Contributions to Mammalogy and Zooarchaeology of Wallacea

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Wallacean Mammalogy and Zooarchaeology: Remembrances and a Renaissance

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The richness of life is not distributed haphazardly across the globe, but instead exhibits profound, non-random patterns. Numbers of species of insects, trees, and frogs, for example, abound in tropical localities, like in Brazil or the Congo, but not in Siberia or the Yukon. Species uniqueness, or endemism, peaks on large, long-isolated islands, like Madagascar or the Philippines. And different continents often have profoundly different assemblages of organisms. These types of observations regarding major patterns in the distribution of life, and their implied histories, formed the original foundation of the science of biogeography. Among the most important developers of this science was Alfred Russel Wallace, one of the architects of evolutionary biology.

One of Wallace's many fundamental biogeographic insights was the realization that the fauna of the "Malay Archipelago", extending from the Malay Peninsula to New Guinea, much of which is now encompassed within the modern nation of Indonesia, can be demarcated into zones of marked Asian and Australian character. (This was an insight based on firsthand fieldwork, collecting biological specimens for museums.) These zones of regional influence merge and meld along the island chain, but nevertheless a particularly sharp demarcation runs between the islands of Borneo and Sulawesi in the north, and Bali and Lombok, in the south. This demarcation is now known as the "Wallace Line" (Wallace, 1869, 1876; Fig. 1), and others later built on these Wallacean insights to identify additional "lines" of biogeographic significance in the archipelago (Fig. 1). We now understand more fully that the profound distinctions in the archipelago result from differential histories of continental connection and movement, with the islands of Sumatra, Java, and Borneo being part of Sundaland-the Asian continental shelf, and New Guinea an extension of the Australian, or Sahulian, continent. The area in between consists of the large island of Sulawesi and the oceanic archipelagos known as the Lesser Sundas (Nusa Tenggara) and the Moluccas (Maluku). These long-isolated islands constitute a geologically complex region that serves both as a zone of faunal transition between the two great continental faunas, as well as a realm unto itself with remarkable endemism. Today this region is called Wallacea by biogeographers, and it is rich in animal life, including mammals.

Most work on mammals in the Wallacean region has focused on Sulawesi, the largest and most centrally located island in the zone. Initial biological exploration on the island demonstrated that the fauna was a mix of mammals of both Asian and Australian genesis, with the island's forests home to native bats, rats, squirrels, shrews, monkeys, tarsiers, civets, pigs, and bovids, as well as marsupialsarboreal possums called cuscuses. Early, sporadic work by European collectors and taxonomists gave way to more systematic expeditionary collecting by British and American collectors in the twentieth century (Musser et al., 2010). This work illuminated the remarkable diversity and endemism of Sulawesi's mammals and led in particular to proliferation in knowledge of the island's rich native murine rodent fauna (e.g., Musser, 1969, 1982, and many similar contributions). From the mid twentieth century, palaeontological excavations on Sulawesi also began to reveal aspects of the deeper Quaternary history of the island's mammals, including the past presence of now-extinct megafauna such as proboscideans and large pigs (Hooijer, 1958, 1975, and many other contributions). This was accompanied by other discoveries of extinct megafauna on islands in Nusa Tenggara, including Sumba, Flores, and Timor, especially of species of the proboscidean genus Stegodon (Hooijer, 1975).

Much better known than the mammals of Wallacea are its birds (Rheindt et al., 2020), which are more colourful, more vocal, easier to find by day, and most importantly were more economically lucrative targets for early natural history collectors working in the region (Coates & Bishop, 1997). Wallacean fruit-eating bats (family Pteropodidae), from tiny blossom bats to massive flying foxes, were commonly collected by early European traders and expeditioners alongside birds and are thus the mammals best represented in historical museum collections. Because of this, much of their distributional patterns of occurrence became reasonably well documented by the turn of the twentieth century (Andersen, 1912) and more firmly fleshed out by the end of the century (Corbet & Hill, 1992; Flannery, 1995). Nevertheless, much remains to be published about the taxonomy of Wallacea's fruit-eating bats, and these species have been largely untouched by the revolution in systematics enabled by integrative approaches involving both molecular phylogenetic and modern morphometric methodologies.

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Figure 1. Regional map of Wallacea, showing the Huxley, Wallace and Lydekker lines. The extent of the continental shelves at 65 ka (accounting for uplift) is indicated by dark grey shading. This map is a modified version of the map appearing in Kealy *et al.* (2018) and has been edited and reproduced with permission.

(Taxonomic revision in these species forms the basis of another volume, currently in preparation for publication.)

Outside Sulawesi and apart from fruit-eating bats, mammals in Wallacea have remained less well known to science. It is these species, represented especially by murine rodents and insectivorous bats, that form the subject matter of many of the contributions in this volume. Our reports in this volume are drawn mainly from two streams of work. One is from modern mammal specimens collected during fieldwork in the Moluccas and Nusa Tenggara since the Second World War, including major initiatives led by the eminent biologist Boeadi in Indonesia and the collecting efforts of Tim Flannery and Darrell Kitchener from Australian museums, along with more recent efforts (see below). The other involves important archaeological excavations undertaken since the mid twentieth century, and especially since the 1990s, on the islands of Timor, Flores, and Morotai, especially by Indonesian and Australian archaeologists including Thomas Sutikna, Rokus Due Awe, Michael Morwood, Peter Bellwood, and Sue O'Connor, among others. This work has taken on greater interdisciplinary interest as archaeological discoveries have increasingly shown the importance of Wallacean islands in hominin and modern human history, and particularly since the discovery of the endemic hominin Homo floresiensis on Flores (Brown et al., 2004; Morwood et al., 2004). Joint insights from modern mammalogy and the study of zooarchaeological remains illuminating past mammal faunas form an especially powerful approach for understanding the ecology and evolution of Wallacean mammals across deep time and constitute a central motivation for the studies in this volume.

Across this deep history, the islands of Wallacea have been impacted by human activities, resulting in removal of rainforest, major land-use changes, hunting of native and endemic wildlife, and the introduction of non-native species like commensal rodents, livestock, and crops. More recently, and especially today, these impacts have taken on an industrial dimension, with logging, fires, mining, and other large-scale environmental perturbations transforming these islands in the face of growing human populations and increasing economic demands. Anthropogenic climate change, with its myriad concomitant environmental effects, is already underway globally, and its changes will be felt across the world, including in Wallacea, especially in the decades ahead. Clearer understanding of past environmental changes and impacts, and the ongoing effects of these modern pressures, are fundamental to identifying which Wallacean mammal species are most in danger of extinction and in need of conservation measures to ensure their survival (Monk *et al.*, 1997; Aplin & Helgen, 2010). There is much still to discover, and corresponding urgency in this work.

Remembrances

We dedicate this Special Issue to the memory of two close colleagues from Indonesia, both giants in their fields, who have passed away in recent years: the eminent zoologist Bapak Boeadi (1935–2021) and the eminent zooarchaeologist Bapak Rokus Due Awe (1942–2015).

Boeadi was born on 13 March 1935 and passed away on 2 August 2021. A mammalogist and herpetologist from East Java, Boeadi was the most renowned Indonesian zoologist of his generation. He published extensively on the vertebrate fauna of the entire Indonesian archipelago, produced important taxonomic revisions, and named many taxa. These include, among mammals, the rodent genus *Komodomys*, the marsupials *Dendrolagus mbaiso* and *Phalanger alexandrae*, the murine rodent *Rattus timorenesis*,



Figure 2. Boeadi (standing), with Tim Flannery (left) and other colleagues in the field, September 1992, on Supiori Island in Cendrawasih Bay (Papua Province, Indonesia)—home to the endemic giant rat *Uromys boeadii*.

and the pteropodid bat *Megaerops kusnotoi* (Musser & Boeadi, 1980; Kitchener *et al.*, 1993; Flannery *et al.*, 1997; Flannery & Boeadi, 1995; Hill & Boeadi, 1978), as well as a variety of frogs and reptiles. Various species have been named in his honour, including the Indonesian endemic mammals *Uromys boeadii*, a giant rat from Biak-Supiori (Fig. 2) in Cenderawasih Bay, western New Guinea (Groves & Flannery, 1994), and *Hipposideros boeadii*, a leaf-nosed (or roundleaf) bat from Sulawesi (Bates *et al.*, 2007).

Boeadi worked extensively with many zoologists from outside Indonesia, including Tim Flannery, who partnered with him on a series of expeditions across Maluku and western New Guinea during the 1990s. In remembering Boeadi, Flannery writes:

It was my great good fortune, on my first visit to Indonesia, to encounter Boeadi. It was in the days before email, and I had decided to drop in to the Zoology Museum in Bogor on my way home to Sydney from researching Europe. When I asked at the museum's front desk to meet someone from the mammal section, Boeadi came to the desk and greeted me. I had arrived around lunchtime, and when I suggested that we could go somewhere for lunch he instantly agreed, leading me into a warren of tiny shops in the market opposite the Museum's main gate. We settled into a dimly-lit and distant corner of a Chinese restaurant where he ordered a dish of pork, explaining that he had resorted to this out-of-the-way place so that none of his workmates might see him.

Boeadi was one of the sunniest and most enthusiastic people I ever met, and he cheerfully shared his life story with me. He had grown up in East Java, and by the time he was in his early teens WW2 was finished and the Indonesians were fighting the Dutch for independence. At the age of 14 Boeadi had become an itinerant cigarette seller, a profession that allowed him to play a role in the struggle for independence. Lugging his supply of cigarettes, he would slip through the Dutch lines with messages for the Indonesian freedom fighters on the other side. That year was also the year of Boeadi's circumcision, a ceremony which in Java is done at adolescence. Boeadi was determined to avoid having the operation done in the village with the other boys. So he saved the money he earned by selling cigarettes to pay for a circumcision done in a hospital, under anesthetic.

As we ate lunch that day, Boeadi also spoke of his career as a wildlife researcher—of trapping Sumatran rhinos and tigers for various breeding programs, of sleeping in remote jungle trees as tigers stalked below, and of climbing to the eternal snows of Mt Jaya in Papua as part of the 1963 military expedition sent to climb to the highest in Indonesia. He still had the letter from President Suharto (which he later showed me) requesting him to instruct the soldiers in jungle survival. He vividly recalled teaching these young, mostly Muslim men how to catch, kill and cook snakes and other wild sources of food.

We had soon set up a partnership that allowed us to do groundbreaking fieldwork in Maluku Utara and Papua. It was a period of relative freedom of travel, though tensions were prone to break out, especially during the First Gulf War, which some Muslims interpreted as an attempt by the West to take over Muslim heartlands. Without Boeadi's sage advice and care in mediating with bureaucrats and villagers, the fieldwork would have been impossible.

By the time we were doing our fieldwork Boeadi had been training researchers and conducting fieldwork throughout Indonesia for decades. He was held in the highest esteem, for not only was he the "guru" of many wildlife officials, but he was regarded as the grand old man of Indonesian mammalogy.

My fieldwork in Indonesia would have simply been impossible without Boeadi. He facilitated the granting of research permits, acquired the necessary surat jalans to work in eastern Indonesia, and obtained export permits. He was also an expert field hand who was never happier than when in the forest, cooking a delicious bush meal or skinning and preparing specimens. He was also a wonderful companion whose never-failing sense of humour made even the most difficult of circumstances bearable.

Boeadi contributed to a number of jointly authored papers, among which was one the naming a spectacular new tree-kangaroo from Papua, Dendrolagus mbaiso. The Australian Museum had borrowed the holotype to allow for its description, and when I returned it to the Zoology Museum in Bogor, Boeadi had organized a small ceremony which included my meeting the Director of the institution, an honour I had not had before. It was perhaps Boeadi's way of ensuring that my reputation as a friend of the Bogor Museum would endure beyond his time.

When our fieldwork ceased, it became difficult to remain in contact. Boeadi's wife Emma passed away, and he was cared for by an aged housekeeper who spoke only Sundanese. She also had few teeth, which made her difficult to understand on the phone. But we continued to exchange Christmas cards for many years. Boeadi was one of the most important, and most generous colleagues I've ever had. I miss him greatly.—Tim Flannery

The other colleague we remember with this Special Issue is Rokus Due Awe. Rokus was born in Flores and spent a lifetime dedicated to archaeological excavation and zooarchaeological investigation in Indonesia. From the 1960s onward, Rokus was involved in excavations at the world-renowned fossil sites in the So'a Basin and at Liang Bua on Flores. Liang Bua eventually was to yield evidence of a rich vertebrate fauna, including many species of extinct endemic rats, as well as Homo floresiensis, for which Liang Bua is the type locality (Brown et al., 2004). Rokus was the first person to correctly identify the original specimens of Homo floresiensis, and he coauthored the major papers documenting these finds. His life and contributions are memorialized further by Veatch et al. (2023) in this volume in their description of a new genus and species of gigantic "shrew rat" from Flores named in his honour. This subfossil rat, thus far known only from Liang Bua deposits, is ecomorphologically very different from any rodent previously named, characterized by a large and relatively robust jaw but miniscule molars.

A Wallacean mammal "renaissance"?

During the last decade or so, mammalogical work in Wallacea has seen a spurt in activity. This is especially true in Sulawesi, where this spurt has been energized by new fieldwork and integrative systematic revisions of small mammals, led especially by Jacob Esselstyn, Kevin Rowe, Anang Achmadi, and colleagues-enabled too, until recently, by the late Guy Musser (e.g., Esselstyn et al., 2012, 2015; Musser et al., 2010). This has led to the documentation of a remarkable number of new species and genera of Sulawesian mammals (e.g., Esselstyn et al., 2021). These taxonomic descriptions have demonstrated not only that Wallacean faunas remain incompletely inventoried, but also, as in the discovery of remarkable new genera like Hyorhinomys and Paucidentomys, that major new ecomorphological "ways of being a mammal" are still out there to be documented. (This type of documentation is continued in this volume especially with the description of a new giant rat genus from Flores: Veatch et al., 2023). Much has also been happening outside Sulawesi. For example, until relatively recently, the nonvolant mammals of the Moluccas were known mainly by a single expeditionary effort undertaken on Seram in 1920 (Thomas, 1920); many Moluccan islands are woefully unexplored for their biodiversity, including for mammals. One of the islands essentially unexplored by mammalogists previously is Kofiau, the subject of mammalogical surveys reported by Wiantoro et al. (2023) in this volume. Kofiau is biogeographically important in being an oceanic island with both Papuan and Moluccan zoogeographic affinities. Only one species of mammal was previously recorded from the island, a number now brought to 20 species by surveys reported in the paper. Fabre et al. (2023) in this volume also summarise results from recent fieldwork from Moluccan islands, including Obi, Halmahera, and Buru. This work has documented several new species of Rattus, which are presented within a comprehensive integrative taxonomic review of Moluccan Rattus. This same fieldwork has also documented previously overlooked taxa and populations in other Moluccan rodent genera, including Melomys and Halmaheramys, reported in earlier papers (Fabre et al., 2013, 2017, 2018). Mammalogical inventories of islands in Nusa Tenggara also remain incomplete, and Parnaby & Helgen

(2023) in this volume report additional important fieldwork from Timor-Leste, reporting the re-discovery of the long-eared bat genus *Nyctophilus* for the first time after a hiatus of 200 years. This discovery is reported in the context of revisionary work on the genus *Nyctophilus*, an Australo-Papuan genus that just penetrates Wallacea. All of the papers in this volume emphasize the importance of new and ongoing fieldwork in the region toward better understanding Wallacean faunas, their deeper histories, and their connections to Asia and Australia.

An increasing motivation for studying wild mammals, and to inventory mammalian biodiversity, is to understand the parasites and pathogens they may harbour, especially where those may be of significance to human and veterinary welfare. Research on the role played by mammals as vectors of infectious disease has increased worldwide since the Second World War and has taken on new urgency in the 21st century as the importance of understanding zoonotic pathogens, including those with potential for pandemic impact, has become clearer (Cook et al., 2020). One paper in this volume, by Mursyid et al. (2023) provides the most comprehensive view yet obtained for the occurrence of trypanosome parasites in Wallacean mammals, based on sampling of hundreds of specimens of bats, shrews, rats, and squirrels across an elevational gradient in central Sulawesi. This provides an important foundation for work of this kind, which is only beginning in the region. Very little is known about parasites and pathogens of species elsewhere in the Moluccas, especially in rodents, but the recent discovery of new virus of medical and veterinary interest in a previously overlooked Moluccan murine, Melomys sp. cf. burtoni from Halmahera (Alfano et al., 2016), indicates the importance of embarking on this work with greater concentration.

The modern faunas of Wallacea, documented by fieldwork in existing and historical habitats, are framed in important resolution by studies of the deep past, and zooarchaeology is a field that has recently burgeoned in visibility in Wallacea recently. In these studies, it has been rats, which numerically dominate the material from some of the most important excavation sites, that take centre stage. In this volume, Aplin et al. (2023) and Veatch et al. (2023) document newly described species of murine rodents from Morotai and Flores, respectively, in the context of important taxonomic and ecomorphological comparisons. This brings to completion the naming of the various rat taxa previously identified in Morotai and Flores subfossil deposits, complementing other recent work from Sumba (Turvey et al., 2017) and Timor (Aplin & Helgen, 2010). Most of the subfossil rats of Timor, however, remain unnamed-a major unfinished task in Wallacean zooarchaeology, and the subject of another forthcoming revision. Taxonomic documentation of these small mammal faunas enables better understanding of insular patterns of evolution and extinction and the spread for commensal and invasive species. It also allows for clearer understanding of past environments and ecological associations in the past, considered increasingly valuable to studies in palaeoanthropology and archaeology (see Louys et al., 2023; and Veatch et al., 2023, in this volume). Indeed, Wallacea has increasingly drawn focal attention in studies of deep human history with the firm demonstration that hominins have histories extending many hundreds of thousands of years, or longer, on islands like Flores and Sulawesi (e.g., Brumm et al., 2016; van den Bergh et al. 2016), and that various Wallacean islands have been important in the history of modern humans, such as for migration (Kealy et al., 2018), cultural expression (Brumm et al., 2021), and genomic introgression (Teixeira et al., 2020).

In our view, scientific explorations of mammal faunas in Wallacea, both modern and ancient, have only just begun—all while we move into a world in which their future is fraught. Perhaps the most important insight from this volume is the urgent need to undertake fieldwork to understand if various species that have not been documented in decades (like the two new species of *Rattus* described here from Taliabu) or much longer (like new subfossil species described here for *Myctophilus* on Timor. Hopefully some of them are still extant, giving us a chance to better enable

their long-term conservation in a changing world. Overall, we take great joy in delivering these current contributions to knowledge of mammalogy and zooarchaeology in the region, in collaboration with many excellent colleagues, and we remember others that have come before us and have now departed the stage.

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Corrigendum

The photographer of Figure 2 was not acknowledged in the work: Helgen, K.M., and R. K. Jones. 2023. Wallacean mammalogy and zooarchaeology: remembrances and a renaissance. *Records of the Australian Museum* 75(5): 623–628. https://doi.org/10.3853/j.2201-4349.75.2023.1780

The figure caption should read.

Figure 2. Boeadi (standing), with Tim Flannery (left) and other colleagues in the field, September 1992, on Supiori Island in Cendrawasih Bay (Papua Province, Indonesia)—home to the endemic giant rat *Uromys boeadii*. (photo: Alexandra Szalay).

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