

BIOGEOGRAPHY OF INDONESIAN FRESHWATER FISHES: CURRENT PROGRESS

Arief Aditya Hutama¹, Renny Kurnia Hadiaty², Nicolas Hubert^{*2,3}

¹Bogor Agricultural University, Faculty of Mathematics and Natural Science, Animal Bioscience,
Jl. Raya Darmaga, Bogor, Jawa Barat 16680, Indonesia

²Museum Zoologicum Bogoriense, Research Centre for Biology, Indonesian Institute of Sciences,
Jl. Raya Jakarta - Bogor Km 46, Cibinong 16911, Indonesia

³Institut des Sciences de l'Evolution, CNRS/IRD/UM2-UMR5554, Université de Montpellier,
Place Eugène Bataillon, 34095 Montpellier Cedex 05, France

*Corresponding author: nicolas.hubert@ird.fr

Received: 25 June 2015; Accepted: 2 December 2015

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).

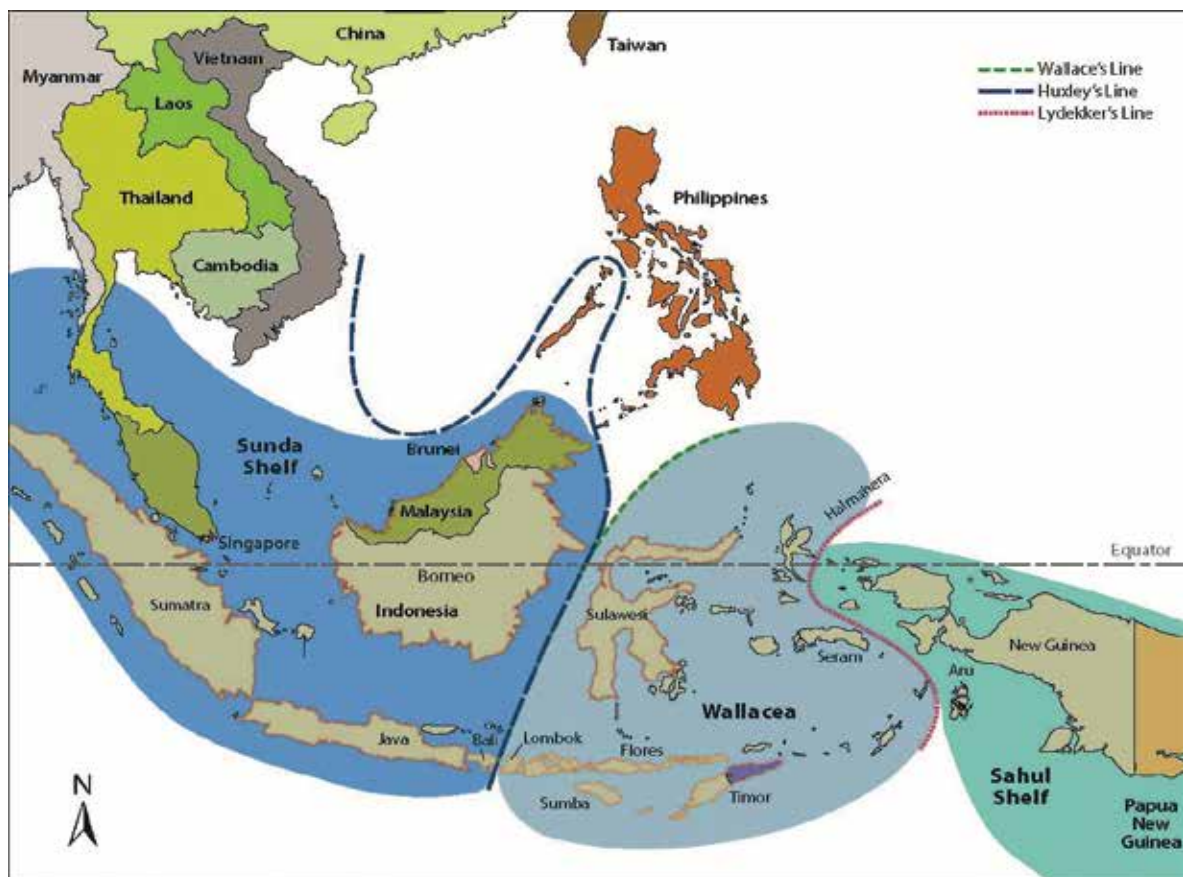


Figure 1. Map of the Indo-Australian Archipelago (IAA) indicating contemporary landmasses, straits, seas, arcs, and faunal lines. Major islands are labeled; different countries in the IAA are indicated by color (modified from Lohmann *et al.* 2011).

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.

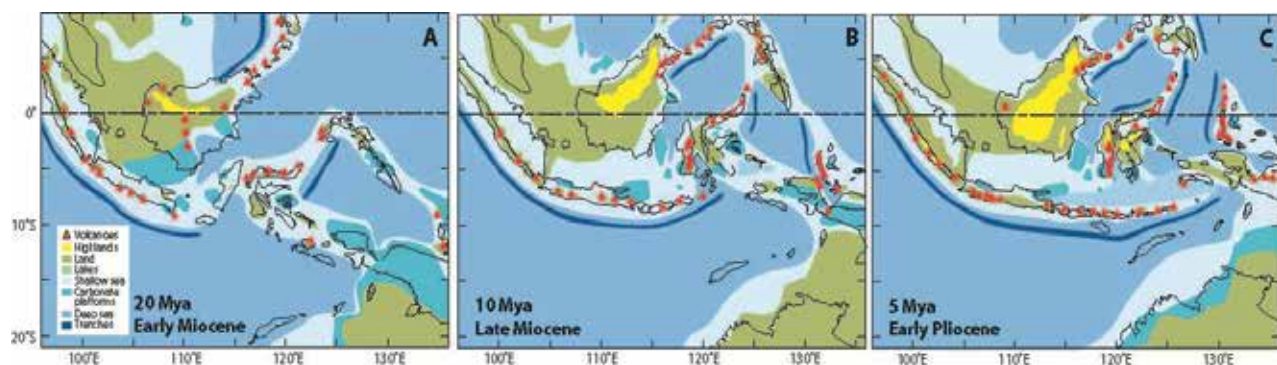


Figure 2. Cenozoic reconstructions of land and sea in the Indo-Australian Archipelago during the last 20 Mys(modified from Lohmann *et al.* 2011)

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

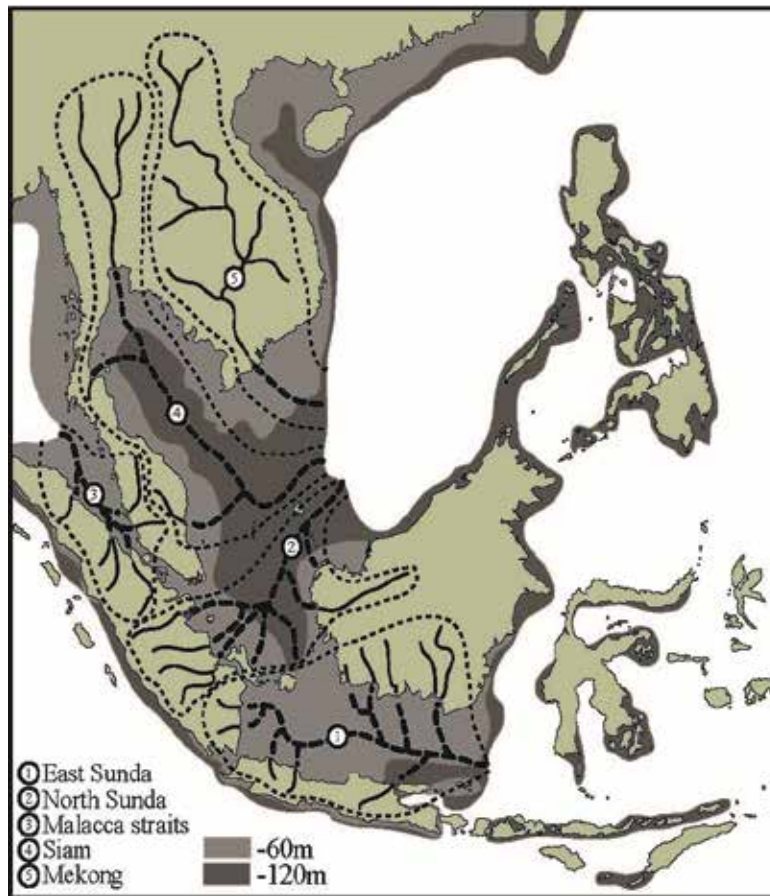


Figure 3. Emerged lands and palaeodrainages during the Pleistocene (modified from Woodruff, 2010).

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 everisi* 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.

ACKNOWLEDGMENTS

The authors would like to thank Dr. Siti Nuramaliati Prijono, Dr. Ir. Witjaksono, M.Sc., Mohammad Irham, M.Sc., Dr. Marlina Adriyani, Dr. Rosichon Ubaidillah, Dr. Daniel Lumbantobing, Dr. Hari Sutrisno and Sopian Sauri at Research Centre for Biology, Dr. Jean-Paul Toutain and Dr. Jean-François Agnèse from the 'Institut de Recherche pour le Développement' and Dr. Bambang Suryobroto at the Bogor Agronomy University for their support as well as the staff of the genetic lab at the Research Centre for Biology and Dr. Lukas Rüber, Dr. Fabian Herder, Dr. Philippe Keith for constructive discussions. The authors also thank Dr. Amir Hamidy and the anonymous reviewer for his insightful comments. This manuscript has ISEM number 2015-223 SUD.

REFERENCES

Allen, G.R. 1981. The "*maccullochi* species group" of rainbowfishes (Melanotaeniidae) with the description of *Melanotaenia papuae*, new species. *Revue Française d'Aquariologie Herpétologie* **8** (2): 47-56.

- Allen, G.R. 1991. Field Guide to the freshwater fishes of New Guinea. Christensen Research Institute. Singapore.
- Allen, G.R. & N.J. Cross 1982. Rainbowfishes of Australia & Papua New Guinea. T.F.H. Publications, New Jersey.
- Allen G.R. & M.V. Erdmann 2012. Reef fishes of the East Indies. Volumes I-III. Tropical reef research, Perth, Australia.
- Allen, G.R. & R.K. Hadiaty 2013. *Melanotaenia sneideri*, a new species of rainbowfish (Melanotaeniidae) from West Papua Province, Indonesia. *Aqua* **19**(3): 137-146.
- Allen, G.R., P.J. Unmack & R.K. Hadiaty 2014a. Three new species of rainbowfishes (Mela-noteniidae) from the Birds Head Peninsula, West Province, Indonesia. *Aqua* **20**(3): 139-158.
- Allen, G.R., R.K. Hadiaty, P.J. Unmack 2014b. *Melanotaenia flavipinnis*, a new species of Rainbowfish (Melanotaeniidae) from Misool island, West Papua Province, Indonesia. *Aqua* **20**(1): 35-52.
- Allen, G.R., P.J. Unmack & R.K. Hadiaty 2015. *Melanotaenia rubrivittata*, a new species of rainbowfish (Melanotaeniidae) from Northwestern Papua Province, Indonesia. *Fishes of Sahul*, **29** (1): 846-858
- Allen, G.R., R.K. Hadiaty, P.J. Unmack & M.V. Erdmann 2015. Rainbowfishes (Melanotaeniidae) of the Aru Islands, Indonesia with descriptions of five new species and redescription of *M. patoti* Weber and *M. senckenbergianus* Weber. *Aqua* **21** (2): 66-108.
- Aurich, H. 1935. Mitteilungen der Wallacea-Expedition Woltereck. Mitteilung XIV. *Fische II. Zoologischer Anzeiger*. **112** (7/8): 161-177.
- Bird, M.I., D. Taylor & C. Hunt 2005. Palaeoenvironments of insular Southeast Asia during the Last Pleistocene. Glacial Period: a savanna corridor in Sundaland?. *Quaternary Science Reviews* **24**: 2228-2242.
- De Bruyn, M., L. Rüber, S. Nylinder, B. Stelbrink, N. R. Lovejoy, S. Lavoué, T. Heok Hui, E. Nugroho, D. Wowor, P. K. L. Ng, M. N. Siti Azizah, T. Von Rintelen, R. Hall & G.R. Carvalho 2013. Paleodrainage basin connectivity predicts evolutionary relationships across three Southeast Asian biodiversity hotspots. *Systematic Biology* **62**: 398-410.
- Dodson, J.J., F. Colombani & P.K.L. Ng 1995. Phylogeographic structure in mitochondrial DNA of a South-east Asian freshwater fish, *Hemibagrus nemurus* (Sluroidei; Bagridae) and Pleistocene sea-level changes on the Sunda shelf. *Molecular ecology* **4**: 331-346.
- Froese, R. & D. Pauly 2011. Fishbase. Worldwide web electronic publication, <http://www.fishbase.org>, version (Accessed on 06/2011).
- Graf, J.A., F. Herder & R.K. Hadiaty 2015. A new species of rainbowfish (Melanotaeniidae), *Melanotaenia garylangei*, from western new guinea (papua province, Indonesia). *ANGFA, Fishes of Sahul* **29**(2): 870-881.
- Hadiaty, R.K. 1996. Keanekaragaman jenis ikan dan ekosistem nya di Taman Nasional Bogani-nani Wartabone, Sulawesi Utara. Laporan teknik penelitian dan pengembangan biota berdaya guna, Puslitbang Biologi – LIPI .
- Hadiaty, R.K. 2001. Fauna ikan di Cagar Alam Muara Kendawangan, Kalimantan Barat. *Jurnal Iktiologi Indonesia* **1**(2): 1-9.
- Hadiaty, R.K. 2005. Keanekaragaman Jenis ikan di Taman Nasional Gunung Leuser, Sumatra. *Jurnal Biologi Indonesia* **3**(9): 379- 388.
- Hadiaty, R.K. 2007. Kajian ilmiah ikan pelangi, *Marosatherina ladigesii* (Ahl 1936), Fauna endemik Sulawesi. *Berita Biologi* **8**(6): 473-479.
- Hadiaty, R.K. 2011a. Diversitas dan hilangnya jenis-jenis ikan di Sungai Ciliwung dan Sungai Cisadane. *Berita Biologi* **10**(4): 491-504.
- Hadiaty, R.K. 2011b. Diversitas dan kehilangan jenis ikan di danau-danau aliran Sungai Cisadane. *Jurnal Iktiologi Indonesia* **2**: 143-157.
- Hadiaty, R.K. 2012. Ikan. Dalam: Suhardjono, Y.R. & R. Ubaidillah (eds.), *Fauna Karst dan Gua Maros, Sulawesi Selatan*. LIPI Press.

- Hadiaty, R.K. 2014. Taxonomic study of the genus *Nemacheilus* (Teleostei: Nemacheilidae) in Indonesia. Doctoral thesis of science, <http://ir.lib.u-ryukyu.ac.jp/handle/123456789/29676> (Accessed on December 2014).
- Hadiaty, R.K. & D.J. Siebert 1998. Two new species of *Osteochilus* (Teleostei: Cyprinidae) from Sungai Lembang, Suag Balimbing Research Station, Gunung Leuser National Park, Aceh, Northwestern Sumatra. *Revue Francaise d'Aquariologie et Herpetologie* **25** (1-2): 1-4.
- Hadiaty, R.K. & M. Kottelat 2009. *Rasbora lacrimula*, a new species of cyprinid fish from eastern Borneo (Teleostei: Cyprinidae). *Ichthyological Exploration of Freshwaters* **20**(2): 105-109.
- Hadiaty, R.K. & S. Wirjoatmodjo 2003. Studi Pendahuluan: Biodiversitas dan Distribusi Ikan Endemik di Danau Matano, Sulawesi Selatan. *Jurnal Iktiologi Indonesia* **2**(2): 23-29.
- Hadiaty, R.K., Nyanti, L. Zainuddin & Suhitno 2003. Biodiversity and Distribution of the Fishes at Pa'Raye, Kayan Mentarang National Park, East Kalimantan, Indonesia. A joint expedition between Indonesia and Malaysia, Funded by ITTO, Dept. of Forestry, LIPI. Published in CD version.
- Hadiaty, R.K., S. Wirjoatmodjo, Sulistiono & M.F. Rahardjo 2004. Perjalanan dan koleksi ikan di Danau Mahalona, Lantoa dan Masapi, Sulawesi Selatan. *Jurnal Iktiologi Indonesia* **4**(1): 31-42
- Hadiaty, R.K., G.R. Allen & M.V. Erdmann 2012. Keanekaragaman jenis ikan Kaimana, Papua Barat. *Jurnal Zoo Indonesia* **21**(2): 35-42.
- Haffer, J. 1969. Speciation in Amazonian Forest Birds. *Science* **165**:131-137.
- Hall, R. 2012. Late Jurassic-Cenozoic reconstructions of the Indonesian region and the Indian ocean. *Tectonophysics* **570-571**:1-41.
- Hall, R. 2013. The palaeogeography of Sundaland and Wallacea since the late jurassic. *Journal of Limnology* **72**:1-17.
- Haq, B.U., J. Hardenbol & P.R. Vail 1987. Chronology of fluctuating sea levels since the triassic. *Science* **235**:1156-1167.
- Hays, J.D., J. Imbrie & N.J. Shackleton 1976. Variations in the Earth's Orbit: Pacemaker of the Ice Ages. *Science* **194**: 1121-1132.
- Herder, F., A.W. Nolte, J. Pfaender, J. Schwarzer, R.K. Hadiaty & U.K. Schliewen 2006. Adaptive radiation and hybridization in Wallace's dreamponds: evidence from sailfin silversides in the malili lakes of sulawesi. *Proceedings of the Royal Society, B* **273**: 2209-2217.
- Herder, F., J. Pfaender & U.K. Schliewen 2008. Adaptive sympatric speciation of polychromatic "roundfin" sailfin silverside fish in Lake Matano (Sulawesi). *Evolution* **62**: 2178-2195.
- Herder, F. & S. Chapuis 2010. *Oryzias hadiatyae*, a new species of ricefish (Atherinomorpha: Beloniformes: Adrianichthyidae) endemic to Lake Masapi, Central Sulawesi, Indonesia. *Raffles Bulletin of Zoology* **58**(2): 269-280.
- Herder, F., R.K. Hadiaty & A. Nolte 2012. Pelvic-fin brooding in a new species of riverine ricefish (Atherinomorpha: Beloniformes: Adryanichthyidae) from Tana Toraja, Central Sulawesi, Indonesia. *The Raffles Bulletin of Zoology* **60**(2): 267-476.
- Hoese, D.F., R.K. Hadiaty & F. Herder 2015. Review of the dwarf *Glossogobius* lacking head pores from the Malili lakes, Sulawesi, with a discussion of the definition of the genus. *Raffles bulletin of Zoology* **63**(1): 14-26.
- Hoffman, M., C. Hilton-Taylor, A. Angulo, M. Böhm, T.M. Brooks, S. H. M. Butchart, K.E. Carpenter, J. Chanson, B. Collen & N.A. Cox 2010. The impact of Conservation on the status of the world's vertebrates. *Science* **330**:1503-1509.
- Hope, G. S. 2007. Paleoecology and paleoenvironments of Papua. In: Marshall, A.J. & B. M. Beehler (eds.), *The ecology of Papua*. Periplus, Singapore.
- Hubert, N., Calcagno, V., Etienne, R., Mouquet & N. Mouquet 2015. Metacommunity speciation models and their implications for diversification theory. *Ecology Letters* **18**: 864-881.

- Hubert, N., Kadarusman, A. Wibowo, F. Busson, D. Caruso, S. Sulandari, N. Nafiqoh, L. Rüber, L. Pouyaud, J. C. Avarre, F. Herder, R. Hanner, P. Keith, and R. K. Hadiaty 2015. DNA barcoding Indonesian freshwater fishes: challenges and prospects. *DNA Barcodes* **3**: 144-169.
- Ivantsoff, W. & G. R. Allen 1984. Two new species of *Pseudomugil* (Pisces: Melanotaeniidae) from Irian Jaya and New Guinea. *Australian Zoologist* **21**(5): 479-489.
- Kadarusman, Sudarto, E. Paradis & L. Pouyaud 2010. Description of *Melanotaenia fasinensis*, a new species of rainbowfish (Melanotaeniidae) from West Papua, Indonesia with comments on the rediscovery of *M. ajamaruensis* and the endangered status of *M. parva*. *Cybium* **34**(2): 207-215.
- Kadarusman, Sudarto, J. Slembrouck & L. Pouyaud 2011. Description of *Melanotaenia salawati*, a new species of rainbowfish (Melanotaeniidae) from Salawati Island, West Papua, Indonesia. *Cybium* **35** (3): 223-230.
- Kadarusman, R.K. Hadiaty, G. Segura, G. Setiawibawa, D. Caruso & L. Pouyaud. 2012. Four new species of Rainbowfishes (Melanotaeniidae) from Arguni Bay, West Papua, Indonesia. *Cybium* **36**(2): 362-382.
- Kadarusman, N. Hubert, R.K. Hadiaty, Sudarto, E. Paradis & L. Pouyaud 2012. Cryptic diversity in Indo-Australian rainbowfishes revealed by DNA Barcoding: implications for conservation in a biodiversity hotspot candidate. *PLoS One* **7**: e40627.
- Keith, P., G.R. Allen, C. Lord & R.K. Hadiaty 2011. Five new species of *Sicyopterus* (Teleostei: Gobioidi: Sicydiinae) from Papua New Guinea & Papua. *Cybium* **35**(4): 299-318
- Keith P. & R.K. Hadiaty 2014. *Stiphodon annieae*, a new species of freshwater goby from Indonesia (Gobiidae). *Cybium* **38**(4): 267-272.
- Kottelat, M. 1989. Zoogeography of the fishes from Indochinese inland water with annotated checklist. *Bulletin Zoologisch Museum Universiteit Van Amsterdam* **12**:1-55.
- Kottelat, M. 1990a. Sailfin silversides (Pisces: Telmatherinidae) of Lakes Towuti, Mahalona and Wawontoa (Sulawesi, Indonesia) with descriptions of two new genera and two new species. *Ichthyological Exploration of Freshwaters* **1**: 35-54.
- Kottelat, M. 1990b. The ricefishes (Oryziidae) of the Malili Lakes, Sulawesi, Indonesia, with description of a new species. *Ichthyological Exploration of Freshwaters* **1**(2): 151-166.
- Kottelat, M. 1991. Sailfin silversides (Pisces: Telmatherinidae) of Lake Matano, Sulawesi, Indonesia, with descriptions of six new species. *Ichthyological Exploration of Freshwaters* **1**:321-344.
- Kottelat, M. 2013. The fishes of the inland waters of Southeast Asia: a catalog and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries. *The Raffles Bulletin of Zoology Supplement* **27**: 1-663.
- Kottelat, M., A. J. Whitten, S. R. Kartikasari, and S. Wirjoatmodjo 1993. Freshwater fishes of western indonesia and sulawesi. Periplus editions, Singapore.
- Kottelat, M. & A. J. Whitten 1996. Freshwater fishes of Western Indonesia and Sulawesi: additions and corrections. Periplus, Hong Kong, 8 pp.
- Kottelat, M. & E. Widjanarti 2005. The fishes of Danau Sentarum National Park and the Kapuas Lakes area, Kalimantan Barat, Indonesia. *Raffles Bull. Zool. Supplement* **13**: 139-173.
- Lamoureux, J. F., J. C. Morrison, T. H. Ricketts, D. M. Olson, E. Dinerstein, M. McKnight, & H. H. Shugart 2006. Global tests of biodiversity concordance and the importance of endemism. *Nature* **440**: 212-214.
- Larson, H. K. & M. Kottelat 1992. A new species of *Mugilogobius* (Pisces: Gobiidae) from Lake Matano, central Sulawesi, Indonesia. *Ichthyological Exploration of Freshwaters* **3**(3): 225-234.
- Larson; H.K., M.F. Geiger, R.K. Hadiaty & F. Herder 2014. *Mugilogobius hitam*, a new species of freshwater goby (Teleostei: Gobioidi: Gobiidae) from Lake Towuti, central Sulawesi, Indonesia. *Raffles Bulletin of Zoology* **62**: 718–725.

- Lohman, K., M. De Bruyn, T. Page, K. Von Rintelen, R. Hall, P. K. L. Ng, H.-T. Shih, G. R. Carvalho & T. von Rintelen 2011. Biogeography of the Indo-Australian archipelago. *Annual Review of Ecology, Evolution and Systematics* **42**:205-226.
- McConnell, S.K.J. 2004. Mapping aquatic faunal exchanges across the Sunda shelf, South-East Asia, using distributional and genetic sets from the cyprinid fish *Barbodes gonionotus* (Bleeker, 1850). *J. Nat. Hist.* **38**(5): 651-670.
- McPeck, M.A. 2008. The ecological dynamics of clade diversification and community assembly. *American Naturalist* **172**:e270-e284.
- Mokodongan, D.F., R. Tanaka & K. Yamahira 2014. A New Ricefish of the Genus *Oryzias* (Beloniformes, Adrianichthyidae) from Lake Tiu, Central Sulawesi, Indonesia. *Copeia* **2014**(3): 561-567.
- Myers, A.A. & P.S. Giller 1988. Process, Pattern and Scale in Biogeography. Pages 3-12 in A. A. Myers and P. S. Giller, editors. *Analytical Biogeography*. Chapman & Hall, London.
- Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca & J. Kent 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853-858.
- Nelson, G.J. & N. Platnick 1981. *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press, New York.
- Nguyen, T.T.T., U. Na-Nakorn, S. Sukmanomon & C. ZiMing 2008. A study on phylogeny and biogeography of mahseer species (Pisces: Cyprinidae) using sequences of three mitochondrial DNA gene regions. *Molecular Phylogenetics and Evolution* **48**: 1223-1231.
- Nores, N. 1999. An alternative hypothesis for the origin of Amazonian bird diversity. *Journal of Biogeography* **26**(3): 475-485.
- Nores, N. 2004. The implications of tertiary and quaternary sea level rise events for avian distribution patterns in the lowlands of northern south america. *Global Ecology and Biogeography* **13**: 149-161.
- Nugraha, M. F. I., Kadarusman, N. Hubert, J. C. Avarre, R. K. Hadiaty, J. Slembrouck, O. Carman, Sudarto, R. Ogistira & L. Pouyaud 2015. Eight new species of Rainbowfishes (Melanotaeniidae) from the Bird's Head Region, West Papua, Indonesia. *Cybium* **39**: 99-130.
- Olden, J., M. Kennard & F. Leprieur 2010. Conservation biogeography of freshwater fishes: recent progress and future challenges. *Diversity and distribution* **16**: 496-513.
- Parenti, L.R. 2008. A phylogenetic analysis and taxonomic revision of ricefishes. *Oryzias* and relatives (Beloniformes, Adrianichthyidae). *Zoological Journal of the Linnean Society* **154**: 494-610.
- Parenti, L. R. & M. C. Ebach 2013. Evidence and hypothesis in biogeography. *Journal of Biogeography* **40**: 813-820.
- Parenti, L. R. & R. K. Hadiaty 2010. A new, remarkably colorful, small ricefish of the genus *Oryzias* (Beloniformes, Adrianichthyidae) from Sulawesi, Indonesia. *Copeia* **2010**: 268-273.
- Parenti, L.R. & B. Soeroto 2004. *Adrianichthys roseni* and *Oryzias nebulosus*, two new ricefishes (Atherinomorpha: Beloniformes: Adrianichthyidae) from Lake Poso, Sulawesi, Indonesia. *Ichthyological Research* **51**(1): 10-19.
- Parenti, L.R., R.K. Hadiaty, D. Lumbantobing & F. Herder 2013. Two new ricefishes of the genus *Oryzias* (Atherinomorpha: Beloniformes: Adrianichthyidae) augment the endemic freshwater fish fauna of southeastern Sulawesi, Indonesia. *Copeia* **2013**: 403-414.
- Pfaender, J., F.W. Miesen, R.K. Hadiaty & F. Herder 2011. Adaptive speciation and sexual dimorphism contribute to diversity in form and function in the adaptive radiation of Lake Matano's sympatric roundfin sailfin silversides. *Journal of Evolutionary Biology* **24**: 2329-2345.
- Pfaender, J., U.K. Schliewen & F. Herder 2010. Phenotypic traits meet patterns of resource use in the radiation of "sharppin" sailfin silverside fish in Lake Matano. *Journal of Evolutionary Ecology* **24**: 957-974.

- Pouyaud, L., Sudarto & E. Paradis 2009. The phylogenetic structure of habitat shift and morphological convergence in Asian *Clarias* (Teleostei, Siluriformes: Clariidae). *Journal of Zoological Systematics and Evolutionary Research* **47**: 344-356.
- Prance, G.T. 1982. A review of the phytogeographic evidences for Pleistocene climate changes in the Neotropics. *Annals of the Missouri Botanical Garden* **69**: 594-624.
- Ricklefs, R.E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* **7**: 1-15.
- Roberts, T.R. 1989. The freshwater fishes of Western Borneo (Kalimantan Barat, Indonesia). California Academy of Sciences.
- Schwarzer, J., F. Herder, B. Misof, R.K. Hadiaty & U.K. Schliewen 2008. Gene flow at the margin of Lake Matano's adaptive sailfin silverside radiation: Telmatherinidae of River Petea in Sulawesi. *Hydrobiologia* **615**: 201-213.
- Tan, H.H. & M. Kottelat 2009. The fishes of Batang Hari drainage, Sumatra, with descriptions of six new species. *Ichthyol. Explor. Freshwat.* **20**:13-69.
- Tittensor, D.P., C. Mora, W. Jetz, H.K. Lotze, D. Ricard, E. Vanden Berghe & B. Worm 2010. Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**: 1098-1103.
- Verstappen, H.T. 1975. On palaeo climates and landform development in Malesia. *Modern Quaternary Research in Southeast Asia* **1**: 3-35.
- Weber, M. 1913. Neue Beiträge zur Kenntnis der Süßwasserfische von Celebes. *Bijdragen tot de Dierkunde* **1913**: 197-213.
- 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 refugium-phase biodiversity. *Biodiversity and Conservation* **19**: 919-941.