Draco sumatranus*	✓	✓	✓	✓
sum.TelukBetung.JAM9074	*Draco sumatranus*	✓	✓	✓	✓
sum.TelukBetung.JAM9075	*Draco sumatranus*	✓	✓	✓	✓
sum.TelukBetung.JAM9076	*Draco sumatranus*	✓	✓	✓	✓
sum.TelukBetung.JAM9078	*Draco sumatranus*	✓	✓	✓	✓
sum.Tinggi.LSUHC4714	*Draco sumatranus*	✓	✓	✓	✓
sum.Tinggi.LSUHC4715	*Draco sumatranus*	✓	✓	✓	✓
sum.Tioman.4007	*Draco sumatranus*	✓	✓	✓	✓

Sample Name	**Species**	**ND2**	**PNN**	**CMOS**	**BDNF**
sum.Tioman.4031	*Draco sumatranus*	✓	✓	✓	✓
sum.Tioman.4038	*Draco sumatranus*	✓	✓	✓	✓
sum.UAndalas.JAM9240	*Draco sumatranus*	✓	✓	✓	✓
sum.UAndalas.JAM9241	*Draco sumatranus*	✓	✓	✓	✓
sum.UAndalas.JAM9242	*Draco sumatranus*	✓	✓	✓	✓
sum.UAndalas.JAM9243	*Draco sumatranus*	✓	✓	✓	✓
sum.UAndalas.JAM9244	*Draco sumatranus*	✓	✓	✓	✓
sumatranus.ID7221	*Draco sumatranus*	✓	✓	✓	✓
supriatnai.3797	*Draco supriatnai*	✓	✗	✓	✓
supriatnai.3800	*Draco supriatnai*	✓	✓	✓	✓
taen.fmnh263336.Cambodia	*Draco taeniopterus*	✓	✗	✗	✗
taen.Mon.CAS222231	*Draco taeniopterus*	✓	✓	✓	✓
taen.Mon.CAS222237	*Draco taeniopterus*	✓	✓	✓	✓
taen.Mon.CAS222278	*Draco taeniopterus*	✓	✓	✓	✓
taen.Mon.CAS222279	*Draco taeniopterus*	✓	✓	✓	✓
taen.Perlis.JAM1063	*Draco taeniopterus*	✓	✓	✓	✓
taen.Shan1.CAS228465	*Draco taeniopterus*	✓	✓	✓	✓
taen.Taninth1.CAS228468	*Draco taeniopterus*	✓	✓	✓	✓
taen.Taninth1.CAS228469	*Draco taeniopterus*	✓	✓	✓	✓
taen.Taninth1.CAS228471	*Draco taeniopterus*	✓	✓	✓	✓
taen.Taninth2.CAS228477	*Draco taeniopterus*	✓	✓	✓	✓
tim.Roti.WAM105619	*Draco timoriensis*	✓	✗	✓	✗
tim.Timor.WAM107005	*Draco timoriensis*	✓	✗	✓	✗
vol.Jakarta.JAM2079	*Draco volans*	✓	✓	✓	✓
WC.spil.Adiadi.j6200	*Draco spilonotus*	✓	✓	✓	✓

CHAPTER 3

HISTORICAL BIOGEOGRAPHY OF SUMATRA AND WESTERN ARCHIPELAGO: INSIGHTS FROM PHYLOGEOGRAPHY AND POPULATION GENETICS OF THE COMMON FLYING LIZARDS *DRACO SUMATRANUS*

INTRODUCTION

Island systems have long held the interest of evolutionary biologists because they can provide independent, isolated natural experiments to test the evolutionary processes that generate and maintain biodiversity. For example, studies of the flora and fauna of oceanic islands such as the Hawaiian and Galapagos Archipelagos have contributed tremendously to our understanding of evolutionary processes generally and in particular to mechanisms underlying speciation (e.g. Gillespie et al. 1994; Grant & Grant 2002; Jokiel 1987; Kizirian et al. 2004; McDowall 2003; Myers 1991; Petren et al. 1999). On the other hand, continental islands like Madagascar and New Zealand have had an important part in our understanding of the mechanisms of vicariance biogeography (e.g. Raxworthy et al. 2008, MORE CITATIONS). Some archipelagic systems, however, contain both islands that are continental and oceanic in nature. These islands may have received their flora and fauna through a combination of dispersal and vicariance events, and can often provide excellent opportunities to test hypotheses regarding the role of population divergence and migration events in shaping modern-day distribution patterns. The Western Archipelago is one example of such systems (see below).

On the analytical front, biogeographers now have the opportunity not only to elucidate historical patterns of occurrence, but also the recent and contemporary roles of migration (gene flow) in maintaining or altering those historical patterns. This can be achieved by combining traditional phylogeny-based biogeographic analysis with recently developed population genetic tools such is IM (Isolation with Migration, Hey & Nielsen 2007). In this chapter I will attempt to utilize molecular data to shed light on the historical biogeography of Western Archipelago—one of the most understudied island systems in the world—by reconstructing its colonization process by the common flying lizard, *Draco sumatranus*.

Study System: *Sumatra & The Western Archipelago*

On the western margin of Indonesia lies Sumatra, the 5th largest island in the world and a major component of Sundaland biodiversity hotspot (Conservation International 2011). This island hosts a diversity of landscapes and thus is home to a wide variety of species, leading the World Wildlife Funds to recognize it as a distinct ecoregion (WWF, 2008). Geologically, Sumatra—along with other Sundaland islands of Borneo and Western Sulawesi—broke off from Gondwanaland roughly 150 million years ago, but its most prominent geographical feature (i.e.the Bukit Barisan Mountain Range; Figure 1) did not emerge until India collided into Asia and produced a secondary thrust that raised this chain of mountains ~70 million years ago (Whitten et al. 2000). Sumatra is a major component of the biogeographic region Sundaland, which throughout the Pleistocene's glaciation cycles and fluctuating sea levels experienced repeated positive land connections with the Malay Peninsula, Borneo and Java (Voris 2000; Sathiamurthy & Voris 2006), forming a continental basin called the Sunda Shelf. This repeated connection influenced the biogeography of the region; for example, a Pleistocene divergence has been suggested to have been responsible for shaping the distribution of the avifauna of Malay Peninsula and Borneo (Lim & Sheldon 2011; Lim et al. 2011).

Along Sumatra's west coast sits an archipelago of comparatively smaller islands (although by no means small—Nias is 4048 km2 in area) that I refer to in this chapter as the Western Archipelago. The Western Archipelago is composed of seven major islands and two island groups, including from north to south: Simeulue, the Banyak Islands, Nias, the Batu Islands, Siberut, Sipora, Pagai Utara, Pagai Selatan, and Enggano. The Western Archipelago is situated approximately 85–150 km off the west coast of Sumatra, and for the most part is separated by a deep-water channel called the Mentawai Strait (Figure 1). Geologically, the Western Archipelago was formed by upward thrusting of oceanic plates in association with India's collision with mainland Asia approximately 60 million years ago (Whitten et al. 2001). Bathymetry studies show that the floor of the Mentawai Strait lies 200–500 m below current sea level except at two places where the water is shallower (Ladage et al. 2006). These two points, which now exist as two clusters of small islands (the Banyak Islands to the north and the Batu Islands to the south), indicate where the historical land bridge connections between Sumatra and the Western Archipelago—particularly the Mentawai Islands—may have occurred. These bathymetry readings, combined with results from studies on Pleistocene sea level fluctuations, suggest that Simeulue, Nias and Enggano have probably never had a land connection with mainland Sumatra—therefore acting as oceanic islands—whereas the remaining islands were probably joined to the mainland anywhere between 250,000 and one million years ago (Dring et al. 1989; Voris 2000; Sathiamurthy & Voris 2006). The subsequent fragmentation sequence experienced by these islands remains unknown.

Having been separated from Sumatra for an extended period of time, the Western Archipelago harbors a wealth of endemic species. For example, the Mentawai Islands, which are restricted to the four islands at the center of the chain (Siberut, Sipora, Pagai Utara & Pagai Selatan), is home to 14 endemic mammal species (Whitten et al. 2000). The island of Simeulue hosts endemic lineages of macaque and pig that are likely to be distinct species, and Enggano has three endemic mammal species (Whitten et al. 2000). Despite this high level of endemism, the Western Archipelago is relatively understudied, with the four Mentawai-endemic primate species receiving the most scientific attention with respect to their ecology, behavior and phylogeny (e.g. Chatterjee 2008; Roos et al. 2003; Tilson 1977; Whittaker 2005; Ziegler et al. 2007). As for their herpetofauna, these islands were mentioned in older records inventorying the reptiles and amphibians of Sundaland and the Indo-Australian Archipelago (e.g. deRooj 1915; vanKampen 1923), and more recently, new publications have updated lists of species occurrence and provided records of newly described species from the area (mostly on the basis of historical museum specimens rather than recent fieldwork; e.g. Das 2005; Das & Lim 2005; Dring et al 1989).

From the handful of publications on the Western Archipelago, some insights can be gleaned regarding the manner in which they were colonized. It has been shown based on mitochondrial sequence data that the dispersal of the endemic tree shrews, tree squirrels and gibbons onto the Mentawai Islands occurred roughly 3–5 million years ago (Chatterjee 2008; den Tex et al. 2011; Roberts et al. 2010). Also based on mtDNA evidence, the endemic "Mentawai macaque" has been shown to consist of two paraphyletic lineages, with one species, *Macaca siberu* on Siberut, showing closer affinity to *M. nemestrina* from Sumatra than to the morphologically uniform *Macaca pagensis* from Pagai islands. Due to this finding, it has been posited that they colonized the Mentawai Islands on two separate occasions, both of which occurred in the early Pleistocene and via Siberut (Roos et al. 2003). To my knowledge, nuclear DNA data was never applied to this question and so there is no way of learning if this had been a case of a more recent mitochondrial introgression between the Siberut species and the Sumatran macaques or if this is a case of incomplete lineage sorting. No molecular biogeographical studies can be found that incorporated Nias, Simeulue or Enggano into their sampling, and so the colonization history of these islands is essentially unknown.

Study System: Draco sumatranus

Flying lizards of the genus *Draco* (Reptilia: Agamidae) are a monophyletic assemblage with remarkable adaptations for arboreal life, including wing-like patagial membranes supported by modified, elongated thoracic ribs, which enable them to glide short distances between trees (McGuire & Alcala 2000; McGuire & Dudley 2005; McGuire & Kiew 2001; McGuire *et al.* 2007). Their distribution ranges from India to southern China and insular South East Asia (Musters 1983). Of the ~45 species that compose the genus, 11 can be found in Sundaland, of which the common flying lizard *Draco sumatranus* has the widest distribution. *Draco sumatranus* occurs on Sumatra, the Malay Peninsula, Borneo, as well as most of Western Archipelago and on a host of other smaller islands in the Singapore Strait, the Strait of Malacca, and the Strait of Karimata. On two of the islands that make up the Western Archipelago, endemic forms occur that are closely related to, and most likely derived from, *D. sumatranus*: *D. modiglianii* on Enggano, and a newly discovered undescribed species on Simeulue (SZL unpublished data). On Java and Bali, *D. volans*, a close relative of *D sumatranus*, fills a similar ecological niche.

Like other *Draco* species, *D. sumatranus* is dietary specialist on ants and arboreal termites (Inger, 1983). However, unlike many other *Draco* species, *D. sumatranus* is a habitat generalist that thrives in open areas as long as there is a sufficient density of trees present. For example, *D. sumatranus* can often be found in stands of the widely cultivated coconut palm, *Cocos nucifera*. The species does occur in natural forest habitats, but seems to be most abundant in forest edge habitats or disturbed patches (e.g. around tree falls), as well as in the forest canopy (J.A. McGuire, pers. com). Nevertheless, they are most frequently encountered in human-altered landscapes, such as coconut groves, plantations, or even on trees growing around human settlements. They are abundant and can often be found in large numbers. Coupled with their wide distribution on the Sunda Shelf, their abundance make *D. sumatranus* an ideal system to study the historical biogeography of Sundaland, including the islands of Sumatra and the Western Archipelago.

Theoretical Framework and Analytical Approach

The question I am trying to tackle concerns whether the islands of Western Archipelago acquired their populations of *D. sumatranus* via overwater dispersal or through vicariance events influenced by the history of land connectivity with Sumatra. It is now known that throughout the glaciation cycles in the Pleistocene, the Malay Peninsula and the islands of Java, Borneo and Sumatra, which are separated by a shallow body of water, were repeatedly connected to each other. During the last glacial maxima (~21ky before present), sea levels dropped to 120 m below current levels and a continental basin emerged in the area, known as Sunda Shelf (Figure 2; Hall 1998; Voris 2000; Sathiamurthy & Voris 2006). It is possible that during this time, the islands of the Western Archipelago experienced a land-positive connection to Sumatra through the shallower parts of the Mentawai Strait, and that *Draco sumatranus* were thereby provided an opportunity to colonize the newly available habitat by direct overland dispersal. If this was the case, populations representing the islands of the Western Archipelago should form a monophyletic clade in phylogenetic analyses. Furthermore, the timing of divergence should date to the late Pleistocene.

Dispersal over water is a more difficult scenario to infer, considering the many routes and sequences that could have taken place. Evidence that would lend weight to this scenario, however, would be if populations representing the islands of the Western Archipelago form monophyletic assemblages not with one another, but rather with populations on the adjacent Sumatran mainland on the opposite side of the Mentawai Strait. Such a finding would suggest multiple independent colonizations of the islands of the Western Archipelago. This pattern of colonization has never been detected in other taxa, and judging from the lack of major drainage system west of the Bukit Barisan mountain range (Voris 2000; Whitten et al. 2000)—typically crucial in facilitating overwater dispersal by carrying "rafts" of living vegetation, dead trees, debris, etc. downstream and into the ocean—is the more unlikely hypothesis of the two.

MATERIALS & METHODS

Sample collection

I collected between 1 and 20 samples of *Draco sumatranus*—a total of 224 samples—from a series of localities throughout the Southeast–Northwest-oriented length of Sumatra, as well as from every major island in the Western Archipelago and on one island each of the Banyak and Batu island groups (see Figure 6 for a map of sampling locations). Specimens were formalin-fixed as museum voucher specimens and deposited either in the Museum Zoologicum Bogoriense (MZB, the national museum of Indonesia) or in the University of California Museum of Vertebrate Zoology (MVZ). Liver tissue samples were taken from each specimen prior to formalin fixation and preserved in either 95% ethanol or RNALater ®. Fifteen additional samples were acquired through museum loans (see Appendix X).

Molecular labwork

For the purpose of phylogenetic analyses, up to five individuals were randomly chosen to represent each locality, totaling 132 individual samples. DNA sequence data were collected from the coding region of one mitochondrial locus (*ND2*; Macey et al. 1997; McGuire and Kiew, 2001), as well as three coding genes (*CMOS, BDNF, PNN*; Saint *et al.* 1998; Townsend *et al.* 2008). To improve the accuracy of demographic parameter estimates, six additional anonymous nuclear loci (*Sum140621*, *Sum140121*, *Sum21353*, *Sum98605*, *Sum140646*, *Sum140675*) were developed using Illumina next generation sequencing, bringing the total of nuclear loci to nine. Primer sequences and annealing temperatures are provided in Table 1. PCR products were purified using ExoSAP-IT, cycle sequenced using BigDye 3.1 terminator sequencing chemistry, and sequenced on ABI3730 automated sequencer.

Sequence alignment & molecular analyses

Sequence data were cleaned and assembled into contigs using GENEIOUS PRO™ (Biomatters, New Zealand). GENEIOUS' implementation of MUSCLE (Edgar 2004) was employed to align sequences of the same locus. Allelic phase was determined computationally using the program PHASE (Stephens et al. 2001), taking the most probable pair of alleles from each individual to be used in all downstream analyses. Because of the triallelic nature of some of the SNP variants in my data set—which can be interpreted as false evidence of recombination under the four-gamete test of recombination (Hudson & Kaplan 1985) due to its assumption of infinite sites model of mutation—I opted to test for recombination in nuclear sequences using the Difference of Summed Squares (DSS) method as implemented in the software TOPALi (Milne *et al.* 2004). The DSS method detected recombination in *CMOS*; therefore, for this locus, only the longest non-recombining block (264 nucleotides) was retained for further analyses.

Phylogenetic analyses were performed using diploid, unphased sequences. I carried out Maximum Likelihood analysis using the program RAxML version 7.0.4 (Stamatakis *et al.* 2006) with 1,000 bootstrap replicates under the GTRGAMMA model of evolution, invoking the [–f a] flag to make RAxML conduct rapid bootstrap analysis and search for the optimal maximum likelihood tree in a single run. Bayesian analysis was performed using MrBayes version 3.1.2 (Huelsenbeck & Ronquist 2001). I conducted two runs with four chains each (one cold and three heated) for thirty million generations, discarding the first fifteen million as burn-in period. The most appropriate models of evolution to be incorporated in Bayesian analysis were selected using Akaike Information Criterion (AIC) as implemented in MrModelTest v. 2.3 (Posada & Crandall 1998), with the protein-coding genes (*ND2*, *CMOS*, *BDNF*, *PNN*) further partitioned into first, second and third codon positions. In both Maximum Likelihood and Bayesian analyses, I used one individual of *Draco volans*—sister to *D. sumatranus* species complex—obtained from Jakarta as the outgroup taxon.

Coalescent Analysis of Divergence

To infer the parameter of divergence within *D. sumatranus*, I employed coalescent methods implemented in the program IMa2 (Isolation with Migration; Nielsen & Wakeley 2001, Hey & Nielsen 2007). Unlike its predecessor, IM, IMa2 is capable of calculating divergence parameters for more than two populations. However, since the number of parameters to be estimated increases dramatically with each additional population, for this analysis I restricted my sampling to include only individuals from the Western Archipelago and the Sumatran clade immediately sister to them according to phylogenetic analyses (see results below), while increasing the number of individuals sampled per population to 10–20 individuals, amounting to a total of 140 individuals included in the analysis. Because my phylogenetic results indicated that the Western Archipelago populations are geographically structured into their island-unit constituents, I further divided these individuals according to their source island populations: Simeulue, Nias, Mentawai Islands, and Enggano—in effect running the program as a 5-population model. I used phased, non-recombining nucleotide sequence data from one mtDNA and nine nuclear loci to determine time of population splitting (t), effective population sizes (θ), and migration rates (m) among all five extant as well as ancestral populations. This is a parameter-rich analysis that our data may not adequately model, and we are currently exploring analyses with fewer parameters in addition to Approximate Bayesian Computation approaches.

In order to convert coalescent estimates of divergence parameters into meaningful demographic quantities, it is necessary to supply the analysis with mutation rates. While dating analyses might benefit from having an island age to be utilized as a calibration point, I am a little wary in placing an age on the islands of Western Archipelago. Hall (2009) pointed out that the complex history of the Sumatran "forearc islands" (i.e., Western Archipelago)—which includes a series of rapid tectonic-driven emergence and subsidence that are later further confounded by glacial and eustatic changes in sea levels that affected their connectivity to the mainland—made it difficult to pinpoint a certain age for these islands. Because of the scarcity of fossils that have been confidently placed as having originated from the Sumatra region (Meijaard 2004; Whitten et al. 2000), I resorted to using a substitution rate of 0.81% per lineage per million years for *ND2* (with a range of 0.62–1.03%), based on the Shoo et al. (2008) relaxed lognormal clock recalibration of the Macey et al. 1998 estimate of the ND2 substitution rate. I did multiple preliminary runs to determine the prior values for parameters before conducting a final run. Because it was not immediately clear how many steps are needed to achieve convergence, I specified a floating number for the duration of the run (`-l 12.0`) while sampling every 100 steps (`-d 100`), in effect keeping the program running indefinitely while producing an output file every 12 hours. My final run consisted of 24 chains (`-hn 24`) heated geometrically (`-hfg`) under heating parameters that vary between 0.95 and 0.88 (`-ha 0.95 -hb 0.88`). The prior values used in the final run are as follows: maximum migration $m = 4$, maximum population size (4Nμ) $q = 20$, maximum time of population splitting $t = 6$. I also specified a generation time $u = 2$.

RESULTS

Phylogenetic Analysis

Both Maximum Likelihood and Bayesian analyses showed with great confidence that most of the islands of the Western Archipelago (including Enggano and Simeulue, which harbor endemic species) form a monophyletic clade with respect to Sumatra (Figure 2 & 3). However, populations from the Batu and Banyak Islands were found to be more closely related to populations from the nearby Northwestern Sumatra clade. The two endemic lineages on Enggano and Simeulue were found to be nested within the Western Archipelago clade. This WA clade is the sister of a clade that is comprised of populations from the Banyak and Batu Islands, as well as Sumatran localities West of the Bukit Barisan Mountain Range and as far South as the town of Panyabungan (Figure 5A).

Within the Western Archipelago itself, both ML and Bayesian methods uncover monophyletic clades that correspond to the islands/island groups that comprise the chain: Simeulue, Nias, Mentawai Islands, and Enggano, while the Batu and Banyak Islands are found to be more closely related to Northwestern Sumatra. The Nias population represents the most basal lineage, suggesting that it had been separated from the remainder of the islands for the longest. The next most basal lineage is the newly discovered species on the island of Simeulue. The island of Enggano, which harbors the endemic *D. modigliani* seems to be the most recent divergence event, as it is sister to the Mentawai Islands populations. Furthermore, my results suggest that the island constituents of Mentawai group seem to form a panmictic population that does not exhibit signs of inter-island divergence.

Also of interest in my phylogenetic results is the discovery of a high degree of geographic structuring within *Draco sumatranus* on Sumatra. Both Maximum Likelihood and Bayesian methods uncover similar deep, divergent lineages: (1) the most basal clade comprising individuals from Southwest Sumatra, (2) Southeast Sumatra, including Natuna Islands and Borneo, (3) Northeast Sumatra and Malay Peninsula, (4) Northwest Sumatra, including individuals from the Banyak and Batu Islands. Each of these clades is well supported, with the exception of the Northeast Sumatra-Malay Peninsula (41% bootstrap support) and the Northwest Sumatra (61% bootstrap support). These clades show between 4–11% corrected mitochondrial divergence based on Tamura-Nei model of sequence evolution (Table 2).

Coalescent Analysis of Divergence

I chose to use IMa2 to conduct divergence dating between sister species because a coalescent model is a better fit for my assumptions and biological system than a multi-species complex, as might be appropriate when using additional divergence dating methods that do not incorporate gene flow (such as BEAST; Drummond et al. 2006). At the time of writing, my coalescent analysis had been running for a total duration of roughly 10 weeks and about 6 million generations, but some of the estimated parameters still exhibit incomplete curves. These include the curve of splitting time between the Western Archipelago and its sister NW Sumatra clade, whose distribution curve seems to have been influenced by the prior at the tail end of the distribution. Here I decided to include this estimate and treat it as a preliminary value, while acknowledging that further adjustment of priors and heating parameters may be necessary before accepting the estimate as a final result. IMa2 estimated that all divergences occurred within the Pleistocene, and the divergence between Sumatra and the Western Archipelago took place at ~556 kya (95% HPD = 404–795 kya; Figure 6). Furthermore, Nias was inferred to have diverged at ~384 kya (105–419 ybp 95% HPD), Simeulue at ~200 kya (220–664 kya 95% HPD), and lastly, the split between Mentawai and Enggano occurred 150 kya (95% HPD = 85–323 kya). I was not able to obtain a reliable figure of migration parameters between the clades due to irregularity of curves for these estimates.

DISCUSSION

Colonization of Western Archipelago

Based on my phylogenetic results, the hypothesis of independent over-water dispersal of *D. sumatranus* onto the islands of the Western Archipelago can be soundly rejected. The monophyly of Simeulue, Nias, Mentawai Islands and Enggano relative to Sumatra, and the exclusion of the Batu and Banyak Islands populations from this clade, suggest that the former had been colonized via the shallower parts of the Mentawai Strait, and were later separated as sea level rose and isolated the islands from Sumatra. By contrast, the Batu and Banyak Islands, which are separated only by shallower water, seem to have shared a more recent connection with Sumatra, forming a panmictic clade with the Northwestern Sumatra clade.

My preliminary coalescent results indicate that the divergence of Simeulue, Nias, Mentawai, and Enggano from Sumatra took place some time in the mid-Pleistocene, a time during which the Sunda Shelf had significantly more land area and rainforest cover (Voris 2000; Sathiamurthy & Voris 2006)—by some estimates up to ~400,000 km^2 more land area than is available today (Cannon et al. 2009). While it has been suggested that Nias and Simeulue, which according to my phylogenetic results were some of the first islands to be colonized, were never connected to the mainland (Whitten et al. 2000; Meijaard 2004), it is conceivable that during a period of glaciation, the expansion of land area caused the body of water separating these islands from the nearby Banyak and Batu Islands to become narrower facilitating the overwater dispersal of *D. sumatranus*. A similar scenario is also a plausible explanation of the colonization of Enggano—which also has never experienced a land-positive connection with Sumatra—via the islands of Mentawai Archipelago.

It is tempting to derive general conclusion regarding the colonization of the Western Archipelago by considering my results together with the evidence from mammal studies. However, I would caution against making a direct comparison to the previous results for a few reasons. First, while they did incorporate samples from the Mentawai Islands as a part of their broader Southeast Asia sampling, these studies did not take into consideration other Western Archipelago islands like Simeulue or Enggano. This means that their findings cannot be safely applied to these islands. Furthermore, despite the superficially similar pattern of monophyly of the island populations, the inferred timing of divergence for mammals vs. *D. sumatranus* could not be reconciled—the mammals are almost uniformly found to have colonized the Mentawai Islands during the late-Pliocene to early Pleistocene. This disparity may simply be an artifact of the dating method used in the mammal studies, as their results are based on molecular clock assumptions inferred strictly from mitochondrial DNA. Recent studies have indicated that relying on mitochondrial DNA to date older divergences may result in overestimation of this parameter (Ho et al. 2005; Zheng et al. 2011). If we were to accept those results at face value, however, it would imply that the Western Archipelago had been populated in multiple waves of colonization—evidence against a singular vicariance event. It is possible that these older divergences of Mentawai fauna can be explained by the fact that these mammals are all forest-dependent, and thus may have been unable to disperse across non-forest habitats that emerged across the Sunda Shelf during the Pleistoene (Bird et al. 2005; Slik et al. 2011). By contrast, *D. sumatranus* is not a forest-obligate and thus would not be as affected by the occurrence of the non-forest corridor, and is therefore more likely to have acquired its modern distribution simply through the emergence of land-bridge connections between Sumatra and the Western Archipelago.

The question of the number of colonization event that have occurred across the Mentawai Strait seems to be the perfect candidate for the application of recently developed hierarchical Approximate Bayesian Computation (HABC) methods that aim to infer simultaneous colonization across co-distributed taxon pairs, such as msBayes (Huang et al. 2011). However, we have not yet employed this approach.

Biogeography of Sumatra & Sunda Shelf

It is not entirely unexpected that the distribution of *D. sumatranus* is geographically structured, considering Sumatra's diversity of landscapes. *Draco sumatranus* is commonly found in low-lying areas, very seldom above the altitude of 1,300 m (personal observation), so it is interesting to discover that their distribution exhibits a marked East-West division around the Bukit Barisan mountain range. It is surprising, however, to find further divergences on either side of the mountain range that do not seem to correspond to the modern-day geography of the island (10.4% and 4.4% corrected mtDNA sequence divergence between the two western and northern clades, respectively). Likewise, the affinity of the northeastern and southeastern Sumatra clades to the Malay Peninsula and Borneo, respectively, presents a biogeographic conundrum. The late-Pleistocene land-positive connection that bridged today's insular Southeast Asia into a continuous landmass (Voris 2000, Sathiamurthy & Voris 2006) does not adequately explain this North-South divide. It is worth noting that a more commonly observed pattern in Sunda Shelf taxa is one that shows a western (Malay Peninsula & Sumatra) vs. eastern (Borneo) divergence (e.g. Meijaard 2004, Woodruff 2010, Lim et al. 2011)—something that has been attributed to the existence of a corridor of grassland savanna that extended along the Malay Peninsula to the far Eastern edge of the shelf during the late Pleistocene (Bird et al. 2005), or a dispersal barrier in the form of sandy soil (Slik et al. 2011). While Lake Toba—which emerged as a result of a supervolcano eruption ~75,000 years ago—has been noted as a zoogeographic barrier for certain species (e.g. orangutans, Nater et al. 2011; various birds species, Whitten et al. 2000; Thomas' leaf monkeys, Aimi & Bakar 1996; white-handed gibbons, Whittaker et al. 2007, Thinh et al. 2010), the clade boundaries within *D. sumatranus* do not seem to coincide with this lake, instead occurring ~300–500 km southeast of the lake. In the case of the eastern clades, it is possible that the North-South divide was caused by Pleistocene rivers that were wide enough to prevent *D. sumatranus* from crossing. The location of these ancient drainages roughly coincide with the break observed in my results (Figure 5B), although this is difficult to ascertain with precision considering the substantial gap in my sampling on the eastern side of the Bukit Barisan Mountain Range.

Consequences for Conservation

The importance of the Western Archipelago in the biogeography theater of the Sunda Shelf cannot be overstated. Regardless of the cause or timing of the split between Sumatra and the WA, my results clearly indicate that the islands of Western Archipelago have been on their own evolutionary trajectory for at least hundreds of thousands of years—something also evident from the level of endemism exhibited by some of these islands (e.g. the Mentawai macaques, the Nias hill mynah, the undescribed species of *Draco* (and *Aphaniotis*) discovered on Simeulue, *D. modigliani* (and a bunch of other endemic herps) on Enggano). Considering that these islands are relatively understudied, I believe this endemism is only the tip of the diversity iceberg, and that many more endemic species and lineages remain to be discovered. It has been demonstrated in other studies that during the last glaciation cycle, these islands remained covered in forests, thus serving as important refugia of forest-dependent species throughout the late-Pleistocene (e.g. Gathorne-Hardy 2002; Meijaard 2003; Bird et al. 2005). Furthermore, Cannon et al. (2009) found that the modern-day distribution of lowland evergreen rain forests on Sundaland reflects a highly atypical refugial state, which implies that the diversity currently inhabiting these areas will serve as source populations during the next glaciation period. Given all of the above, it is paramount that the islands of Western Archipelago be considered as candidates for conservation areas. It is unknown what the current rate of deforestation is on these islands, but personal observation from my fieldwork on the islands of the Western Archipelago confirmed that logging and agricultural land conversion remain a major threat to biodiversity. Indeed, Nias Island seems to host little to no natural lowland rainforest. At the moment, the Mentawai Islands—easily the most actively studied group of the Western Archipelago—are the only region with a government-sanctioned conservation area, hosting the Siberut National Park on the northernmost island in the group. While *D. sumatranus*—with its generalist habitat preference and resiliency in human-altered environments—is not in danger of extinction from habitat degradation, this lack of protection status does not bode well for the long-term survival of the forest-dependent species that call these islands home.

CONCLUSION

The Western Archipelago seemed to have been colonized by *D. sumatranus* through a single radiation event that took place approximately 550,000 years before present, likely during a glacial period when land cover was much more extensive and the body of water separating the Western Archipelago from Sumatra was narrower. While this is suggestive of a vicariant diversification, cautious comparison of my results with findings in mammals indicate that there may have been multiple waves of colonization into Western Archipelago. Sumatra is revealed to be a fascinating biogeography theater in and of itself, with deep divergences occurring on both sides of the Bukit Barisan mountain range and merits further study. Lastly, the monophyly of

Western Archipelago implies that the islands have a distinct evolutionary trajectory that has played an important role in shaping the region's biodiversity. Their refugial role during past glaciation cycles and the ongoing deforestation means they are in dire need of a government-sanctioned conservation status.

References

Aimi M, Bakar A. 1996. Distribution and deployment of *Presbytis melalophos* group in Sumatera, Indonesia. *Primates* 37: 399–409.

Cannon, C.H., R.J. Morley, A.B.G. Bush. 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.

Chatterjee, H.J. 2006. Phylogeny and biogeography of gibbons: A dispersal-vicariance analysis. *International Journal of Primatology* 27(3): 699–712.

Conservation International. 2011. *Sundaland.* http://www.biodiversityhotspots.org/xp/hotspots/sundaland/Pages/default.aspx#indepth. Accessed on 12 September, 2011.

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.

Das, I. & K.K.P. Lim. 2005. New species of Dibamus (Squamata: Dibamidae) from Pulau Nias, Indonesia. *Journal of Herpetology* 39(1): 113—117.

denTex, R.J., R. Thorington, J.E. Maldonado & J.A. Leonard. 2010. Speciation dynamics in the SE Asian tropics: Putting a time perspective on the phylogeny and biogeography of Sundaland tree squirrels, *Sundasciurus*. *Molecular Phylogenetics & Evolution* 55(2): 711–720.

deRooj, N. 1917. The reptiles of the Indo-Australian Archipelago, Vol. I & II. E.J. Brill, Ltd., Leiden.

Dring, J.C.M., C.J. McCarthy & A.J. Whitten. 1989. The terrestrial herpetofauna of the Mentawai Islands, Indonesia. *Indo-Malayan Zoology* 6: 119–132.

Drummond, A.J., S.Y. Ho, M.J. Phillips, and A. Rambaut. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biology* 4:e88.

Edgar, R.C. 2004. Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acid Research*. **32**: 1792–1797.

Gathorne-Hardy, F.J., Syaukani, R.G. Davies, P. Eggleton & D.T. Jones. 2002. Quaternary rainforest refugia in south-east Asia: Using termites (Isoptera) as indicators. *Biol. J. Linn. Soc.* 75: 453–466.

Gillespie, R.G., H.B. Croom & S.R. Palumbi. 1994. Multiple origins of a spider radiation in Hawaii. *Proceedings of the National Academy of Sciences* 91: 2290–2294.

Grant, P.R. & B.R. Grant. 2002. Adaptive radiation of Darwin's Finches. *American Scientist 90(2):* 130–139.

Hall, R. 2009. Southeast Asia's changing palaeogeography. *Blumea* 54: 148–161.

Hey, J. & R. Nielsen. 2007. Integration within the Felsenstein equation for improved Markov chain Monte Carlo methods in population genetics. *Proceedings of the National Academy of Sciences* 104 (8): 2785–2790.

Ho, S.Y.W., M.J. Phillips, A. Cooper & A.J. Drummond. 2005. Time dependency of molecular rate estimates and systematic overestimation of recent divergence times. *Molecular Biology & Evolution* 22(7): 1561–1568.

Huang, W., N. Takebayashi, Y. Qi & M. Hickerson. MTML-msBayes: Approximate Bayesian comparative phylogeographic inference from multiple taxa and multiple loci with rate heterogeneity. *BMC Bioinformatics* 12(1): 1–14.

Hudson, R.R. & N.L. Kaplan. 1985. Statistical properties of the number of recombination events in the history of a sample of DNA sequences. *Genetics* **111**(1): 147–164.

Huelsenbeck, J. P. and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17:754–755.

Jokiel, P.L. 1987. Ecology, biogeography and evolution of corals in Hawaii. *Trends in Ecology & Evolution* 2(7): 179–182.

Kizirian, D., A. Trager, M.A. Donnelly & J.W. Wright. 2004. Evolution of Galapagos Island lava lizards (Iguania: Tropiduridae: Microlophus). *Molecular Phylogenetics & Evolution* 32(3): 761–769.

Ladage, S., W. Weinrebe, C. Gaedicke, U. Barckhausen, E.R. Flueh, I. Heyde, A. Krabbenhoeft, H. Kopp, S. Fajar & Y. Djajadihardja. 2006. Bathymetric survey images structure off Sumatra. *EOS transactions* 87(17): 165, 168.

Lim, H.C. & F.H. Sheldon. 2011. Multilocus analysis of the evolutionary dynamics of rainforest bird populations in Southeast Asia. *Molecular Ecology* 20(16): 3414–3438.

Lim, H.C., M.A. Rahman, S.L. Lim, R.G. Moyle & F.H. Sheldon. 2011. Revisiting Wallace's haunt: Coalescent simulations and comparative niche modeling reveal historical mechanisms that promoted avian population divergence in the Malay Archipelago. *Evolution* 65: 321–334.

Macey, J. R., A. Larson, N. B. Ananjeva, and T. J. Papenfuss. 1997b. Evolutionary shifts in three major structural features of the mitochondrial genome among iguanian lizards. *J. Mol. Evol.* 44:660–674.

Macey, J.R., J.A. Schulte II, N.B. Ananjeva, A. Larson, N. Rastegar-Pouyani, S.M. Shammakov & T.J. Papenfuss. 1998. Phylogenetic relationships among agamid lizards of the Laudakia caucasia species group: testing hypotheses of biogeographic fragmentation and an area cladogram for the Iranian Plateau. *Molecular Phylogenetics & Evolution* 10: 118–131.

McDowall, R.M. 2003. Hawaiian biogeography and the islands′ freshwater fish fauna. *Journal of Biogeography* 30(5): 703–710.

McGuire, J.A. & A.C. Alcala. 2000. A taxonomic revision of the flying lizards (Iguania: Agamidae: *Draco*) of the Philippine Islands, with a description of a new species. *Herpetological monographs* 14(2000): 81–138.

McGuire, J.A. & B.H. Kiew. 2001. Phylogenetic systematics of Southeast Asian flying lizards (Iguania: Agamidae: *Draco*) as inferred from mitochondrial DNA sequence data. *Biological Journal of the Linnean Society* 72: 203–229.

McGuire, J.A. & R. Dudley. 2005. The cost of living large: Comparative gliding performance in flying lizards (*Draco*). *American Naturalist* 166: 93–106.

McGuire, J.A., R.M. Brown, Mumpuni, A. Riyanto & N. Andayani. 2007. The flying lizards of the *Draco lineatus* group (Squamata: Iguania: Agamidae): A taxonomic revision with descriptions of two new species. *Herpetological Monographs* 21: 179–212.

Meijaard, E. 2003. Mammals of South-east Asian islands and their Pleistocene environments. *Journal of Biogeography* 30: 1245–1257.

Meijaard, E. 2004. Solving Mammalian Riddles : A reconstruction of the Tertiary and Quaternary distribution of mammals and their palaeoenvironments in island South-East Asia. Australian National University Ph.D. Thesis. Downloaded on August 15, 2011 from http://hdl.handle.net/1885/47989.

Milne, W., F. Wright, G. Rowe, D.F. Marshall, D. Husmeier & G. McGuire. 2004. TOPALi: software for automatic identification of recombinant sequences within DNA multiple alignments. *Bioinformatics* 20 (11): 1806–1807.

Musters, C.J.M. 1983. Taxonomy of the genus *Draco* L. (Agamidae, Lacertilia, Reptilia). *Zool. Verhandelingen* 199: 1–120.

Myers, A.A. 1991. How did Hawaii accumulate its biota? A test from the Amphipoda. *Global Ecology and Biogeography Letters* 1: 24–29.

Nater, A., P. Nietlisbach, N. Arora, C.P. Van Schaik, M.A. Van Noordwijk, E.P. Willems, I. Singleton, S.A. Wich, B. Goossens, K.S. Warren, E.J. Verschoor, D. Perwitasari-Farajallah, J. Pamungkas, M. Krutzen. 2011. Sex-Biased dispersal and volcanic activities shaped phylogeographic patterns of extant orangutans (genus: *Pongo*). *Molecular Biology and Evolution* 28(8): 2275–2288.

Nielsen, R. and J. Wakeley 2001. Distinguishing migration from isolation: a Markov chain Monte Carlo approach. *Genetics* 158:885-896.

Petren, K., B.R. Grant & P.R. Grant. 1999. A phylogeny of Darwin's finches based on microsatellite DNA length variation. *Proceedings of the Royal Society of London Series B: Biological Sciences* 266 (1417): 321–329.

Posada, D. & K.A. Crandall. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14(9): 817–818.

Raxworthy, C.J., R.G. Pearson, B.M. Zimkus, S. Reddy, A.J. Deo, R.A. Nussbaum & C.M. Ingram. Continental speciation in the tropics: contrasting biogeographic patterns of divergence in the *Uroplatus* leaf-tailed gecko radiation of Madagascar. *Journal of zoology* 275(4): 423–440.

Roberts, T.E., H.C. Lanier, E.J. Sargis & L.E. Olson. 2011. Molecular phylogeny of treeshrews (Mammalia: Scandentia) and the timescale of diversification in Southeast Asia. *Molecular Phylogenetics & Evolution* 60(3): 358–372.

Roos, C., T. Ziegler, J.K. Hodges, H. Zischler & C. Abegg. 2003. Molecular phylogeny of Mentawai macaques: taxonomic and biogeographic implications. *Molecular Phylogenetic & Evolution* 29(1): 139–150.

Sathiamurthy, E. & H.K. Voris. 2006. Maps of Holocene sea transgression and submerged lakes on the Sunda Shelf. *Natural History Journal of Chulalongkorn University,* Supplement 2:1–43.

Shoo, L.P., R. Rose, P. Doughty, J.J. Austin & J. Melville. 2008. Diversification patterns of pebble-mimic dragons are consistent with historical disruption of important habitat corridors in arid Australia. *Molecular Phylogenetics & Evolution* 48: 528–542.

Slik, J.W.F, S.I. Aiba, M. Bastian, F.Q. Brearley, C.H. Cannon, K.A.O. Eichhorn, G. Fredriksson, K. Kartawinata, Y. Laumonier, A. Mansor, A. Marjokorpi, E. Meijaard, R.J. Morley, H. Nagamasu, R. Nilus, E. Nurtjahya, J. Payne, A. Permana, A.D. Poulsen, N. Raes, S. Riswan, C.P. vanSchaik, D. Sheil, K. Sidiyasa, E. Suzuki, J.K.C.H. vanValkenburg, C.O. Webb, S. Wich, T. Yoneda, R. Zakaria & N. Zweifel. 2011. Soils on exposed Sunda Shelf shaped biogeographic patterns in the equatorial forests of Southeast Asia. *Proceedings of the National Academy of Sciences* 108 (30): 12343–12347.

Stephens, M., N.J. Smith, P. Donnelly. 2001. A new statistical method for haplotype reconstruction from population data. *Journal of Human Genetics*. 68: 978–989.

Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, **22**: 2688–2690.

Thinh V.N., A.R. Mootnick, T. Geissmann, M. Li, T. Ziegler, M. Agil, P. Moisson, N. Tilo, L. Walter & C. Roos. 2010. Mitochondrial evidence for multiple radiations in the evolutionary history of small apes. *BMC Evolutionary Biology*. 10:74.

Townsend, T.M., R.E. Alegre, S.T. Kelly, J.J. Wiens & T.W. Reeder. 2008. Rapid development of multiple nuclear loci for phylogenetic analysis using genomic resources: An example from squamate reptiles. *Molecular Phylogenetics & Evolution*, 47(1): 129–142.

vanKampen, P.N. 1923. *The Amphibia of the Indo-Australian Archipelago*. E.J. Brill, Ltd., Leiden.

Voris, H.K. 2000. Maps of Pleistocene sea levels in Southeast Asia: Shorelines, river systems and time durations. *Journal of Biogeography* 27(5): 1153–1167.

Whittaker, D.J. 2005. New population estimates for the endemic Kloss′s gibbon *Hylobates klossii* on the Mentawai Islands, Indonesia. *Oryx* 39: 458–461.

Whitten, T., S.J. Damanik, J. Anwar & N. Hisyam. 2000. *The ecology of Sumatra*. Periplus Editions, Hong Kong: xxxiii + 478 pp.

Woodruff, D.S. 2010. Biogeography and conservation in Southeast Asia: how 2.7 million years of repeated environmental fluctuations affect today's patterns and the future of the remaining refugial-phase biodiversity. *Biodiversity & Conservation* 19 (4): 919–941.

World Wildlife Fund (Lead Author); Mark McGinley (Topic Editor) "Sumatran lowland rain forests". In: Encyclopedia of Earth. Eds. Cutler J. Cleveland (Washington, D.C.: Environmental Information Coalition, National Council for Science and the Environment). [First published in the Encyclopedia of Earth September 17, 2008; Last revised Date September 17, 2008; Retrieved September 14, 2011]. <http://www.eoearth.org/article/Sumatran_lowland_rain_forests>

Zheng, Y., R. Peng, M. Kuro-o, X. Zeng. 2011. Exploring patterns and extent of bias in estimating divergence time from mitochondrial DNA sequence data in a particular lineage: A case study of salamanders (Order Caudata). *Molecular Biology & Evolution* 28(9): 2521–2534.

Ziegler, T., C. Abegg, E. Meijaard, D.P. Farajallah, L. Walter, J.K. Hodges & C. Roos. 2007. Molecular phylogeny and evolutionary history of Southeast Asian macaques forming the *M. silenus* group. *Molecular Phylogenetics & Evolution* 42(3): 807–816.

Table 1. List of primers and PCR conditions used in this study.

Locus Name	Primer name	Sequence (5' → 3')	Annealing Temp. (°C)	Reference
NADH-2 (ND2)	MetF1 (PCR-External)	AAGCAGTTGGGCCCATRCC	50-48-45 (step-down)	Macey et al. 1997
	AlaR2 (PCR-External)	AAAGTGTCTGAGTTGCATTCRG		
	ND2F5 (Sequencing-internal)	AACCAAACCCAACTACGAAAAAT	N/A	
	ND2R6 (Sequencing-internal)	ATTTTTCGTAGTTGGGTTTGRTT	N/A	
CMOS	G73	GCGGTAAAGCAGGTGAAGAAA	54	Townsend et al. 2008
	G74	TGAGCATCCAAAGTCTCCAATC		
BDNF	BDNF-F	GACCATCCTTTTCCTKACTATG	50	Townsend et al. 2008
	BDNF-R	CTATCTTCCCCTTTTAATGGTC		
PNN	PNN-L	TGCCAGCAGATGGTGAACAG	57	Townsend et al. 2008
	PNN-R	TATCCCTTCGCTTCCGATCC		
Sum21353	Sum21353-F	GCTATGCCATTCCGTTTATTTC	60	This study
	Sum21353-R	CAGATCGTGCAACAAGGTTAGA		
Sum98605	Sum98605-F	GTTGACGCTTGTGGGACTTC	60	This study
	Sum98605-R	GTGGCCTAAATGGGAAAAGG		
Sum140121	Sum140121-F	ATGCACCGAATGTTAGACAAAA	60	This study
	Sum140121-R	TTCTCATCTTTTCTTCCCTTGC		
Sum140621	Sum140621-F	CATGGCTGATCAACCTGAAATA	60	This study
	Sum140621-R	TCCTTCTGACATCCAGAGAGTG		
Sum140646	Sum140646-F	ACATCTGCAGTGGCACAGAT	60	This study
	Sum140646-R	ATTTGCTCCCGCTTAACAATAA		
Sum140675	Sum140675-F	GATTTTTCTCAGTGCAGACGTG	60	This study
	Sum140675-R	GCCTTCCCTTTCCCTCTAATAA		

Table 2. Corrected pairwise population divergence, based on Tamura-Nei model. Values below diagonals are from mtDNA sequence data, and above diagonals are from concatenated nuclear sequence data. All values are significant.

Population	Nias	Mentawai	Simeulue	Enggano	NW Sumatra	SW Sumatra	NE Sumatra + MP	SE Sumatra + Borneo
Nias		0.162	0.049	0.630	0.063	0.264	0.156	0.261
Mentawai	5.304		0.204	0.589	0.150	0.225	0.173	0.236
Simeulue	5.610	6.496		0.669	0.044	0.304	0.179	0.284
Enggano	11.121	10.832	11.606		0.596	0.529	0.592	0.574
NW Sumatra	4.394	4.815	5.364	8.519		0.200	0.106	0.203
SW Sumatra	11.954	12.219	12.825	11.096	10.441		0.230	0.215
NE Sumatra+MP	4.903	5.502	6.224	8.811	1.393	11.191		0.078
SE Sumatra+Borneo	5.201	5.272	5.652	9.066	3.293	10.326	4.408	

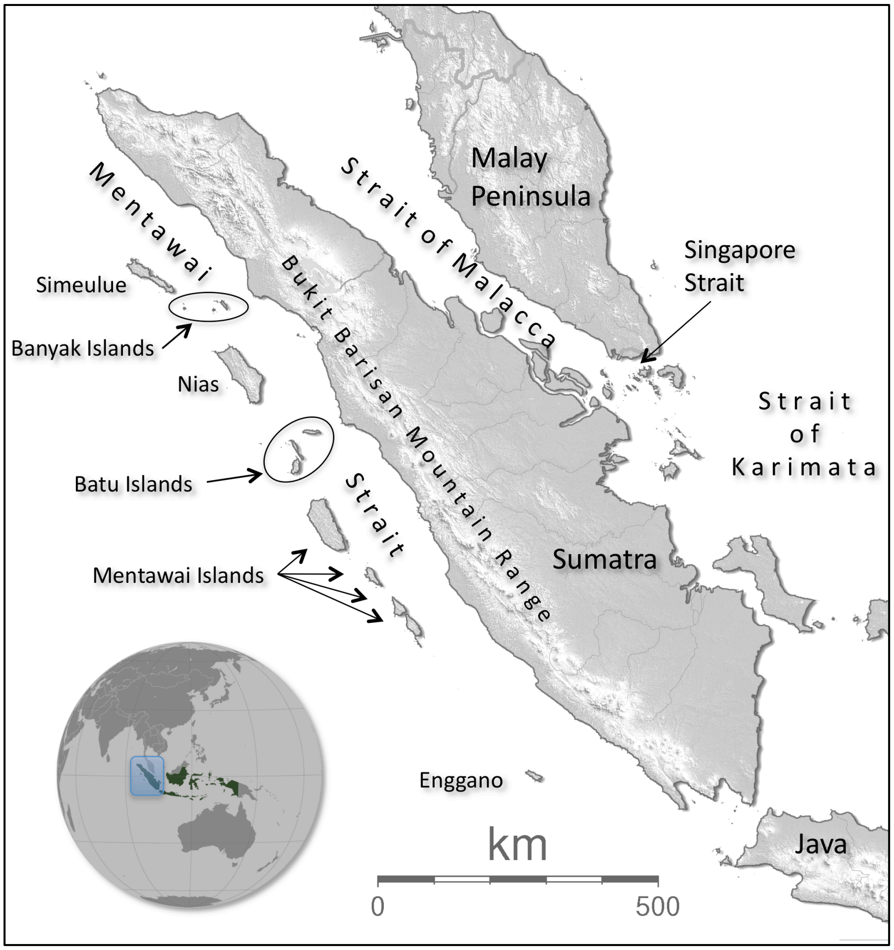


Figure 1. Map of Sumatra and the islands comprising Western Archipelago.

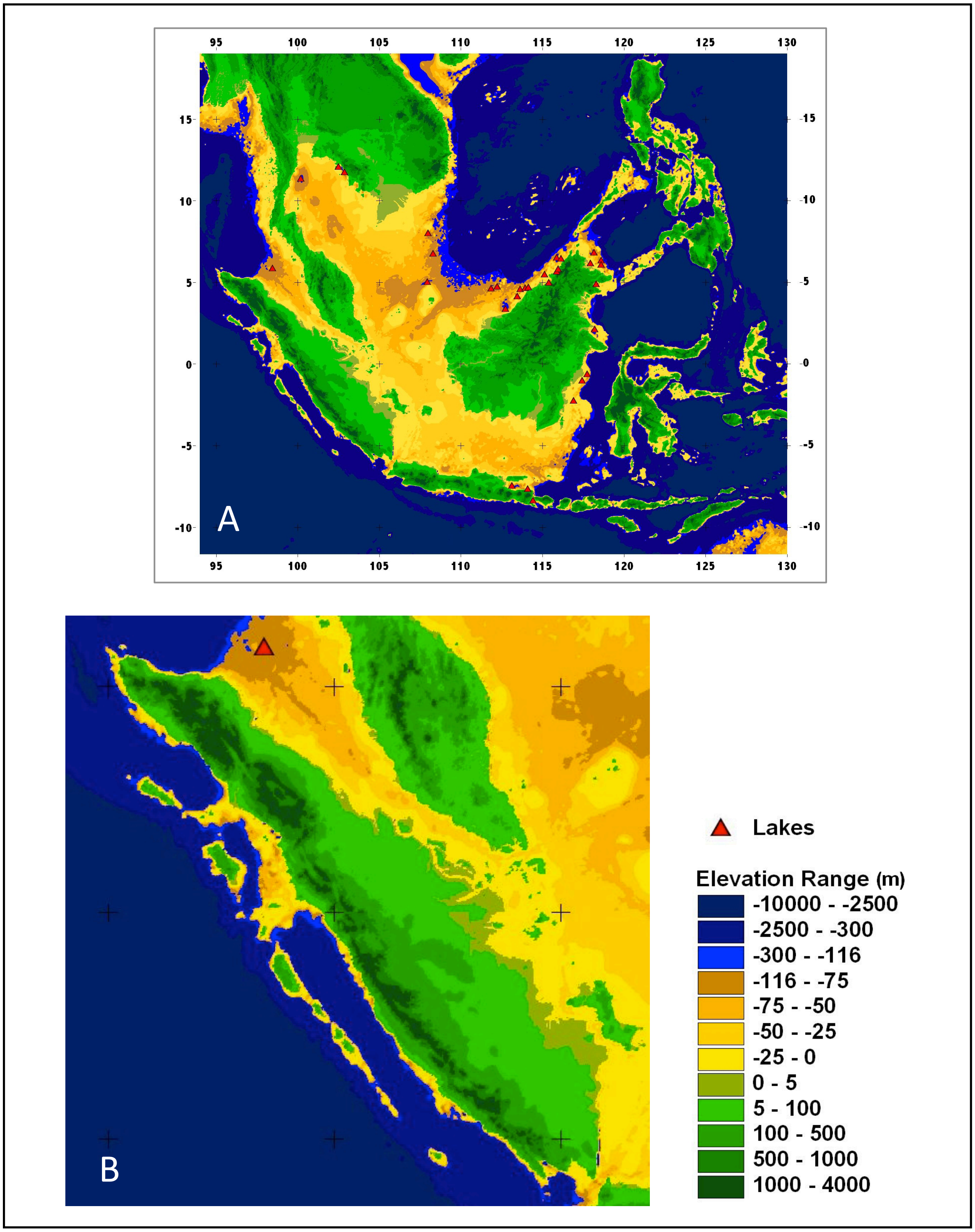


Figure 2. Map showing Sunda Shelf (A) and Sumatra and Western Archipelago (B) and the extent of land cover during the last glacial maximum in the Pleistocene, ca. 21,000 years before present (from Sathiamurthy & Voris 2006).

Figure 3. Maximum Likelihood phylogeny of *Draco sumatranus* under GTRGAMMA model in RAxML Version 7.0.4. Bootstrap values for major clades are indicated at nodes, with values lower than 50% highlighted in red.

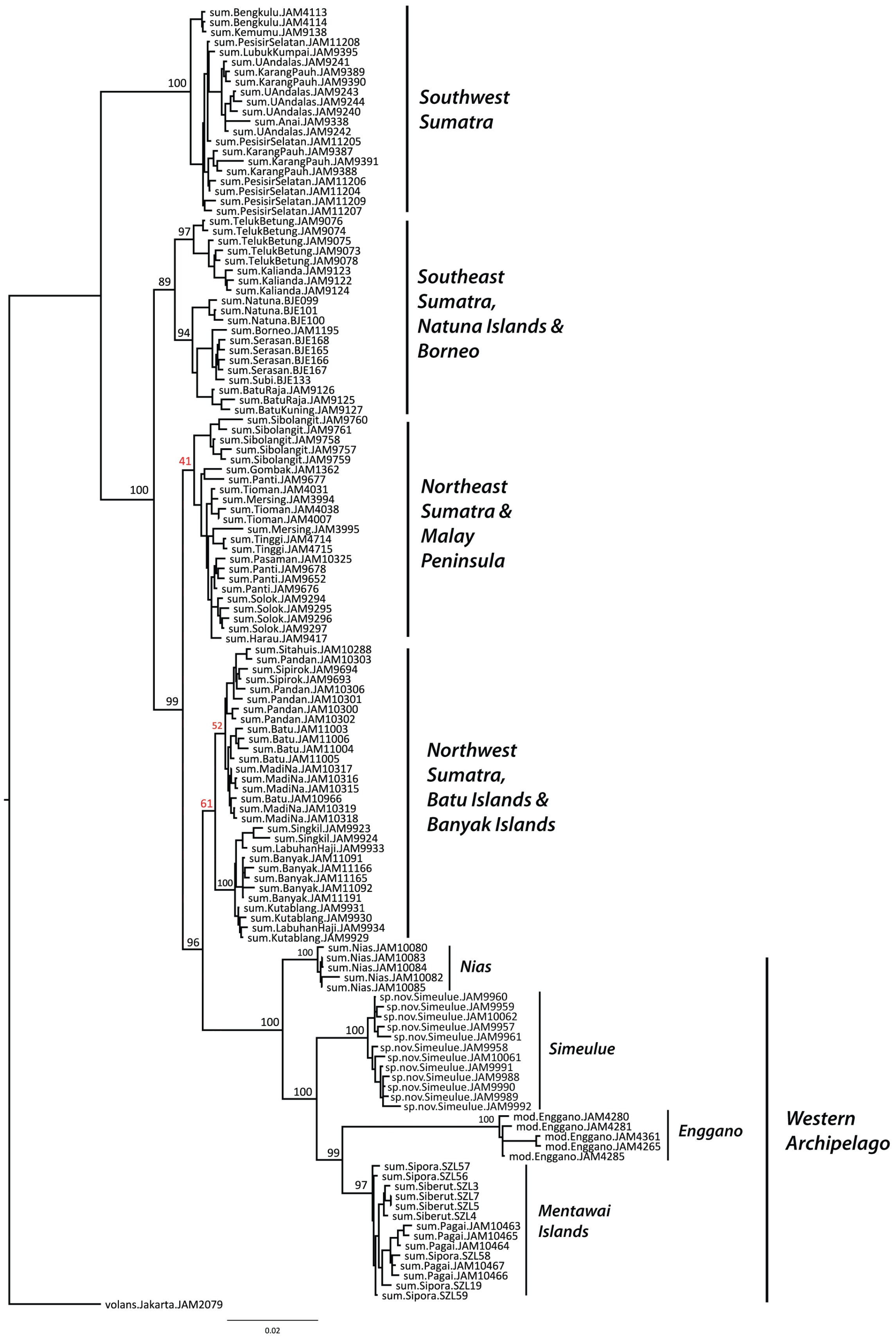
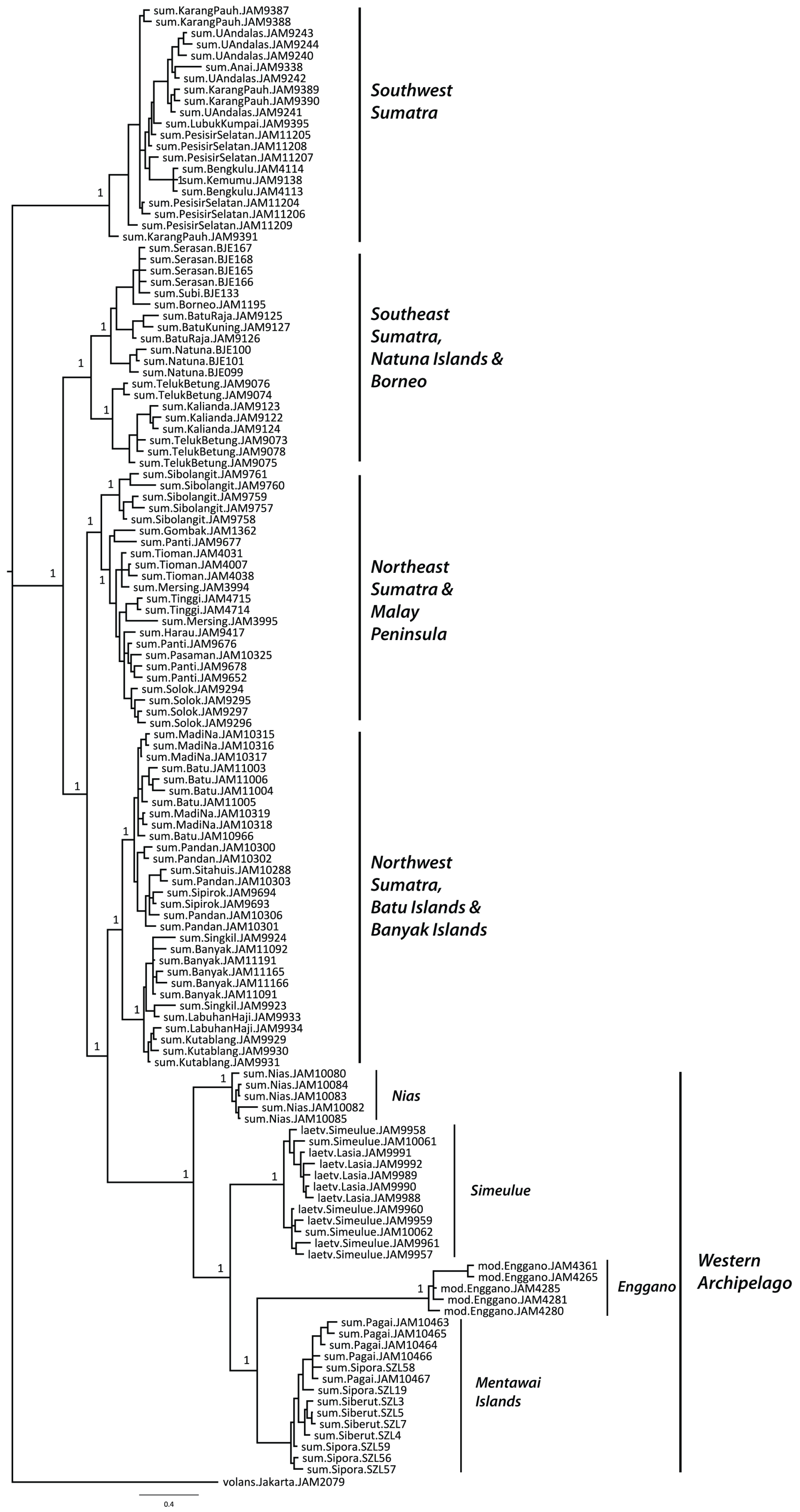

sum.Bengkulu.JAM4113
sum.Bengkulu.JAM4114
sum.Kemumu.JAM9138
sum.PesisirSelatan.JAM11208
sum.LubukKumpai.JAM9395
sum.UAndalas.JAM9241
sum.KarangPauh.JAM9389
sum.KarangPauh.JAM9390
sum.UAndalas.JAM9243
sum.UAndalas.JAM9244
sum.UAndalas.JAM9240
sum.Anai.JAM9338
sum.UAndalas.JAM9242
sum.PesisirSelatan.JAM11205
sum.KarangPauh.JAM9387
sum.KarangPauh.JAM9391
sum.KarangPauh.JAM9388
sum.PesisirSelatan.JAM11206
sum.PesisirSelatan.JAM11204
sum.PesisirSelatan.JAM11209
sum.PesisirSelatan.JAM11207
100
Southwest Sumatra
sum.TelukBetung.JAM9076
sum.TelukBetung.JAM9074
sum.TelukBetung.JAM9075
sum.TelukBetung.JAM9073
sum.TelukBetung.JAM9078
sum.Kalianda.JAM9123
sum.Kalianda.JAM9122
sum.Kalianda.JAM9124
sum.Natuna.BJE099
sum.Natuna.BJE101
sum.Natuna.BJE100
sum.Borneo.JAM1195
sum.Serasan.BJE168
sum.Serasan.BJE165
sum.Serasan.BJE166
sum.Serasan.BJE167
sum.Subi.BJE133
sum.BatuRaja.JAM9126
sum.BatuRaja.JAM9125
sum.BatuKuning.JAM9127
97
89
94
Southeast Sumatra, Natuna Islands & Borneo
sum.Sibolangit.JAM9760
sum.Sibolangit.JAM9761
sum.Sibolangit.JAM9758
sum.Sibolangit.JAM9757
sum.Sibolangit.JAM9759
sum.Gombak.JAM1362
sum.Panti.JAM9677
sum.Tioman.JAM4031
sum.Mersing.JAM3994
sum.Tioman.JAM4038
sum.Tioman.JAM4007
sum.Mersing.JAM3995
sum.Tinggi.JAM4714
sum.Tinggi.JAM4715
sum.Pasaman.JAM10325
sum.Panti.JAM9678
sum.Panti.JAM9652
sum.Panti.JAM9676
sum.Solok.JAM9294
sum.Solok.JAM9295
sum.Solok.JAM9296
sum.Solok.JAM9297
sum.Harau.JAM9417
41
100
Northeast Sumatra & Malay Peninsula
sum.Sitahuis.JAM10288
sum.Pandan.JAM10303
sum.Sipirok.JAM9694
sum.Sipirok.JAM9693
sum.Pandan.JAM10306
sum.Pandan.JAM10301
sum.Pandan.JAM10300
sum.Pandan.JAM10302
sum.Batu.JAM11003
sum.Batu.JAM11006
sum.Batu.JAM11004
sum.Batu.JAM11005
sum.MadiNa.JAM10317
sum.MadiNa.JAM10316
sum.MadiNa.JAM10315
sum.Batu.JAM10966
sum.MadiNa.JAM10319
sum.MadiNa.JAM10318
sum.Singkil.JAM9923
sum.Singkil.JAM9924
sum.LabuhanHaji.JAM9933
sum.Banyak.JAM11091
sum.Banyak.JAM11166
sum.Banyak.JAM11165
sum.Banyak.JAM11092
sum.Banyak.JAM11191
sum.Kutablang.JAM9931
sum.Kutablang.JAM9930
sum.LabuhanHaji.JAM9934
sum.Kutablang.JAM9929
99
52
61
100
Northwest Sumatra, Batu Islands & Banyak Islands
sum.Nias.JAM10080
sum.Nias.JAM10083
sum.Nias.JAM10084
sum.Nias.JAM10082
sum.Nias.JAM10085
100
96
Nias
sp.nov.Simeulue.JAM9960
sp.nov.Simeulue.JAM9959
sp.nov.Simeulue.JAM10062
sp.nov.Simeulue.JAM9957
sp.nov.Simeulue.JAM9961
sp.nov.Simeulue.JAM9958
sp.nov.Simeulue.JAM10061
sp.nov.Simeulue.JAM9991
sp.nov.Simeulue.JAM9988
sp.nov.Simeulue.JAM9990
sp.nov.Simeulue.JAM9989
sp.nov.Simeulue.JAM9992
100
100
100
Simeulue
mod.Enggano.JAM4280
mod.Enggano.JAM4281
mod.Enggano.JAM4361
mod.Enggano.JAM4265
mod.Enggano.JAM4285
100
Enggano
sum.Sipora.SZL57
sum.Sipora.SZL56
sum.Siberut.SZL3
sum.Siberut.SZL7
sum.Siberut.SZL5
sum.Siberut.SZL4
sum.Pagai.JAM10463
sum.Pagai.JAM10465
sum.Pagai.JAM10464
sum.Sipora.SZL58
sum.Pagai.JAM10467
sum.Pagai.JAM10466
sum.Sipora.SZL19
sum.Sipora.SZL59
99
97
Mentawai Islands
Western Archipelago
volans.Jakarta.JAM2079
0.02

Figure 4. Bayesian phylogeny of *Draco sumatranus* based on concatenated sequences from mtDNA and nine nuclear loci. Posterior probabilities for each node is indicated, with values lower than 0.85 marked in red.


sum.KarangPauh.JAM9387
sum.KarangPauh.JAM9388
sum.UAndalas.JAM9243
sum.UAndalas.JAM9244
sum.UAndalas.JAM9240
sum.Anai.JAM9338
sum.UAndalas.JAM9242
sum.KarangPauh.JAM9389
sum.KarangPauh.JAM9390
sum.UAndalas.JAM9241
sum.LubukKumpai.JAM9395
sum.PesisirSelatan.JAM11205
sum.PesisirSelatan.JAM11208
sum.PesisirSelatan.JAM11207
sum.Bengkulu.JAM4114
sum.Kemumu.JAM9138
sum.Bengkulu.JAM4113
sum.PesisirSelatan.JAM11204
sum.PesisirSelatan.JAM11206
sum.PesisirSelatan.JAM11209
sum.KarangPauh.JAM9391
Southwest Sumatra
sum.Serasan.BJE167
sum.Serasan.BJE168
sum.Serasan.BJE165
sum.Serasan.BJE166
sum.Subi.BJE133
sum.Borneo.JAM1195
sum.BatuRaja.JAM9125
sum.BatuKuning.JAM9127
sum.BatuRaja.JAM9126
sum.Natuna.BJE100
sum.Natuna.BJE101
sum.Natuna.BJE099
sum.TelukBetung.JAM9076
sum.TelukBetung.JAM9074
sum.Kalianda.JAM9123
sum.Kalianda.JAM9122
sum.Kalianda.JAM9124
sum.TelukBetung.JAM9073
sum.TelukBetung.JAM9078
sum.TelukBetung.JAM9075
Southeast Sumatra, Natuna Islands & Borneo
sum.Sibolangit.JAM9761
sum.Sibolangit.JAM9760
sum.Sibolangit.JAM9759
sum.Sibolangit.JAM9757
sum.Sibolangit.JAM9758
sum.Gombak.JAM1362
sum.Panti.JAM9677
sum.Tioman.JAM4031
sum.Tioman.JAM4007
sum.Tioman.JAM4038
sum.Mersing.JAM3994
sum.Tinggi.JAM4715
sum.Tinggi.JAM4714
sum.Mersing.JAM3995
sum.Harau.JAM9417
sum.Panti.JAM9676
sum.Pasaman.JAM10325
sum.Panti.JAM9678
sum.Panti.JAM9652
sum.Solok.JAM9294
sum.Solok.JAM9295
sum.Solok.JAM9297
sum.Solok.JAM9296
Northeast Sumatra & Malay Peninsula
sum.MadiNa.JAM10315
sum.MadiNa.JAM10316
sum.MadiNa.JAM10317
sum.Batu.JAM11003
sum.Batu.JAM11006
sum.Batu.JAM11004
sum.Batu.JAM11005
sum.MadiNa.JAM10319
sum.MadiNa.JAM10318
sum.Batu.JAM10966
sum.Pandan.JAM10300
sum.Pandan.JAM10302
sum.Sitahuis.JAM10288
sum.Pandan.JAM10303
sum.Sipirok.JAM9694
sum.Sipirok.JAM9693
sum.Pandan.JAM10306
sum.Pandan.JAM10301
sum.Singkil.JAM9924
sum.Banyak.JAM11092
sum.Banyak.JAM11191
sum.Banyak.JAM11165
sum.Banyak.JAM11166
sum.Banyak.JAM11091
sum.Singkil.JAM9923
sum.LabuhanHaji.JAM9933
sum.LabuhanHaji.JAM9934
sum.Kutablang.JAM9929
sum.Kutablang.JAM9930
sum.Kutablang.JAM9931
Northwest Sumatra, Batu Islands & Banyak Islands
sum.Nias.JAM10080
sum.Nias.JAM10084
sum.Nias.JAM10083
sum.Nias.JAM10082
sum.Nias.JAM10085
Nias
laetv.Simeulue.JAM9958
sum.Simeulue.JAM10061
laetv.Lasia.JAM9991
laetv.Lasia.JAM9992
laetv.Lasia.JAM9989
laetv.Lasia.JAM9990
laetv.Lasia.JAM9988
laetv.Simeulue.JAM9960
laetv.Simeulue.JAM9959
sum.Simeulue.JAM10062
laetv.Simeulue.JAM9961
laetv.Simeulue.JAM9957
Simeulue
mod.Enggano.JAM4361
mod.Enggano.JAM4265
mod.Enggano.JAM4285
mod.Enggano.JAM4281
mod.Enggano.JAM4280
Enggano
sum.Pagai.JAM10463
sum.Pagai.JAM10465
sum.Pagai.JAM10464
sum.Pagai.JAM10466
sum.Sipora.SZL58
sum.Pagai.JAM10467
sum.Sipora.SZL19
sum.Siberut.SZL3
sum.Siberut.SZL5
sum.Siberut.SZL7
sum.Siberut.SZL4
sum.Sipora.SZL59
sum.Sipora.SZL56
sum.Sipora.SZL57
Mentawai Islands
Western Archipelago
volans.Jakarta.JAM2079
0.4

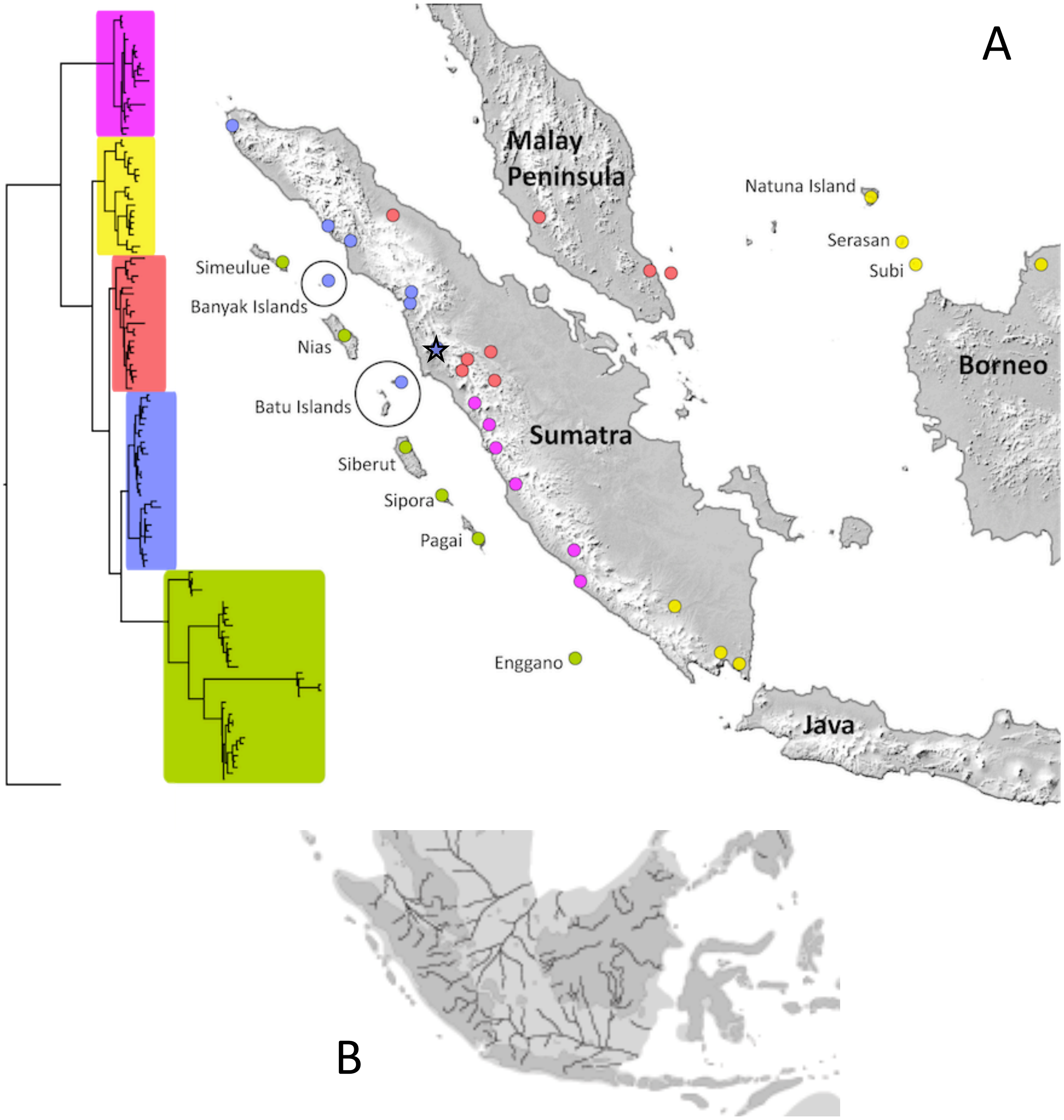


Figure 5. (A) map showing the geographical distribution of *Draco sumatranus* clades. Each circle on the map corresponds to a sampling locality. Panyabungan—the southern boundary of the Northwestern Sumatra clade—is indicated by the hollow star. (B) schematic map of Pleistocene drainage system (Voris 2000).

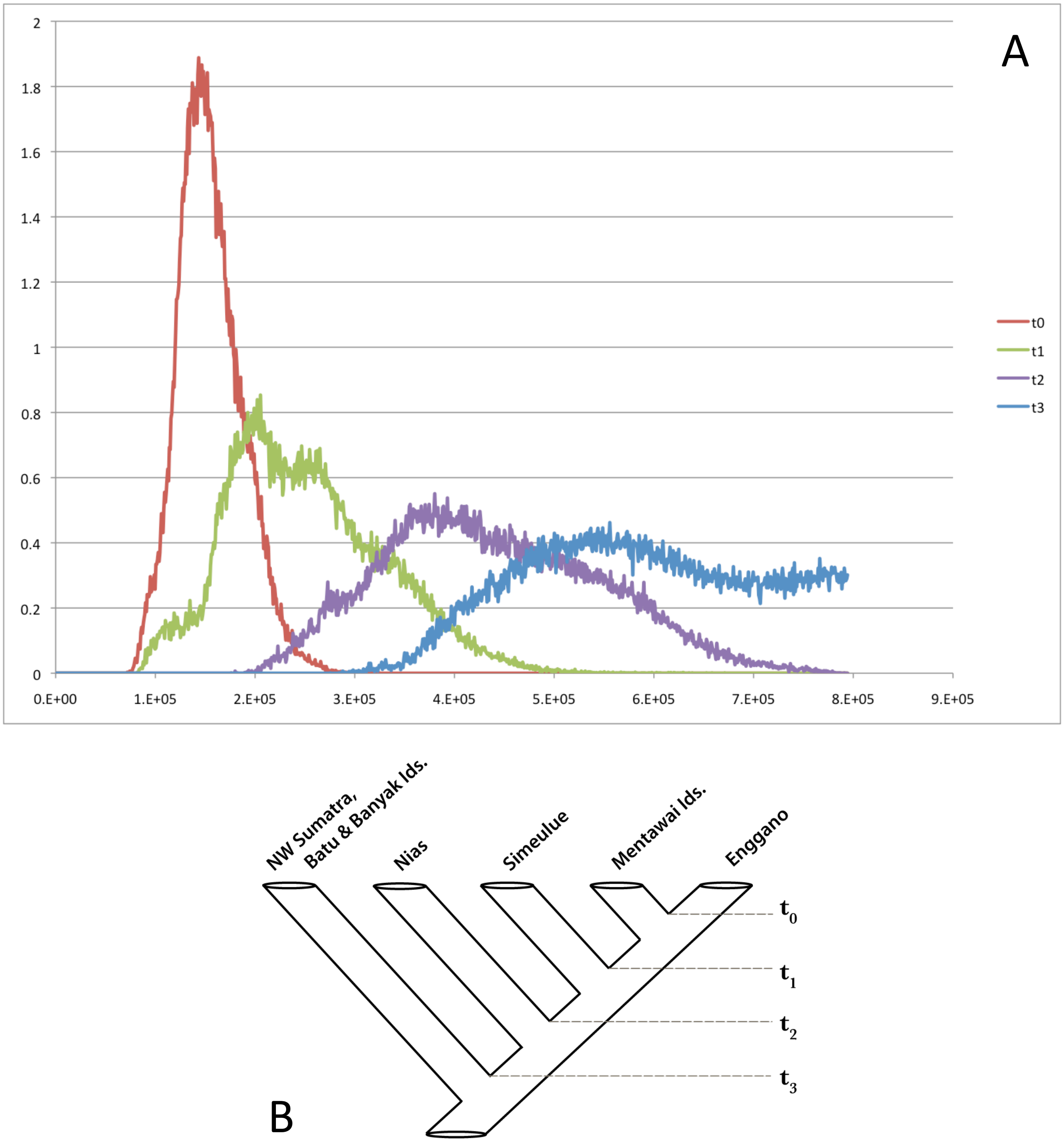


Figure 6. (A) Posterior distribution of population divergence times as inferred by the software IMa2. (B) A schematic diagram illustrating the populations represented in the analysis, and their respective divergence time parameters.

Appendix 1. List of samples included in this study and their localities.

Name in study	Locality	ID	Long.	Lat.	Phylogenetic	Coalescent
mod.Enggano.JAM4116	Enggano	JAM4116	102.272	-5.348		Yes
mod.Enggano.JAM4120	Enggano	JAM4120	102.272	-5.348		Yes
mod.Enggano.JAM4122	Enggano	JAM4122	102.272	-5.348		Yes
mod.Enggano.JAM4125	Enggano	JAM4125	102.272	-5.348		Yes
mod.Enggano.JAM4131	Enggano	JAM4131	102.272	-5.348		Yes
mod.Enggano.JAM4265	Enggano	JAM4265	102.232	-5.375	Yes	Yes
mod.Enggano.JAM4280	Enggano	JAM4265	102.232	-5.375	Yes	Yes
mod.Enggano.JAM4281	Enggano	JAM4281	102.232	-5.375	Yes	Yes
mod.Enggano.JAM4285	Enggano	JAM4285	102.232	-5.375	Yes	Yes
mod.Enggano.JAM4361	Enggano	JAM4361	102.232	-5.375	Yes	Yes
sp.nov.Simeulue.JAM10061	Simeulue	JAM10061	96.336	2.390	Yes	Yes
sp.nov.Simeulue.JAM10062	Simeulue	JAM10062	96.336	2.390	Yes	Yes
sp.nov.Simeulue.JAM9957	Simeulue	JAM9957	96.336	2.390	Yes	Yes
sp.nov.Simeulue.JAM9958	Simeulue	JAM9958	96.336	2.390	Yes	Yes
sp.nov.Simeulue.JAM9959	Simeulue	JAM9959	96.336	2.390	Yes	Yes
sp.nov.Simeulue.JAM9960	Simeulue	JAM9960	96.336	2.390	Yes	Yes
sp.nov.Simeulue.JAM9961	Simeulue	JAM9961	96.336	2.390	Yes	Yes
sp.nov.Simeulue.JAM9988	Lasia Island	JAM9988	96.650	2.170	Yes	Yes
sp.nov.Simeulue.JAM9989	Lasia Island	JAM9989	96.650	2.170	Yes	Yes
sp.nov.Simeulue.JAM9990	Lasia Island	JAM9990	96.650	2.170	Yes	Yes
sp.nov.Simeulue.JAM9991	Lasia Island	JAM9991	96.650	2.170	Yes	Yes
sp.nov.Simeulue.JAM9992	Lasia Island	JAM9992	96.650	2.170	Yes	Yes
sum.Anai.JAM9338	Anai, West Sumatra	JAM9338	100.335	-0.483	Yes	
sum.Banyak.JAM11091	Haloban, Banyak Islands	JAM11091	97.234	2.214	Yes	Yes
sum.Banyak.JAM11092	Haloban, Banyak Islands	JAM11092	97.234	2.214	Yes	Yes
sum.Banyak.JAM11165	Haloban, Banyak Islands	JAM11165	97.234	2.214	Yes	Yes
sum.Banyak.JAM11166	Haloban, Banyak Islands	JAM11166	97.234	2.214	Yes	Yes
sum.Banyak.JAM11191	Haloban, Banyak Islands	JAM11191	97.234	2.214	Yes	Yes
sum.Banyak.JAM11192	Haloban, Banyak Islands	JAM11192	97.234	2.214		Yes
sum.Banyak.JAM11193	Haloban, Banyak Islands	JAM11193	97.234	2.214		Yes
sum.Banyak.JAM11200	Haloban, Banyak Islands	JAM11200	97.234	2.214		Yes
sum.Banyak.JAM11201	Haloban, Banyak Islands	JAM11201	97.234	2.214		Yes
sum.Banyak.JAM11202	Haloban, Banyak Islands	JAM11202	97.234	2.214		Yes
sum.Batu.JAM10966	Labuhan Bajau, Batu Islands	JAM10966	98.839	0.085	Yes	Yes
sum.Batu.JAM11003	Labuhan Bajau, Batu Islands	JAM11003	98.839	0.085	Yes	Yes
sum.Batu.JAM11004	Labuhan Bajau, Batu Islands	JAM11004	98.839	0.085	Yes	Yes
sum.Batu.JAM11005	Labuhan Bajau, Batu Islands	JAM11005	98.839	0.085	Yes	Yes
sum.Batu.JAM11006	Labuhan Bajau, Batu Islands	JAM11006	98.839	0.085	Yes	Yes
sum.Batu.JAM11014	Labuhan Bajau, Batu Islands	JAM11014	98.852	0.105		Yes
sum.Batu.JAM11071	Labuhan Bajau, Batu Islands	JAM11071	98.852	0.105		Yes
sum.Batu.JAM11072	Labuhan Bajau, Batu Islands	JAM11072	98.852	0.105		Yes
sum.Batu.JAM11073	Labuhan Bajau, Batu Islands	JAM11073	98.852	0.105		Yes
sum.Batu.JAM11074	Labuhan Bajau, Batu Islands	JAM11074	98.852	0.105		Yes
sum.BatuKuning.JAM9127	Batu Kuning, South Sumatra	JAM9127	104.135	-4.108	Yes	
sum.BatuRaja.JAM9125	Baturaja, South Sumatra	JAM9125	104.180	-4.131	Yes	
sum.BatuRaja.JAM9126	Baturaja, South Sumatra	JAM9126	104.180	-4.131	Yes	
sum.Bengkulu.JAM4113	Bengkulu	JAM4113	102.256	-3.801	Yes	
sum.Bengkulu.JAM4114	Bengkulu	JAM4114	102.256	-3.801	Yes	
sum.Borneo.JAM1195	Borneo	JAM1195	113.001	2.557	Yes	
sum.Gombak.JAM1362	Malay Peninsula	JAM1362	101.639	3.290	Yes	
sum.Harau.JAM9417	Sumatra Barat	JAM9417	100.669	0.112	Yes	
sum.Kalianda.JAM9122	Kalianda, Lampung	JAM9122	105.616	-5.722	Yes	

Name in study	Locality	ID	Long.	Lat.	Phylogenetic	Coalescent
sum.Kalianda.JAM9123	Kalianda, Lampung	JAM9123	105.616	-5.722	Yes	
sum.Kalianda.JAM9124	Kalianda, Lampung	JAM9124	105.616	-5.722	Yes	
sum.KarangPauh.JAM9387	Karang Pauh, West Sumatra	JAM9387	100.539	-1.310	Yes	
sum.KarangPauh.JAM9388	Karang Pauh, West Sumatra	JAM9388	100.539	-1.310	Yes	
sum.KarangPauh.JAM9389	Karang Pauh, West Sumatra	JAM9389	100.539	-1.310	Yes	
sum.KarangPauh.JAM9390	Karang Pauh, West Sumatra	JAM9390	100.539	-1.310	Yes	
sum.KarangPauh.JAM9391	Karang Pauh, West Sumatra	JAM9391	100.539	-1.310	Yes	
sum.Kemumu.JAM9138	Kemumu, Bengkulu	JAM9138	102.267	-3.424	Yes	
sum.Kutablang.JAM9929	Kutablang, Aceh	JAM9929	97.151	3.296	Yes	Yes
sum.Kutablang.JAM9930	Kutablang, Aceh	JAM9930	97.151	3.296	Yes	Yes
sum.Kutablang.JAM9931	Kutablang, Aceh	JAM9931	97.151	3.296	Yes	Yes
sum.LabuhanHaji.JAM9933	Labuhan Haji, Aceh	JAM9933	97.044	3.496	Yes	Yes
sum.LabuhanHaji.JAM9934	Labuhan Haji, Aceh	JAM9934	97.044	3.496	Yes	Yes
sum.LubukKumpai.JAM9395	Lubuk Kumpai, West Sumatra	JAM9395	100.525	-1.304	Yes	
sum.MadiNa.JAM10315	Mandailing-Natal, N. Sumatra	JAM10315	99.825	0.642	Yes	Yes
sum.MadiNa.JAM10316	Mandailing-Natal, N. Sumatra	JAM10316	99.825	0.642	Yes	Yes
sum.MadiNa.JAM10317	Mandailing-Natal, N. Sumatra	JAM10317	99.825	0.642	Yes	Yes
sum.MadiNa.JAM10318	Mandailing-Natal, N. Sumatra	JAM10318	99.825	0.642	Yes	Yes
sum.MadiNa.JAM10319	Mandailing-Natal, N. Sumatra	JAM10319	99.825	0.642	Yes	Yes
sum.Mersing.JAM3994	Mersing, Malay Peninsula	JAM3994	103.831	2.436	Yes	
sum.Mersing.JAM3995	Mersing, Malay Peninsula	JAM3995	103.831	2.436	Yes	
sum.Natuna.BJE099	Natuna Island	BJE099	108.143	3.946	Yes	
sum.Natuna.BJE100	Natuna Island	BJE100	108.143	3.946	Yes	
sum.Natuna.BJE101	Natuna Island	BJE101	108.143	3.946	Yes	
sum.Nias.JAM10080	Nias	JAM10080	97.590	1.337	Yes	Yes
sum.Nias.JAM10082	Nias	JAM10082	97.590	1.337	Yes	Yes
sum.Nias.JAM10083	Nias	JAM10083	97.590	1.337	Yes	Yes
sum.Nias.JAM10084	Nias	JAM10084	97.590	1.337	Yes	Yes
sum.Nias.JAM10085	Nias	JAM10085	97.590	1.337	Yes	Yes
sum.Nias.JAM10086	Nias	JAM10086	97.590	1.337		Yes
sum.Nias.JAM10087	Nias	JAM10087	97.590	1.337		Yes
sum.Nias.JAM10090	Nias	JAM10088	97.590	1.337		Yes
sum.Nias.JAM10091	Nias	JAM10089	97.590	1.337		Yes
sum.Nias.JAM10092	Nias	JAM10090	97.590	1.337		Yes
sum.Nias.JAM10093	Nias	JAM10091	97.590	1.337		Yes
sum.Nias.JAM10094	Nias	JAM10092	97.590	1.337		Yes
sum.Nias.JAM10135	Nias	JAM10135	97.536	1.400		Yes
sum.Nias.JAM10138	Nias	JAM10138	97.536	1.400		Yes
sum.Nias.JAM10140	Nias	JAM10140	97.536	1.400		Yes
sum.Nias.JAM10141	Nias	JAM10141	97.536	1.400		Yes
sum.Nias.JAM10144	Nias	JAM10144	97.536	1.400		Yes
sum.Nias.JAM10150	Nias	JAM10150	97.792	1.075		Yes
sum.Nias.JAM10151	Nias	JAM10151	97.792	1.075		Yes
sum.Nias.JAM10152	Nias	JAM10152	97.792	1.075		Yes
sum.Pagai.JAM10463	S. Pagai, Mentawai Island	JAM10463	100.283	-3.077	Yes	Yes
sum.Pagai.JAM10464	S. Pagai, Mentawai Island	JAM10464	100.283	-3.077	Yes	Yes
sum.Pagai.JAM10465	S. Pagai, Mentawai Island	JAM10465	100.283	-3.077	Yes	Yes
sum.Pagai.JAM10466	S. Pagai, Mentawai Island	JAM10466	100.283	-3.077	Yes	Yes
sum.Pagai.JAM10467	S. Pagai, Mentawai Island	JAM10467	100.283	-3.077	Yes	Yes
sum.Pagai.JAM10468	S. Pagai, Mentawai Island	JAM10468	100.283	-3.077		Yes
sum.Pagai.JAM10469	S. Pagai, Mentawai Island	JAM10469	100.283	-3.077		Yes
sum.Pagai.JAM10470	S. Pagai, Mentawai Island	JAM10470	100.283	-3.077		Yes
sum.Pagai.JAM10471	S. Pagai, Mentawai Island	JAM10471	100.283	-3.077		Yes
sum.Pagai.JAM10472	S. Pagai, Mentawai Island	JAM10472	100.283	-3.077		Yes

Name in study	Locality	ID	Long.	Lat.	Phylogenetic	Coalescent
sum.Pagai.JAM10473	S. Pagai, Mentawai Island	JAM10473	100.283	-3.077		Yes
sum.Pagai.JAM10532	S. Pagai, Mentawai Island	JAM10532	100.290	-3.063		Yes
sum.Pagai.JAM10542	S. Pagai, Mentawai Island	JAM10542	100.290	-3.063		Yes
sum.Pagai.JAM10543	S. Pagai, Mentawai Island	JAM10543	100.290	-3.063		Yes
sum.Pagai.JAM10544	S. Pagai, Mentawai Island	JAM10544	100.290	-3.063		Yes
sum.Pagai.JAM10545	S. Pagai, Mentawai Island	JAM10545	100.290	-3.063		Yes
sum.Sipora.JAM10546	S. Pagai, Mentawai Island	JAM10546	100.290	-3.063		Yes
sum.Sipora.JAM10719	Sipora, Mentawai Islands	JAM10719	100.290	-3.063		Yes
sum.Sipora.JAM10720	Sipora, Mentawai Islands	JAM10720	100.290	-3.063		Yes
sum.Sipora.JAM10721	Sipora, Mentawai Islands	JAM10721	100.290	-3.063		Yes
sum.Sipora.JAM10722	Sipora, Mentawai Islands	JAM10722	100.290	-3.063		Yes
sum.Sipora.JAM10723	Sipora, Mentawai Islands	JAM10723	100.290	-3.063		Yes
sum.Pandan.JAM10300	Pandan, North Sumatra	JAM10300	98.850	1.644	Yes	Yes
sum.Pandan.JAM10301	Pandan, North Sumatra	JAM10301	98.850	1.644	Yes	Yes
sum.Pandan.JAM10302	Pandan, North Sumatra	JAM10302	98.850	1.644	Yes	Yes
sum.Pandan.JAM10303	Pandan, North Sumatra	JAM10303	98.850	1.644	Yes	Yes
sum.Pandan.JAM10306	Pandan, North Sumatra	JAM10304	98.850	1.644	Yes	Yes
sum.Panti.JAM9652	Panti, West Sumatra	JAM9652	100.050	0.354	Yes	
sum.Panti.JAM9676	Panti, West Sumatra	JAM9676	100.050	0.354	Yes	
sum.Panti.JAM9677	Panti, West Sumatra	JAM9677	100.050	0.354	Yes	
sum.Panti.JAM9678	Panti, West Sumatra	JAM9678	100.050	0.354	Yes	
sum.Pasaman.JAM10325	Pasaman, North Sumatra	JAM10325	99.988	0.591	Yes	
sum.PesisirSelatan.JAM11204	Pesisir Selatan, Bengkulu	JAM11204	100.952	-1.997	Yes	
sum.PesisirSelatan.JAM11205	Pesisir Selatan, Bengkulu	JAM11205	100.952	-1.997	Yes	
sum.PesisirSelatan.JAM11206	Pesisir Selatan, Bengkulu	JAM11206	100.952	-1.997	Yes	
sum.PesisirSelatan.JAM11207	Pesisir Selatan, Bengkulu	JAM11207	100.952	-1.997	Yes	
sum.PesisirSelatan.JAM11208	Pesisir Selatan, Bengkulu	JAM11208	100.952	-1.997	Yes	
sum.PesisirSelatan.JAM11209	Pesisir Selatan, Bengkulu	JAM11209	100.952	-1.997	Yes	
sum.Serasan.BJE165	Serasan Island (Natuna)	BJE165	109.039	2.518	Yes	
sum.Serasan.BJE166	Serasan Island (Natuna)	BJE166	109.039	2.518	Yes	
sum.Serasan.BJE167	Serasan Island (Natuna)	BJE167	109.039	2.518	Yes	
sum.Serasan.BJE168	Serasan Island (Natuna)	BJE168	109.039	2.518	Yes	
sum.Siberut.JAM10328	Siberut, Mentawai Islands	JAM10328	98.966	1.082		Yes
sum.Siberut.JAM10329	Siberut, Mentawai Islands	JAM10329	98.966	1.082		Yes
sum.Siberut.JAM10330	Siberut, Mentawai Islands	JAM10330	98.966	1.082		Yes
sum.Siberut.JAM10331	Siberut, Mentawai Islands	JAM10331	98.966	1.082		Yes
sum.Siberut.JAM10332	Siberut, Mentawai Islands	JAM10332	98.966	1.082		Yes
sum.Siberut.JAM10462	Siberut, Mentawai Islands	JAM10462	98.966	1.082		Yes
sum.Siberut.SZL14	Siberut, Mentawai Islands	SZL14	98.939	-1.127		Yes
sum.Siberut.SZL15	Siberut, Mentawai Islands	SZL15	98.939	-1.127		Yes
sum.Siberut.SZL16	Siberut, Mentawai Islands	SZL16	98.939	-1.127		Yes
sum.Siberut.SZL18	Siberut, Mentawai Islands	SZL18	98.939	-1.127		Yes
sum.Siberut.SZL20	Siberut, Mentawai Islands	SZL20	98.939	-1.127		Yes
sum.Siberut.SZL21	Siberut, Mentawai Islands	SZL21	98.939	-1.127		Yes
sum.Siberut.SZL3	Siberut, Mentawai Islands	SZL3	98.939	-1.127	Yes	Yes
sum.Siberut.SZL4	Siberut, Mentawai Islands	SZL4	98.939	-1.127	Yes	Yes
sum.Siberut.SZL45	Siberut, Mentawai Islands	SZL45	98.939	-1.127		Yes
sum.Siberut.SZL46	Siberut, Mentawai Islands	SZL46	98.939	-1.127		Yes
sum.Siberut.SZL5	Siberut, Mentawai Islands	SZL5	98.939	-1.127	Yes	Yes
sum.Siberut.SZL7	Siberut, Mentawai Islands	SZL7	98.939	-1.127	Yes	Yes
sum.Siberut.SZL9	Siberut, Mentawai Islands	SZL9	98.939	-1.127		Yes
sum.Sibolangit.JAM9757	Sibolangit, North Sumatra	JAM9757	98.597	3.347	Yes	
sum.Sibolangit.JAM9758	Sibolangit, North Sumatra	JAM9758	98.597	3.347	Yes	
sum.Sibolangit.JAM9759	Sibolangit, North Sumatra	JAM9759	98.597	3.347	Yes	

Name in study	**Locality**	**ID**	**Long.**	**Lat.**	**Phylogenetic**	**Coalescent**
sum.Sibolangit.JAM9760	Sibolangit, North Sumatra	JAM9760	98.597	3.347	Yes	
sum.Sibolangit.JAM9761	Sibolangit, North Sumatra	JAM9761	98.597	3.347	Yes	
sum.Singkil.JAM9923	Singkil, Aceh	JAM9923	97.639	2.896	Yes	Yes
sum.Singkil.JAM9924	Singkil, Aceh	JAM9923	97.639	2.896	Yes	Yes
sum.Sipirok.JAM9693	Sipirok, North Sumatra	JAM9693	99.189	1.641	Yes	
sum.Sipirok.JAM9694	Sipirok, North Sumatra	JAM9694	99.189	1.641	Yes	
sum.Sipora.JAM10724	Sipora, Mentawai Islands	JAM10724	99.589	2.033		Yes
sum.Sipora.JAM10725	Sipora, Mentawai Islands	JAM10725	99.589	2.033		Yes
sum.Sipora.JAM10726	Sipora, Mentawai Islands	JAM10726	99.589	2.033		Yes
sum.Sipora.JAM10727	Sipora, Mentawai Islands	JAM10727	99.589	2.033		Yes
sum.Sipora.JAM10728	Sipora, Mentawai Islands	JAM10728	99.589	2.033		Yes
sum.Sipora.SZL100	Sipora, Mentawai Islands	SZL100	99.588	-2.029		Yes
sum.Sipora.SZL101	Sipora, Mentawai Islands	SZL101	99.588	-2.029		Yes
sum.Sipora.SZL19	Sipora, Mentawai Islands	SZL19	99.588	-2.029	Yes	Yes
sum.Sipora.SZL56	Sipora, Mentawai Islands	SZL56	99.588	-2.029	Yes	Yes
sum.Sipora.SZL57	Sipora, Mentawai Islands	SZL57	99.588	-2.029	Yes	Yes
sum.Sipora.SZL58	Sipora, Mentawai Islands	SZL58	99.588	-2.029	Yes	Yes
sum.Sipora.SZL59	Sipora, Mentawai Islands	SZL59	99.588	-2.029	Yes	Yes
sum.Sipora.SZL70	Sipora, Mentawai Islands	SZL70	99.588	-2.029		Yes
sum.Sipora.SZL71	Sipora, Mentawai Islands	SZL71	99.588	-2.029		Yes
sum.Sipora.SZL72	Sipora, Mentawai Islands	SZL72	99.588	-2.029		Yes
sum.Sipora.SZL77	Sipora, Mentawai Islands	SZL77	99.588	-2.029		Yes
sum.Sipora.SZL78	Sipora, Mentawai Islands	SZL78	99.588	-2.029		Yes
sum.Sipora.SZL79	Sipora, Mentawai Islands	SZL79	99.588	-2.029		Yes
sum.Sipora.SZL80	Sipora, Mentawai Islands	SZL80	99.588	-2.029		Yes
sum.Sipora.SZL97	Sipora, Mentawai Islands	SZL97	99.588	-2.029		Yes
sum.Sipora.SZL98	Sipora, Mentawai Islands	SZL98	99.588	-2.029		Yes
sum.Sipora.SZL99	Sipora, Mentawai Islands	SZL99	99.588	-2.029		Yes
sum.Sitahuis.JAM10288	Sitahuis, North Sumatra	JAM10288	98.785	1.827	Yes	
sum.Solok.JAM9294	Solok, West Sumatra	JAM9294	100.658	0.874	Yes	
sum.Solok.JAM9295	Solok, West Sumatra	JAM9295	100.658	0.874	Yes	
sum.Solok.JAM9296	Solok, West Sumatra	JAM9296	100.658	0.874	Yes	
sum.Solok.JAM9297	Solok, West Sumatra	JAM9297	100.658	0.874	Yes	
sum.Subi.BJE133	Subi Island (Natuna)	BJE133	108.843	2.922	Yes	
sum.TelukBetung.JAM9073	Teluk Betung, Lampung	JAM9073	105.207	-5.430	Yes	
sum.TelukBetung.JAM9074	Teluk Betung, Lampung	JAM9074	105.207	-5.430	Yes	
sum.TelukBetung.JAM9075	Teluk Betung, Lampung	JAM9075	105.207	-5.430	Yes	
sum.TelukBetung.JAM9076	Teluk Betung, Lampung	JAM9076	105.207	-5.430	Yes	
sum.TelukBetung.JAM9078	Teluk Betung, Lampung	JAM9077	105.207	-5.430	Yes	
sum.Tinggi.JAM4714	Tinggi, Malay Peninsula	JAM4715	104.118	2.305	Yes	
sum.Tinggi.JAM4715	Tinggi, Malay Peninsula	JAM4715	104.118	2.305	Yes	
sum.Tioman.JAM4007	Tioman Island	JAM4007	N/A	N/A	Yes	
sum.Tioman.JAM4031	Tioman Island	JAM4031	N/A	N/A	Yes	
sum.Tioman.JAM4038	Tioman Island	JAM4038	N/A	N/A	Yes	
sum.UAndalas.JAM9240	Andalas Univ. West Sumatra	JAM9240	100.462	-0.910	Yes	
sum.UAndalas.JAM9241	Andalas Univ. West Sumatra	JAM9241	100.462	-0.910	Yes	
sum.UAndalas.JAM9242	Andalas Univ. West Sumatra	JAM9242	100.462	-0.910	Yes	
sum.UAndalas.JAM9243	Andalas Univ. West Sumatra	JAM9243	100.462	-0.910	Yes	
sum.UAndalas.JAM9244	Andalas Univ. West Sumatra	JAM9244	100.462	-0.910	Yes	
volans.Jakarta.JAM2079	Jakarta	JAM2079	N/A	N/A	Yes	