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BIOGEOGRAPHY OF INDONESIAN FRESHWATER FISHES: CURRENT PROGRESS

Arief Aditya Hutama, Renny Kurnia Hadiaty, Nicolas Hubert

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Hadi Dahrudin

DNA barcoding: foundations and applications for southeast asian freshwater fishes

TREUBIA, December 2016, Vol. 43, pp. 1–16.

Identifying and delineating species are the primary tasks of taxonomy. Owing to the decreasing interest of the nations for taxonomy and the inventory of living beings, funds have been drastically decreasing during the last two decades for taxonomic studies. As a consequence, the worldwide pool of taxonomists has dramatically decreased. DNA barcoding, as an automated tool for species delineation and identification, proved to rejuvenate the field of taxonomy and open new perspectives in ecology and conservation. In the present review, we will discuss how DNA barcoding established as a new paradigm in taxonomy and how DNA barcoding has been recently integrated in taxonomic studies. We will further details the potential applications for species identifications and discuss how DNA barcoding may positively impact the inventory and conservation of living beings, particularly in Biodiversity hotspots. We emphasize the benefit of DNA barcoding for the conservation of Southeast Asian freshwater fishes.

(Hadi Dahrudin, Renny Kurnia Hadiaty and Nicolas Hubert)

Key words: biodiversity hotspots, DNA barcoding, integrative taxonomy, species delineation, species identification

UDC: 597:574.9(594)

Arief Aditya Hutama

Biogeography of Indonesian freshwater fishes: current progress

TREUBIA, December 2016, Vol. 43, pp. 17–30.

Southeast Asia is one of the most geologically complex tropical regions on Earth, in which the intricate interactions among plate tectonics, volcanism and Pleistocene climatic fluctuations led to complex patterns of species distribution. An increasing number of biogeographic studies of the Indonesian ichthyofauna have already partially uncovered the potential mechanisms at the origin of present day species distribution. These studies are currently scattered in the literature and the present review aims at presenting recent progress. Here, we propose a review of this literature with the aim to provide a broad overview of the current progress in the field of Indonesian freshwater fishes biogeography. First, we will briefly present the geology of the Indo-Australian Archipelago (IAA) and highlight the time frame of the geographical settlement of the Indonesian archipelago. Second, we will present the palaeoecological history of Sundaland during the Pleistocene. Finally, we will present the results of recent biogeographic studies across the three biogeographic provinces (Sundaland, Wallacea, Sahul) and discuss how these results fit with geological and palaeoecological scenarios in Indonesia.

(Arief Aditya Hutama, Renny Kurnia Hadiaty and Nicolas Hubert)

Key words: Biogeography, Indonesia, freshwater fishes, plate tectonics, Pleistocene climate

UDC: 599.41:519.23(594.31)

Sigit Wiantoro

Morphological and genetic study of the masked flying fox, *Pteropus personatus*; with a new subspecies description from Gag Island

TREUBIA, December 2016, Vol. 43, pp. 31-46.

Study on the specimens of Masked Flying Fox, *Pteropus personatus* from Gag and Moluccas islands had been done by using the morphological and genetic analysis. Morphologically, four specimens from Gag Island differs from the other populations in Moluccas Islands by its smaller size of skull, dental and external measurements. All of these four specimens was identified as *P. personatus acityae* n. subsp. The phylogenetic reconstruction based on partial cytochrome *b* sequences also support the differences of *P. Personatus acityae* n. subsp. Thus, recently two subspecies of *P. personatus* known from its distribution areas.

(Sigit Wiantoro and Ibnu Maryanto)

Key words: flying fox, Gag Island, new subspecies, *Pteropus personatus*

results of this study show that Gunung Halimun-Salak National Park has the highest richness of bird species in Java-Bali region and the conservation of its endemic and threatened species should be given the main priority.

(Dewi M. Prawiradilaga)

Key words: Birds, conservation status, endemism, gunung Halimun-Salak National Park, threatened status

UDC: 598.2(594.53)

Fransisca Noni Tirtaningtyas

Morphometric and molt of the crescent-cheded babbler (*stachyris melanothorax*) in Cisarua forest, West Java

TREUBIA, December 2016, Vol. 43, pp. 71–78.

Crescent-cheded Babbler is endemic to the island of Java and Bali, Indonesia and protected by the Indonesian Government Regulation No. 7/ 1999. Its population is suspected to be declining due to ongoing habitat destruction and fragmentation. Information on its eco-biology is very poorly known. There is a need to obtain those information in order to conserve this species and its habitat. Morphometric and molt stages were recorded from 23 individuals captured by mistnets between February and April 2016. There were variation in morphometric measurement in weight, head bill, wing length and tail length in Cisarua Forest habitat. This habitat have sufficient resource for Crescent-cheded Babbler do the molt activity during the study.

(Fransisca Noni Tirtaningtyas, Yeni Aryati Mulyani, Dewi Malia Prawiradilaga, and Joseph Adiguna Hutabarat and Iis Sabahudin)

Key words: morphometric, molt, *Stachyris melanothorax*, threat, West Java

UDC: 598.2:502.3(594.53)

Dewi M. Prawiradilaga

Birds of Halimun-Salak National Park, West Java, Indonesia: endemism, conservation and threatened status

TREUBIA, December 2016, Vol. 43, pp. 47–70.

Bird surveys and long-term bird monitoring in Gunung Halimun-Salak National Park were conducted between 1998 and 2009 to obtain comprehensive data on the bird species in the area. Compilation of bird data from this study and other studies have recorded a total of 279 species which is about 55.3% of the total Javan birds (507 species) or 17.4% of the total Indonesia birds (1605 species). As an important bird area, Gunung Halimun-Salak National Park is a home of 43 Indonesian and Javan endemic species. Among the endemics, 32 species are restricted range species. Gaps in the protection status of the bird species are discussed. The

UDC: 595.132:599.322(594)

Kartika Dewi

General review of the genus *Syphacia* (nematoda: oxyuridae) from murine rodents in Indonesia and neighboring areas

TREUBIA, December 2016, Vol. 43, pp. 79–104.

The pinworms of the genus *Syphacia* are of special interest because they have coevolutionary relationship with their host murines. In the areas from Southeast Asia to Australia, 21 species in four subgenera, of which two were endemic to Sulawesi, have been recorded. Their biogeographical distribution and dispersal process are discussed herein. Based on the morphological characteristics of the cephalic ends, the species of the subgenus *Syphacia* are divided into three lineages with square (S), round (R) and laterally-elongated (LE) cephalic shapes. The LE type is considered to be primitive, and the S and R types are derived from the LE type. The species composition of *Syphacia* seems to be mosaic among the islands, especially in Wallacea. A hypothesis on the formation of the host-parasite relationships between murines and subgenus *Syphacia* in the areas is presented. A key to *Syphacia* species recorded is also provided.

(Kartika Dewi, Hideo Hasegawa and
Mitsuhiko Asakawa)

Key words: Indonesia, murine rodents, Southeast Asia to Australia, *Syphacia*

BIOGEOGRAPHY OF INDONESIAN FRESHWATER FISHES: CURRENT PROGRESS

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ABSTRACT

Southeast Asia is one of the most geologically complex tropical regions on Earth, in which the intricate interactions among plate tectonics, volcanism and Pleistocene climatic fluctuations led to complex patterns of species distribution. An increasing number of biogeographic studies of the Indonesian ichthyofauna have already partially uncovered the potential mechanisms at the origin of present day species distribution. These studies are currently scattered in the literature and the present review aims at presenting recent progress. Here, we propose a review of this literature with the aim to provide a broad overview of the current progress in the field of Indonesian freshwater fishes biogeography. First, we will briefly present the geology of the Indo-Australian Archipelago (IAA) and highlight the time frame of the geographical settlement of the Indonesian archipelago. Second, we will present the palaeoecological history of Sundaland during the Pleistocene. Finally, we will present the results of recent biogeographic studies across the three biogeographic provinces (Sundaland, Wallacea, Sahul) and discuss how these results fit with geological and palaeoecological scenarios in Indonesia.

Key words: Biogeography, freshwater fishes, Indonesia, plate tectonics, Pleistocene climate

INTRODUCTION

Biogeography is a field of evolutionary biology that aims at uncovering the origin of the distribution of Earth's living beings (Nelson & Platnick 1981, Myers & Giller 1988). Understanding the evolutionary history of species across space and time is a fundamental field of research that not only impacts our perception of biological complexity, but also provides guidelines for the conservation of biodiversity. Biogeography provides basic information about species distribution and faunal composition, which are further used to explore patterns of diversity and evolutionary processes (Myers *et al.* 2000, Ricklefs 2004, McPeck 2008). Biodiversity is not evenly distributed on Earth and accumulates in centers of exceptional richness that host a substantial part of the world's biodiversity (Myers *et al.* 2000). Some of these centers, however, have been exposed to increasing levels of anthropogenic pressures (*i.e.* biodiversity hotspots) and are currently threatened by astonishing high rates of extinction (Myers *et al.* 2000, Lamoureux *et al.* 2006, Hoffman *et al.* 2010, Tittensor *et al.* 2010). Given the high numbers of endemic species, coupled with the strong anthropogenic pressures exerted, these regions have been identified as top priority targets for conservation. Establishing efficient conservation policies, however, requires a spatially explicit understanding of species accumulation and maintenance in communities (Lamoureux *et al.* 2006, Hubert *et al.* 2015).

Among the 25 world's terrestrial hotspots, two are in Indonesia, namely Sundaland and Wallacea, and are currently the world's most threatened hotspots by human activities (Lamoureux *et al.* 2006, Hoffman *et al.* 2010). Indonesia is part of the Indo-Australian Archipelago (hereafter the IAA) also known as the Malay Archipelago (Fig. 1). The IAA probably constitutes one of the most geographically complex tropical regions on earth that expands across more than 20,000 islands, straddles the equator, and comprises several major biogeographic provinces (*i.e.* Sundaland, Wallacea, Sahul). The current geography of the IAA is the result of a complex geological history that expended through the last 50 millions years. Plate tectonics and intense volcanic activities led to several major vicariance events that gave rise to remarkable patterns in the distribution of higher taxa. More recently, the rising and falling of sea levels during the Pleistocene caused islands on the Sunda Shelf to be repeatedly merged with each other and/or the mainland as the sea floor was exposed and then submerged (Woodruff 2010, Lohman *et al.* 2011, Hall 2012 & 2013). The complex geological and palaeoecological history of the IAA has given rise to highly diverse and endemic biotas. Although it occupies just 4% of the planet's land area, the IAA is home to nearly one-quarter of the world's terrestrial species. Worth mentioning, the Indonesian archipelago hosts nearly 51,090 km² of coral reefs representing the world's most species-rich coral reefs (Allen & Erdmann 2012).

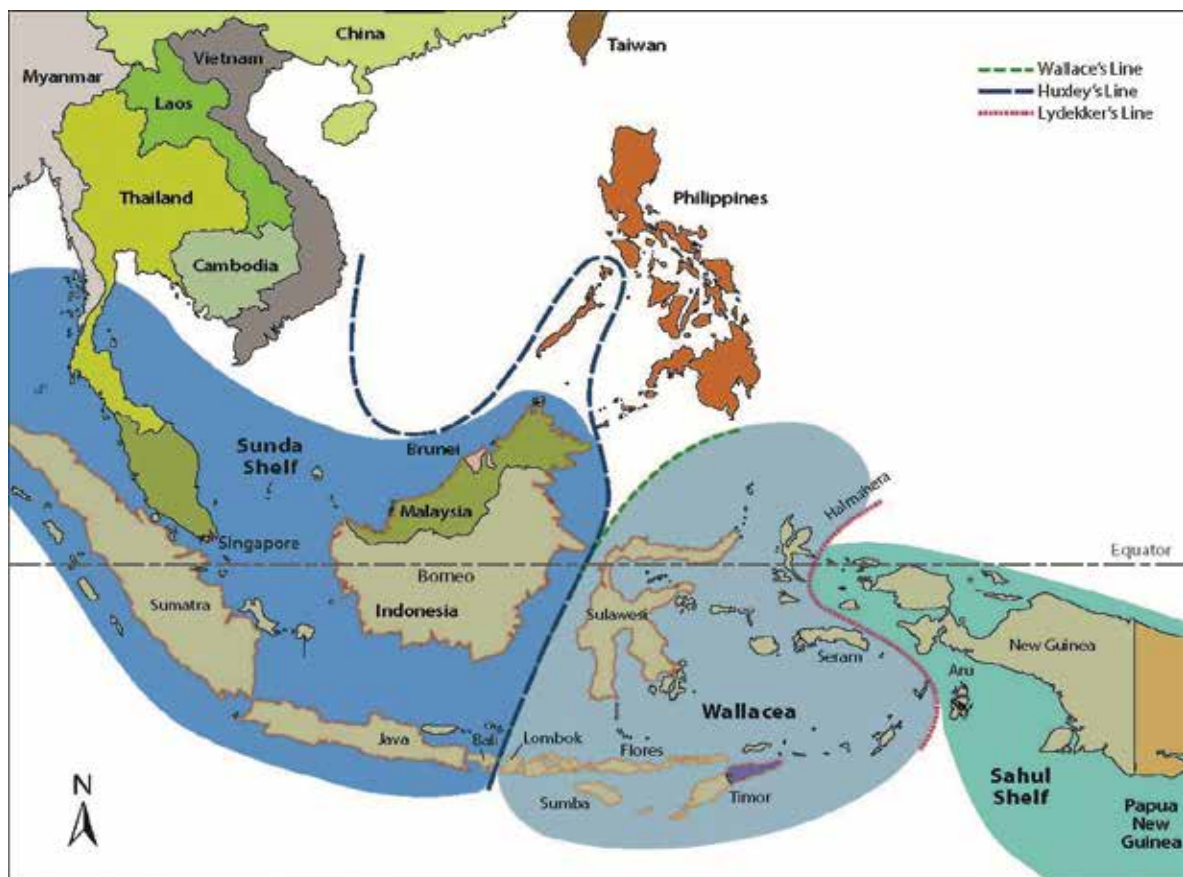


Figure 1. Map of the Indo-Australian Archipelago (IAA) indicating contemporary landmasses, straits, seas, arcs, and faunal lines. Major islands are labeled; different countries in the IAA are indicated by color (modified from Lohmann *et al.* 2011).

Fishes constitutes the most speciose group of vertebrate and the vertebrate biotas of the IAA are no exception (Froese & Pauly 2011). Given its approximately 5000 native species of marine, brackish and freshwater fishes that account for nearly 15 percent of the 33,100 known species of fish worldwide, Indonesia is one of the world's most species-rich countries (Froese & Pauly 2011). Owing to their high diversity and endemism, freshwater fishes of Indonesia provide a prime example that reflects the complex geological and biogeographical history of the IAA. The high diversity and endemism of Indonesian freshwater fishes stem largely from the fact that freshwaters are embedded within terrestrial landscapes that are fragmented by numerous volcanic arches that limit dispersal among watersheds. As a consequence, most freshwater fishes occupy only a fraction of the localities where they might otherwise thrive due to the important fragmentation of the Indonesian lakes and rivers. This constrained geography is at least partially responsible for the fantastic diversity of freshwater fishes observed there (Olden *et al.* 2010).

The aim of the present synthesis is to present an overview of the knowledge that has accumulated during the last decades on the biogeography of the IAA freshwater fishes, with a particular emphasis on the Indonesian hotspots. First, we will briefly cover the last 20 million years (Mys) of geological history of the IAA until the geographical settlement of the archipelago in its present form. Second, we will present the palaeoecological history of the IAA during the Pleistocene with a particularly emphasis on sea levels fluctuations. Finally, we will discuss the recent advances on the IAA freshwater fishes biogeography that originated from the increasing use of DNA sequences and molecular phylogenetics to infer species evolutionary history.

GEOLOGICAL HISTORY OF THE IAA DURING THE LAST 20 MYS

The network of islands in the IAA result from a complex geological history that started at the beginning of the Cenozoic ca. 65 millions years ago (Ma). At that time, Sundaland was still embedded in the Eurasia plate in the Southeast as an emergent terrestrial region crossing the equator (Hall 2012 & 2013). During the Cretaceous, Australia started to move rapidly northward from approximately 45 Ma and the subduction beneath Indonesia caused widespread volcanism at the active margin prompting the rise of chains of islands that contributed later to the Philippines archipelago. At the time, the Sunda arc stretched eastward, while subduction zones surrounded Sundaland until the Miocene (Lohman *et al.* 2011).

The geographic settlement of the IAA in its modern configuration is largely the result of the tectonic activity during the last 20 Mys (Fig. 2; Lohman *et al.* 2011). During the Miocene ca. 23 Ma (Fig. 2 A,B), the eastward movement of Australia prompted subduction beneath Sundaland near Sulawesi, resulting in the counter-clockwise rotation of Sundaland. From approximately 20 Ma, the subduction of Australia prompted the emergence of New Guinea, which was probably

initiated as a series of small islands that further connected to each other to form a large landmass (Fig. 2B,C). During the late Miocene *ca.* 10 Ma, Sundaland started to differentiate from the western mainland and the subduction prompted the rise of a large mountain range in Borneo (Fig. 2B,C). The rise of mountains and the changes in ocean circulation probably contributed towards a generally wetter climate in Sundaland from the Miocene onward (Lohman *et al.* 2011). Despite the uplift of Borneo, shallow seas area expanded and resulted in the reduction of land area in Sundaland until the end of the Miocene *ca.* 5 Ma (Fig. 2C). Collision of Australia resulted in the emergence of more land areas in Wallacea and the emergence of temporary land connection with the emerging New Guinea (Fig. 2C). From the early Pliocene onward (Fig. 2C), the counter clockwise rotation of Borneo resulted in its separation from other landmasses in Sundaland, while volcanic activities due to the subduction of Australia beneath Sundaland resulted in the emergence of Java and the lesser Sunda islands (Bali, Lombok, Flores, Sumbawa, Timor) (Fig. 2C). At the time, several terranes in Sulawesi aggregated as a consequence of a complex pattern of subduction that subsequently led to their separation from the emerging New Guinea (Fig. 2C). New Guinea and Australia separated during the last 5 Mys with temporary land bridges that probably have connected them repeatedly throughout the Quaternary.

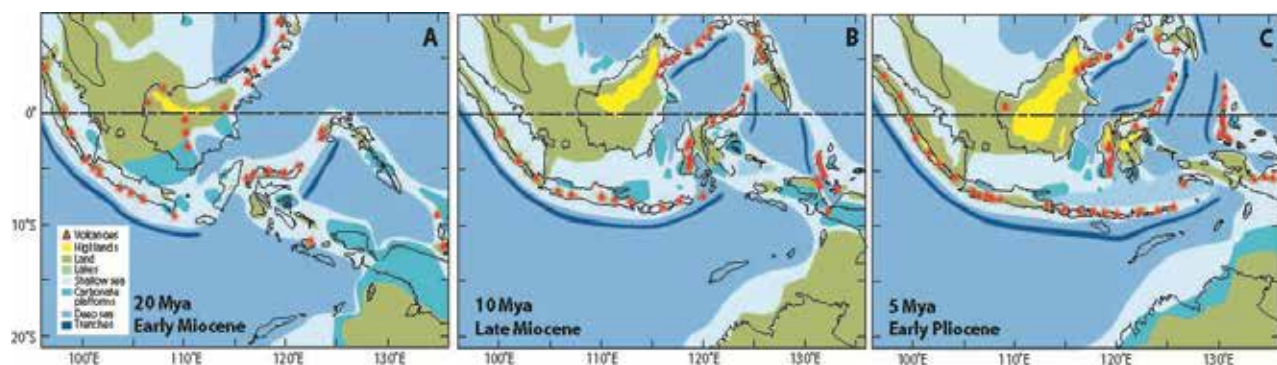


Figure 2. Cenozoic reconstructions of land and sea in the Indo-Australian Archipelago during the last 20 Mys(modified from Lohmann *et al.* 2011)

Pleistocene climatic fluctuations, sea levels and paleodrainages

The impact of collective effects of cyclic changes in the Earth's movement (*i.e.* eccentricity of Earth orbit, axial tilt and precession) upon climate has been formalized in the Milankovitch theory predicting that Earth orbital properties impact Earth climates in a predictable and cyclical way (*i.e.* Milankovitch cycles; Hays *et al.* 1976). Under given combinations of Earth's orbit, surface temperatures decreased (*i.e.* Glacial Maxima), leading to the substantial thickening of ice sheets and the low-stand of sea levels (Haq *et al.* 1987). The alternation of glacial maxima and warmer periods has been documented throughout the Pleistocene based on either the deep-ocean isotopic analyses or the reconstruction of past forest cover (Nores 1999, 2004, Woodruff 2010). These cycles not only

affected the distribution of landmasses through the drastic fluctuations of sea levels, but also affected climates and forest cover (Haffer 1969, Prance 1982) and the IAA is no exception (Verstappen 1975, Kottelat *et al.* 1993, Woodruff 2010).

Based on a synthesis of global sea level fluctuations from deep-ocean foraminifera $\delta^{18}\text{O}$ isotope ratios and fluctuations in tropical lowland forest extent in Southeast Asia, Woodruff (2010) proposed a map of emerged land during sea levels fall of 60m (*i.e.* the sea level corresponding to the average area of the Sunda shelf during the Pleistocene) and 120 m (*i.e.* the maximum sea level fall during the Pleistocene) (Fig. 3). This palaeo-reconstruction of landmasses in Southeast Asia during the late Pleistocene shed light on the past patterns of connectivity among the major island of Sundaland. During the sea level low-stand, Borneo, Sumatra and Java were connected to the mainland, and rivers got connected through the development of four main palaeodrainages straddling among islands (Kottelat *et al.* 1993). Such temporary connections during sea level low-stands happened repeatedly during the late Pleistocene (Woodruff, 2010). The development of these large palaeodrainages during the final geographical settlement of Sundaland offered temporary connections and prompted dispersal among rivers that are currently separated. Along the same line, the climate had been cooler and drier during glacial maxima, but everwet conditions appear to have persisted in northern Sumatra, western and northern Borneo, and parts of the emergent Sunda Shelf (Bird *et al.* 2005). During cooler intervals, only North Borneo and possibly small areas of north Sumatra were high enough to have been capped by ice, whereas New Guinea had extensive montane glaciers (Hope 2007). By contrast, estimating the Quaternary distribution of emerged lands in Wallacea is challenging because of the relatively more recent geological age of Wallacea islands compared to Sundaland (Lohman *et al.* 2011). Although the paleogeography of Wallacea is uncertain, it is clear that deep marine areas persisted between the Sahul and Sunda shelves and there was no land connection (Hall 2012, 2013).

BIOGEOGRAPHY OF INDONESIAN FRESHWATER FISHES

Species diversity and general considerations

With 1,218 species belonging to 84 families and 630 endemic species, Indonesia has the most species-rich ichthyofauna of Southeast Asia (Hubert *et al.* 2015). The inventory of Indonesian freshwater fishes has been ongoing since the second half of the 18th century and many new species are still discovered and described every year. Nevertheless, it has been challenged since its earliest development by several limitations: (1) the Indonesian archipelago hosts nearly 17,000 islands and most of them are remote islands with limited access, (2) tracing the type specimens has been sometimes challenging, particularly for the species described before the 1950's, (3) the Indonesian ichthyofauna demonstrates several large radiations of morphologically

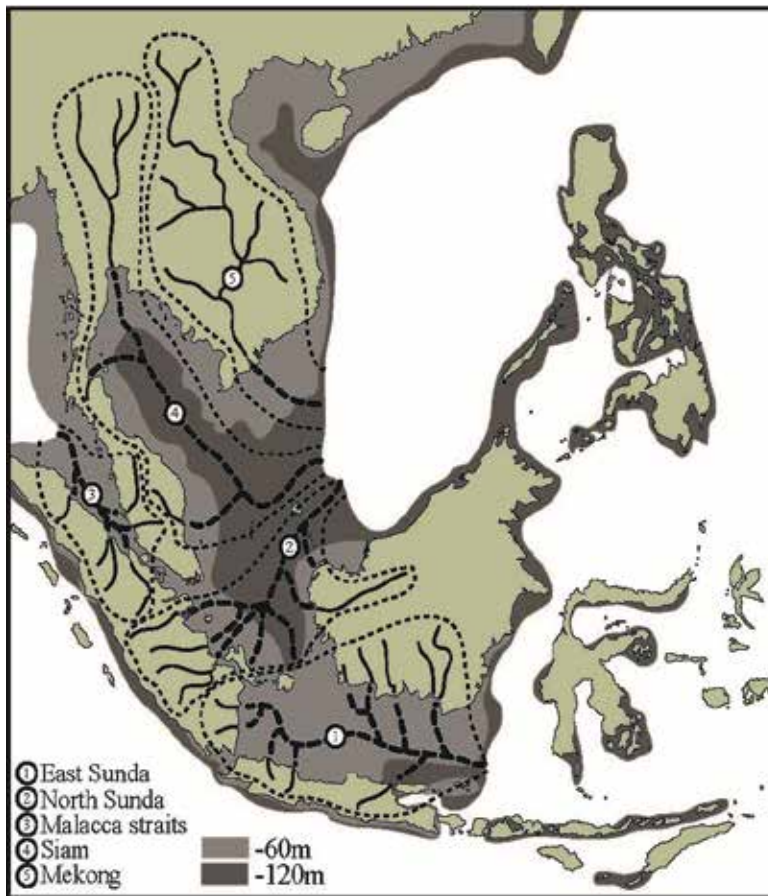


Figure 3. Emerged lands and palaeodrainages during the Pleistocene (modified from Woodruff, 2010).

similar species that have been subject to either multiple descriptions, recurrent systematic revisions or overlooked diversity (Kottelat 2013).

With a density of 0.6 species per 1,000 km², Indonesia hosts one of the world highest density of fish species ahead of Brazil (0.37 species per 1,000 km²) and the Democratic Republic of Congo (0.48 species per 1,000 km²), two countries known to host some the world largest and speciose tropical rivers (Froese & Pauly 2011, Hubert *et al.* 2015). The main reasons for this exceptional diversity can be attributed to the important fragmentation of the rivers across the numerous islands of the archipelago, together with the occurrence of several major biogeographical boundaries (Fig. 1). These major biogeographical provinces are each dominated by different families depending on their past connection to the main land (*i.e.* Eurasia, Australia). Families of primary freshwater fishes such as Cyprinidae (241 species), for instance, dominate Sundaland (Hadiaty 2001, 2005, 2011a,b, Hadiaty & Siebert, 1998, Hadiaty & Kottelat 2009, Hadiaty *et al.* 2003, Kottelat 2013, Kottelat *et al.* 1993, Kottelat & Whitten 1996, Kottelat & Widjanarti 2005, Roberts 1989, Tan & Kottelat 2009). By contrast, Wallacea and Sahul host predominantly families with an ancestral marine origin or displaying larval marine stages such as the family Gobiidae (Allen 1991, Hadiaty 1996, 2007, 2012, Hadiaty & Wirjoatmodjo 2003, Hadiaty *et al.* 2004, 2012, Hoese *et al.* 2015, Larson & Kottelat 1992, Larson *et al.* 2014, Keith & Hadiaty 2014, Keith *et al.* 2011, Parenti *et al.* 2013,

Poyaud *et al.* 2013). Several endemic radiations of primary freshwater fishes, however, are present in Wallacea and Sahul such as the Telmatherinidae (17 endemic species in Wallacea, and 1 endemic species in Sahul; Aurich 1935, Ivantsoff & Allen 1984, Kottelat 1990ab, 1991, Weber 1913), Adrianichthyidae (18 endemic species in Wallacea, Herder & Chapuis 2010, Herder *et al.* 2012, Mokodongan *et al.* 2014, Parenti 2008, Parenti & Hadiaty 2010, Parenti *et al.* 2013) and Melanotaeniidae (47 endemic species in Sahul, Allen 1981, Allen & Cross 1982, Allen & Hadiaty 2013, Allen *et al.* 2014ab, 2015ab, Graf *et al.* 2015, Kadarusman *et al.* 2010, 2011, 2012a), respectively.

Biogeography of Sundaland

Sea level fluctuations associated to Milankovitch cycles have deeply impacted the distribution of freshwater fishes in Sundaland throughout the Pleistocene by providing multiple opportunities for dispersal during sea level low-stands and subsequent fragmentation during sea level high-stands. For instance, Kottelat (1989) stated from 263 species of fish known from the Malay Peninsula (Peninsular Malaysia) at that time, 44 % occurred in Mekong, 47% in the Chao Phraya and 66% in Borneo. Kottelat (1989) attributed this close similarity between Peninsular Malaysia and Borneo as a consequence of past connections related with sea level fluctuations. Along the same line, Dodson and colleagues (1995) noted that the similarity in the genetic diversity of the populations from western Borneo and southeastern Sumatra of the catfish *Hemibagrus nemurus* were a consequence of past drainage connectivity during sea level low-stands. The same pattern was later observed by McConnell (2004) who studied faunal exchanges across the Sunda shelf through phylogeographic inferences of *Barbodes gonionotus*. More recently, Hadiaty (2014) made similar observations in the genus *Nemacheilus* with cases of species with trans-islands range distribution.

Recent studies in the phylogeography of Sundaland fishes confirmed that the evolutionary history of Sundaland fishes was marked by the landmass dynamic during the Pleistocene as a consequence of eustatic changes. In their study of the cyprinid genus *Tor*, Nguyen and colleagues (2008) evidenced that the widely distributed species in Sundaland, such as *Tor douronensis*, display several closely related phylogeographic lineages exhibiting phylogenetic relationships that straddles across distinct islands. Along the same line, De Bruyn *et al.* (2013) demonstrated that species boundaries and phylogeographic structure in the genus *Dermogenys*, *Nomorhamphus* and *Hemirhamphodon* were rather matching palaeodrainages during times of low sea levels than current islands boundaries. The study by Pouyaud and colleagues (2009) on the catfish genus *Clarias* yielded similar results as several molecular lineages were detected inside species with wide distribution ranges in Sundaland (*e.g.* *C. olivaceus*, *C. meladerma*, *C. punctatus* and *C. nieuhoftii*). Furthermore, the distribution of these lineages is rather matching palaeodrainage boundaries than present geography.

Biogeography of Wallacea

The biogeography of Wallacea's ichthyofauna is markedly distinct from the biogeography of the Sundaland's ichthyofauna. Besides of amphidromous lineages with marine larval stages, the Wallacea's ichthyofauna is characterized by several radiations that happened within several ancient lake systems in Sulawesi and resulting in several endemic species flocks (Parenti & Ebach, 2013). The Sulawesi sailfin silversides (Telmatherinidae) and ricefish (Adrianichthyidae) constitute prime examples of such radiations that happened through adaptive shifts across ecological habitats of the Malili lakes (Kottelat 1990ab, 1991). Herder and colleagues (Herder *et al.* 2006, Herder *et al.* 2008, Pfaender *et al.* 2010, Pfaender *et al.* 2011) have demonstrated, for instance, that the silversides radiation was characterized by the existence of introgressive hybridization during early diversification as well as trophic specialization related to a dynamic of niche partitioning and sexual selection. Schwarzer and colleagues (2008) also demonstrated that ongoing gene flow between sharpfin silversides of Lake Matano and Petea river was balanced by adaptive morphometric differences among stream and lake habitats resulting in gradients of gene flow and morphometric similarities between each habitat types. Herder *et al.* (2006) has described the consequences of introgressive hybridization on the match between gene trees and species trees of stream- and river-dwelling sailfin silversides from Malili Lakes systems.

Similar processes are also expected to obscure the phylogenetic relationships among Sulawesi's ricefishes (Herder *et al.* 2012). *Oryzias eversi* has a pelvic brooding strategy and inhabit stream habitat of Sulawesi, while the other known pelvic brooders live in Sulawesi's lakes. The broad ecological requirements of *Oryzias* spp. might facilitate contact of lake- and stream-dwelling species, and may have facilitated reticulate evolution (Herder *et al.* 2012). The family Adrianichthyidae comprises two genera and 35 species (*Oryzias*: 33 species; *Adrianichthys*: two species), only two of which are not endemic to Sulawesi (Parenti & Soeroto 2004, Parenti 2008, Parenti & Hadiaty 2010, Herder & Chapuis 2010, Herder *et al.* 2012, Asai *et al.* 2011, Parenti *et al.* 2013, Mokodongan *et al.* 2014). In her publication of the phylogenetic analysis and taxonomic revision of the ricefishes, Parenti (2008:497) refined the species range distributions of the group and highlighted that the high endemism in Sulawesi was likely the result of higher speciation rates.

Biogeography of Sahul

The biodiversity of New Guinea has been subject to much less ichthyological explorations than the Sundaland and Sahul provinces and the complicated, yet poorly understood, geological history of the island is responsible for the paucity of biogeographic studies in the literature. Recently, Kadarusman and colleagues (2012b) have detected 30 mitochondrial lineages among the 13 nominal species of *Melanotaenia* in the Bird's head, all being distributed in allopatry and restricted to a single watershed. This cryptic diversity has been further confirmed by high level of

genetic differentiation based on microsatellite genotyping and the discovery of several diagnostic morphological characters (Nugraha *et al.* 2015). In their study, the authors reported four clades exhibiting range distribution to be related with the uplift of the Lengguru massif at the southern tip of the bird's head and suggesting that the spatial expansion of the *Melanotaenia* species across New Guinea and Australia probably originated from western Papua New Guinea.

CONCLUSIONS

Indonesia is one of the most geologically complex tropical regions that gave birth to an extraordinary biodiversity. Molecular approaches on biogeography provided an unprecedented improvement to our understanding on the biogeography of the freshwater fishes in Indonesia. The present review highlights that each biogeographic provinces experienced markedly distinct geological and palaeoecological histories resulting in contrasting biogeographic patterns. So far, several hypotheses have been proposed to account for biogeographic patterns in Indonesia. From an historical perspective, sea level fluctuations in Sundaland during the Pleistocene have been the first hypothesis proposed to account for the spatial distribution of freshwater fish species. Particularly for Wallacea and Sahul, alternative hypotheses have been proposed based on adaptive radiation in endorheic basins and plate tectonics. These hypotheses are not mutually exclusive and highlight the complex history of the Indonesian archipelago. The present review also highlight the paucity of biogeographic studies in Indonesia and we hope that the present review will trigger new studies that will improve our understanding of Indonesian freshwater fishes biogeography.

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MacKinnon, J. & K. Phillips 1993. *Field Guide to the Birds of Borneo, Sumatra, Java and Bali*. Oxford University Press, Oxford, 491 pp.

Natural History Museum 2013. Wallace100 - celebrating Alfred Russel Wallace's life and legacy. [Online] <<http://www.nhm.ac.uk/nature-online/science-of-natural-history/wallace/index.html>> [Accessed 11 October 2013].

Stork, N.E. 1994. Inventories of biodiversity: more than a question of numbers. *In*: Forey, P.L., C.J. Humphries & R.I. Vane-Wright (eds.), *Systematics and Conservation Evaluation*. Clarendon Press (for the Systematics Association), Oxford, pp. 81-100.

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