



Mammals of south-east Asian islands and their Late Pleistocene environments

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Abstract

Aim The environments that existed in south-east Asian islands during the last glacial are poorly known, limiting our understanding of mammalian biogeography in the region. The objective of this research is to investigate the ecological characteristics of mammal faunas on small islands, and to see whether the habitat requirements of the species in those faunas can be used to deduce the vegetation types that existed on islands before becoming isolated by rising sea levels.

Location The maps presented here cover the small islands of tropical south-east Asia, including the Burmese, Thai and Cambodian islands in the north, the islands off the coast of west Sumatra in the west, the islands around Java in the south, and the islands off the east coast of Borneo in the east, including the Philippine islands of Palawan and those in the Sulu Archipelago.

Methods The presence records of mammal species on 215 small islands in the region were compiled, and the habitat requirements for each of these species was assessed (species that had probably been introduced by humans were excluded from the analysis). For each island location (longitude and latitude), maximum altitude of the island, total area, depth to nearest land, distance to nearest island, and distance to nearest mainland were assessed. Geographical and statistical analyses were used to investigate patterns of mammalian habitat requirements.

Results The geographical analysis showed that forest-dependent species, i.e. species that are only found in primary forest (lowland and mountainous), appear to be concentrated on islands off west Sumatra, in the Lingga and Riau Archipelagos, around Palawan, and around Bunguran Island; they are absent mostly from the islands of the Java Sea, those off the east coast of eastern Borneo, from most islands in the Sunda Strait, several islands in the northern South China Sea, and from all islands off the west coast of the Malay/Thai Peninsula and in the Gulf of Thailand. Species that generally occur outside primary forest, that is those in secondary forest, gardens, plantations and open areas mostly occurred on islands where the forest-dependent species were absent. The statistical analysis showed that latitude and size of islands were important factors that determined the absence and presence of forest-dependent species on small islands.

Main conclusions The data suggest that during the last glacial there were several areas in the Sundaic region that remained forest covered: west of Sumatra, north-west of Borneo, the Malacca Straits and around Palawan. Other areas may have been covered by more open vegetation types like tree savanna, or open deciduous forest: on and to the east of the Malay/Thai Peninsula, the Java Sea area, including the Sunda Strait, and eastern Borneo.

Keywords

Biogeography, mammal, palaeoenvironment, Pleistocene, sea levels, south-east Asia.

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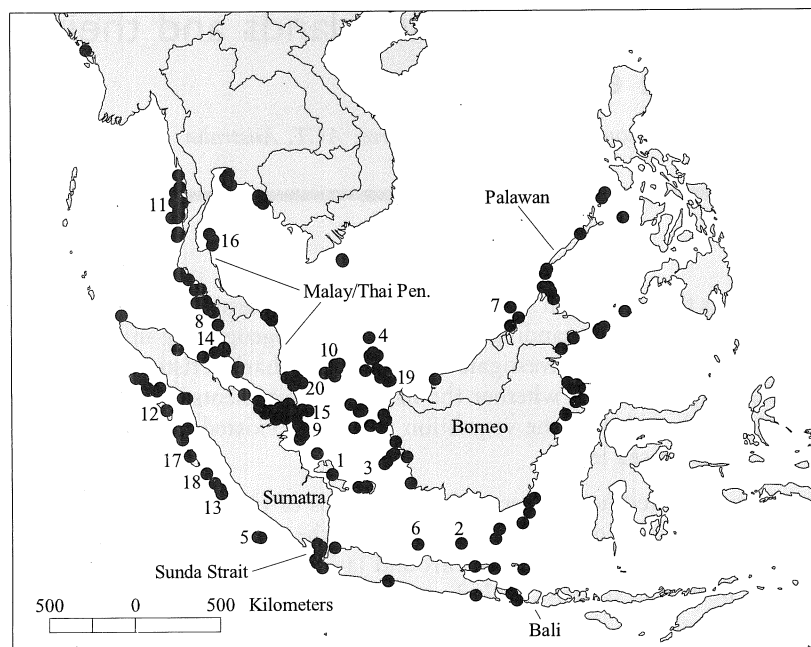


Figure 1 Islands for which mammal faunas were assessed. Numbers refer to the following islands: (1) Bangka; (2) Bawean; (3) Belitung; (4) Bunguran; (5) Enggano; (6) Karimun Jawa; (7) Labuan; (8) Langkawi; (9) Lingga Archipelago; (10) Matak/Siantan; (11) Mergui Archipelago; (12) Nias; (13) Pagai Islands; (14) Penang; (15) Riau Archipelago; (16) Samui; (17) Siberut; (18) Sipura; (19) Sirhassen; and (20) Tioman.

INTRODUCTION

The south-east Asian island (see Fig. 1) is among the richest in the world in terms of its biodiversity (Myers *et al.*, 2000), mainly because of its dynamic geological past (Holloway & Hall, 1998), relatively stable climatic conditions (Gathorne-Hardy *et al.*, 2002) and associated rapid speciation processes (e.g. Whitmore, 1987). The zoogeography of this region is complicated (e.g. Heaney, 1984, 1986; Ruedi, 1996), and after more than a century of research and debate among scientists, many biogeographical questions remain unanswered. Many of these questions are related to the changing sea levels during the Pleistocene and concomitant land bridges. This is especially the case in Sundaland, the area covering the zoogeographical unit of the Sunda Shelf, i.e. the Malayan Peninsula south of the Isthmus of Kra, the larger islands of Sumatra, Borneo, Palawan, Java, Bali and many smaller islands (see Fig. 1). During the last glacial maximum (LGM), when sea levels were much lower than today, all the individual land areas of Sundaland were connected into one large land mass (Molengraaff & Weber, 1920; Beaufort, 1926; Verstappen, 1975, 1980; Tjia, 1980). Many authors (e.g. Beaufort, 1926; Kahlke, 1972; von Koenigswald, 1981; Heaney, 1985; MacKinnon *et al.*, 1996) have therefore characterized Sundaland as a system through which most species could freely move during glacial periods, up until *c.* 10,000 years (10 Ka) ago when higher sea levels once more physically separated the islands. Others (e.g. Brandon-Jones, 1996; Inger & Voris, 2001) recognized that, during much of the Pleistocene, dispersal between the landmasses of Sundaland, especially by terrestrial species, was limited. Despite the Late Pleistocene existence of land connections between Borneo, Java, Sumatra and the Malay Peninsula, present-day distribution patterns of, for instance,

large mammals indicate that dispersal between the individual parts of Sundaland was restricted and there appear to have been considerable barriers to animal movement. The Leopard [*Panthera pardus* (Linnaeus)], for instance, occurs on Java and in the Malay Peninsula, but neither recent nor fossil records indicate their presence on the landmasses between these two, Borneo and Sumatra. The question is how the species ended up in Java without leaving its traces in Borneo and Sumatra. Orangutans [*Pongo pygmaeus* (Linnaeus) and *P. abelii* (Lesson)] provide another riddle. These two species of Borneo and Sumatra have long been thought to be similar – they were considered as one species until quite recently – but morphological (Groves *et al.*, 1992; Uchida, 1998) and genetic data (Xu & Arnason, 1996; Zhi *et al.*, 1996; Warren *et al.*, 2001; Zhang *et al.*, 2001) have shown that Bornean and Sumatran are, in fact, quite distinct, and have probably been separated genetically for some 1–2.5 million years. It is known that Borneo was connected with Sumatra until relatively recently, so why did the two species remain separated? Either a geographical – for instance, the very large rivers that dissected the exposed Sunda Shelf – or an ecological barrier may have existed.

During the glacial periods, climates may have been drier, colder and more seasonal (Verstappen, 1975, 1980, 1997; Gupta *et al.*, 1987; Stuijts *et al.*, 1988; Thorp *et al.*, 1990; Thomas *et al.*, 1999). Some authors have therefore suggested that during the LGM, the land between Borneo, Sumatra, Java and the mainland was covered in savanna-type vegetation (Muller, 1975; Morley, 1981; Morley & Flenley, 1987; Broecker *et al.*, 1988; Caratini & Tissot, 1988; Heaney, 1991; Gathorne-Hardy *et al.*, 2002), although monsoon forest (Whitmore, 1981; Whitten *et al.*, 1996; Morley, pers. comm. in Adams & Faure, 1997; Taylor *et al.*, 1999) has also been suggested. If such

vegetation types indeed existed on the exposed Sunda Shelf it would explain why rainforest-dependent species like orangutans were unable to cross from Borneo to Sumatra or vice versa. The savanna hypothesis is, however, not supported by all, and data by Geyh *et al.* (1979), Emmel & Curray (1982), Pope (1984), Page *et al.* (1999), Anshari *et al.* (2000), Kershaw *et al.* (2001) and Taylor *et al.* (2001) indicated that during the LGM, forests not unlike those found in the area today persisted in much of Sundaland. These conflicting opinions may indicate that rather than thinking of large, homogenous zones of a certain vegetation type, a more gradual and heterogeneous model may be required (P. Kershaw, pers. comm., 1999).

In this research LGM vegetation types were further investigated by looking at the ecological characteristics of mammal faunas on islands that became isolated at the end of the LGM when sea levels rose. It relies on the assumption that habitat requirements of these island species carry a signal of the vegetation types that existed when the islands became isolated. The aim is to assess geographical patterns in these habitat requirements, and to see whether these can be related to palaeoenvironmental reconstructions obtained by other methods.

METHODS

All small islands in the region were listed (Appendix 1, Fig. 1) for which the presence of mammal species was reported in the literature. For this, the following literature sources on mammalian island faunas were used: Miller (1900a, b, 1901, 1903, 1905, 1906a, b), Vorderman (1901), Lyon (1906a, b, 1911, 1916), Kloss (1919), Chasen & Kloss (1928a, b, 1931a, b), van der Meer Mohr (1930), Taylor (1934), Chasen (1937), Sody (1937, 1940), Hoogstraal (1951), Sanborn (1952), Hoogerwerf (1967), Lekagul & McNeely (1977), Heaney (1979), van der Zon (1979), WWF (1980), Musser (1981), Musser & Newcomb (1983), Payne *et al.* (1985), van Strien (1986, 2001), Tenaza (1987), Scott (1989), Corbet & Hill (1992), Dans (1993) and Kirk (1994).

For each island location (longitude and latitude), maximum altitude of the island, total area, depth to nearest land, distance to nearest island and distance to nearest mainland were assessed. Depth to nearest land was determined as much as possible using bathymetric charts of the region. This included the maps by Badan Koordinasi Survei dan Pemetaan Nasional (BAKOSURTANAL, 1992) for Indonesia, and the maps by the Hydrographic Department of Thailand (1978). The distance to the nearest island on maps of the area was calculated using ArcView 3.2a software, by measuring in kilometres the distance to the nearest similar-sized or larger island, or to the nearest continent if there was no nearer island. It was not possible to find the locations of two islands – Chance and Panau.

For each of the island species the vegetation type in which they are generally found was assessed by using data from the literature. For this purpose the following classes were created: montane forest, primary lowland forest, secondary forest, forest gardens and plantations, and open areas. These

classes were combined when necessary to express as closely as possible all vegetation types in which a species occurs. The likelihood of human-aided introductions of certain species [*Rattus rattus* (Linnaeus) and *Suncus murinus* (Linnaeus) were already excluded from research] was also investigated by looking for evidence in the literature.

The geographical patterns of species habitat requirements was analysed to see to what extent these can be related to vegetation types during the LGM using ArcView 3.2a software.

RESULTS

Information on the presence of mammal species was obtained for 215 islands in the region (see Appendix 1), which added up to 1218 records of species presence on these islands, varying from one on many small islands to thirty for Bangka Island (for locations of some islands see Fig. 1). Of the 1218 species records, 357 were excluded from the analysis, because it was more likely that these species had been introduced; this included records for the following species: *Bandicota indica* (Bechstein), *Bos javanicus* (d'Alton), *Bubalus bubalis* (Linnaeus), *Callosciurus nigrovittatus* (Horsfield), *C. notatus* (Boddaert), *C. prevostii* (Desmarest), *Cervus porcinus* (Zimmermann), *C. timorensis* (Blainville), *C. unicolor* (Kerr), *Macaca fascicularis* (Raffles), *M. nemestrina* (Linnaeus), *Mus musculus* (Linnaeus), *Paradoxurus hermaphroditus* (Pallas), *R. argentiventer* (Robinson and Kloss), *R. exulans* (Peale), *R. norvegicus* (Berkenhout), *R. tiomanicus* (Miller) and *Sus scrofa* (Linnaeus).

The geographical analysis showed that forest-dependent species, i.e. species that are only found in primary forest (lowland and mountainous), appear to be concentrated on islands off west Sumatra, in the Lingga and Riau Archipelagos, around Palawan, and around Bunguran Island; they are absent mostly from the islands of the Java Sea, those off the east coast of eastern Borneo, from most islands in the Sunda Strait, several islands in the northern South China Sea, and from all islands off the west coast of the Malay/Thai Peninsula and in the Gulf of Thailand (Fig. 2). The number of forest-dependent species correlated significantly with the size of the island on which they occurred (Spearman's correlation coefficient = 0.432, $P < 0.001$). Therefore the number of forest-dependent species was recalculated by dividing it by the $_{10}\log$ area of the island to account for the effect of island size on the total number of species. The analysis showed that there was a relatively large number of forest-dependent species on the following islands and island groups: Siberut, Sipura and the Pagai Islands off west Sumatra, the Riau Archipelago and, to a lesser extent, the Lingga Archipelago, Bunguran Island, Bangka Island, Labuan Island just offshore Sabah, and the Philippine island of Palawan and the many smaller islands surrounding it, including Banggi and Balembangan offshore Sabah.

When the species that are also found in the secondary forest were added, the geographical patterns were similar to those found for the species limited to the primary forest. Mapping the ratio of forest-dependent species (including

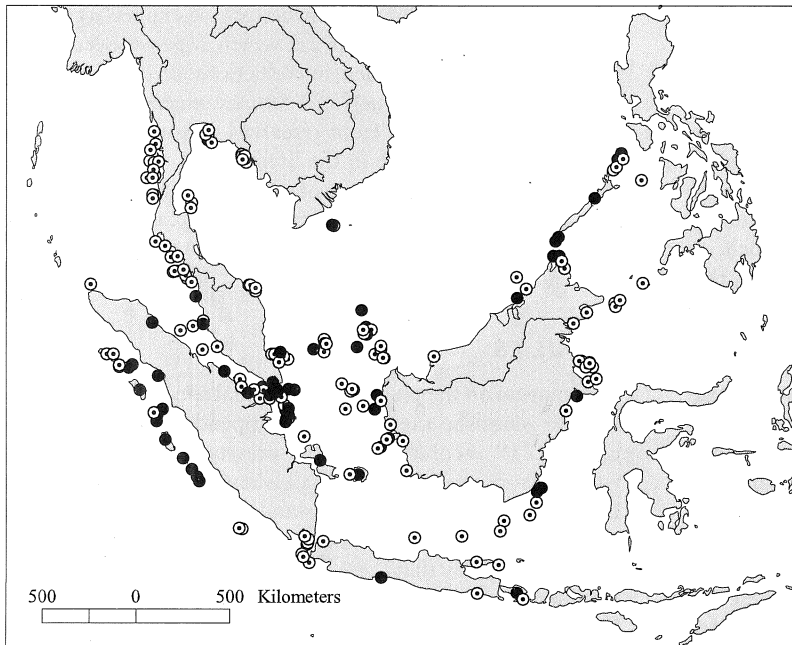


Figure 2 Islands where forest-dependent species occur (solid black circles). Islands where these species are absent are indicated by open circles.

those found in secondary forest) divided by the $10 \log$ island area showed a concentration of these species on the Mentawai Islands (Siberut, Sipura and the Pagai Islands), the Riau Archipelago and Tioman, Bunguran and Sirhassen, Penang, Palawan and the surrounding islands, and the islands in the Mergui Archipelago and in the Gulf of Thailand.

Finally, the geographical patterns of species that generally occur outside primary forest were analysed, that is those in

secondary forest, gardens, plantations and open areas. The number of those species divided by the $10 \log$ island area showed a more or less reversed pattern of that found for forest-dependent species (Fig. 3). These species are concentrated in the Java Sea, Panaitan Island in the Sunda Strait, the islands of Langkawi, Samui and Tao, on either side of the Malay/Thai Peninsula, Enggano off the south-west coast of Sumatra, and many islands in the Mergui Archipelago.

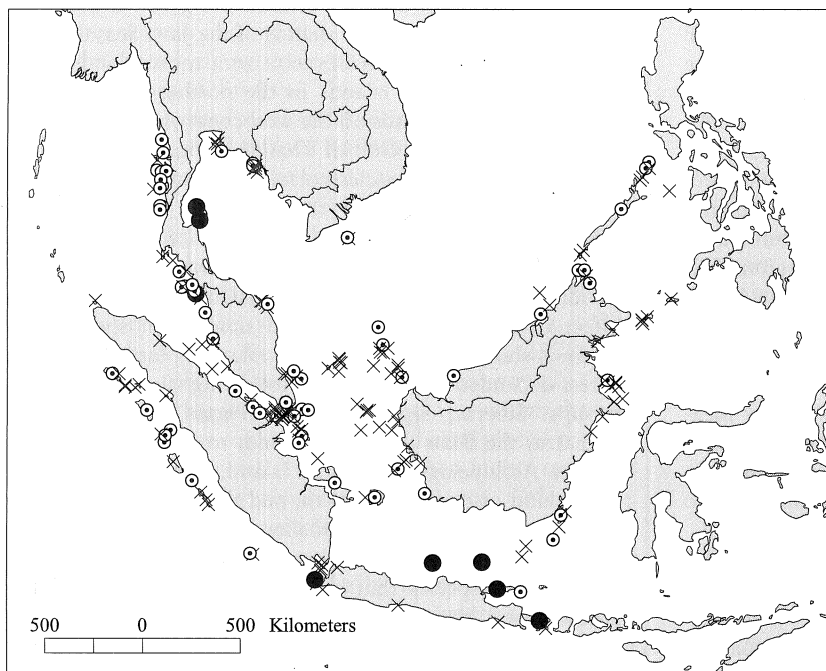


Figure 3 The presence of all island species that do not occur in the primary forest, and are mostly found in more open vegetation types, expressed as the ratio between number of species and the $10 \log$ of the island area. Large solid black circles are for values between 0.5 and 1, smaller open circles for values < 0.5 , and crosses for islands without any of these species.

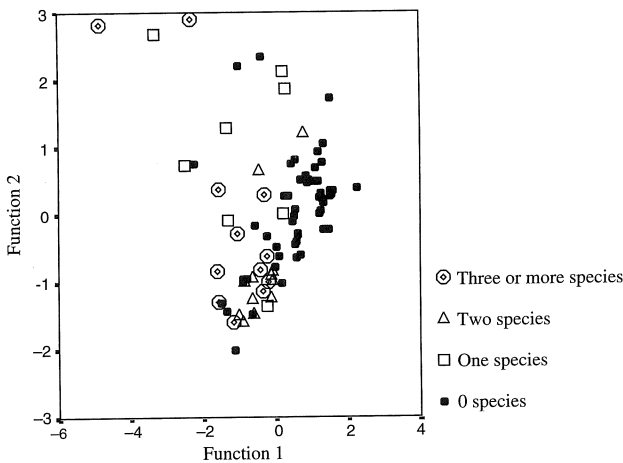


Figure 4 Discriminant analysis of factors that are related to the number of forest-dependent species that occur on islands. The islands in the top left corner of the diagram are Sipura, Siberut and Bunguran.

Table 1 Correlation matrix for discriminant analysis of forest-dependent species

	Function	
	1	2
Latitude	0.69	0.47
Area	-0.61	0.48
Distance to nearest island	-0.30	0.53
Altitude	-0.15	0.40
Distance to mainland	-0.36	0.37
Longitude	-0.15	0.21
Minimum depth	0.05	0.15

To further investigate which geographical factors (island area, latitude, longitude, altitude, distance to nearest island and distance to nearest mainland) most strongly correlated with the number of species with certain ecological characteristics, multivariate statistics was used. A discriminant analysis of the factors that are related to the number of forest-dependent species (mountain and primary forest) showed that there was some separation between islands with and without these species; the differentiation was primarily along the horizontal axis, i.e. function 1 (72% of total variance), which most strongly correlated with island latitude and island size (Fig. 4 and Table 1). Function 2, which accounted for 24% of the total variance, correlated strongly with distance to nearest island.

DISCUSSION

This research has revealed some interesting patterns in the geographical distribution of mammalian characteristics on south-east Asian islands. Forest-dependent species appear to be concentrated off the west coast of Sumatra, in the Riau and Lingga Archipelagos, around Bunguran Island and

around Palawan. The species are mostly absent on islands of the Malay/Thai Peninsula, and on islands in the Java Sea and Sunda Strait. There are three important aspects to this issue. First, are the observed patterns real or apparent, i.e. are they biased by sampling effort. Secondly, we need to ask whether the present-day geographical patterns of ecological traits are related to present-day vegetation types only, or whether they also tell us something about the past environments. Thirdly, can we say with any degree of certainty that if a forest-dependent species is found on an island that became separated after the post-LGM sea-level rise, that the island must have been covered in forest before its isolation?

Sampling bias could arise from two different sources: a preference of the collectors and surveyors for islands in a certain region or with a certain vegetation type, or a preference of the collectors and surveyors for species of certain ecological characteristics. Figure 1 shows that coverage of the islands appears to be equally distributed across the region, and the investigated literature sources indicate that all of the larger islands have been surveyed at least once. Therefore, there does not seem to be a sampling bias to islands in a certain part of the region. One could argue that forest-dependent species may be more difficult to collect than species occurring in more open vegetation types, and that the former group may thus be under-sampled. Still, even if this is the case, this effect is more likely to be equally strong across the region and would not affect the geographical patterns in the data. All the literature sources were reports of general collection and survey work, none of them specifically targeting a particular ecological group. It can therefore be expected that sampling effort has little effect on the patterns in this research, although it is possible that new records, especially of forest-dependent species, could change the patterns to some extent.

The comparison of the geographical distribution of ecological traits with the present-day vegetation types suggested that the two were not directly related. For instance, none of the islands in the Sunda Strait area, all of which were covered in tropical rain forest before these forests were cut down (MacKinnon, 1997), contain forest-dependent species. One would expect islands like Panaitan, Sebesi and Siuncal, none of which are very small, to have retained some forest-dependent species. A similar situation exists off the east coast of Borneo, where islands covered by tropical forest lack any of the forest-dependent species. In the eastern Java Sea, where all islands are within the semi-evergreen forest zone, none of the islands have forest-dependent species; a similar situation is found on islands on either side of the Malay/Thai Peninsula. Also, the Mergui Archipelago, which Mackinnon (1997) classified as having originally been covered by tropical evergreen forest, lacks forest-dependent species. The absence and presence of species on islands depends on a lot more than the island's vegetation, but it can tentatively be concluded that distribution patterns of island species in south-east Asia are partly correlated with past environmental conditions, perhaps those dating back to the LGM.

To establish whether the occurrence of forest-dependent species on an island is indicative of the presence of closed

forest before the islands were isolated by rising sea levels, it is important to establish when climates started to become wetter and warmer, and when rising sea levels isolated species on newly formed islands. A detailed discussion for each island group follows.

Islands off west Sumatra

Apart from three (Nias, Simeulue and Enggano), all islands off the west coast of Sumatra are separated by sea < 120 m deep. The lowest sea levels during the LGM occurred between 29.5 and 18.3 Ka ago (Schönfeld & Kudrass, 1993) and were *c.* 120 m below present day level (e.g. Chappell, 1998). This means that these islands were connected with mainland Sumatra at least until 18.3 Ka. Nias and Simeulue, which are separated from the mainland by sea depths of *c.* 275 and 421 m, respectively, probably remained islands during the LGM, and, in fact, Whitten *et al.* (1987) suggested that the latter island might never have had a land connection with Sumatra. The presence of forest species on Nias, such as *Arctictis binturong* (Raffles), *Chiropodomys gliroides* (Blyth), and *Tragulus napu* (F. Cuvier) provides a strong indication that during the LGM, Nias remained at least partly covered in tropical rainforest. Other islands further south (e.g. N. and S. Pagai, Sipura, Siberut, Tana Bala and Tana Masa) have even more forest-dependent species than Nias, and although these islands were probably connected with Sumatra during the LGM, the presence of many forest endemics strongly indicates that these islands also remained forest covered during the LGM.

Riau and Lingga Archipelagos

Islands in the Riau and Lingga Archipelagos also have many forest-dependent species. These islands, however, are all surrounded by shallow seas, and it has even been suggested that these island groups remained connected with the Malay Peninsula until very recently (see Obdeijn, 1942). It may therefore well be that the presence of forest-dependent species on these islands reflects the vegetation history of the island only for the last few thousand years, and tells us little about conditions during the LGM.

Palawan

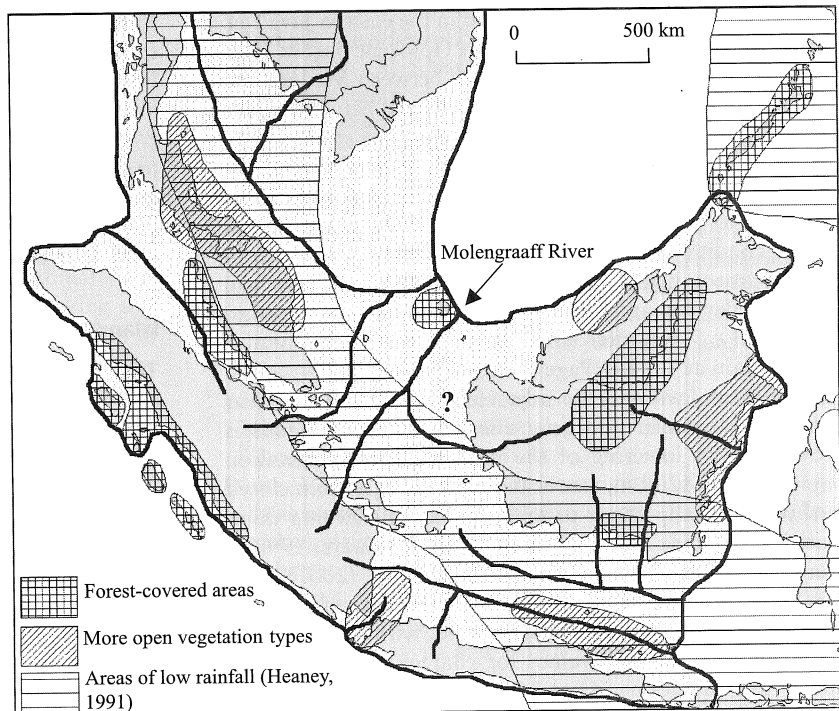
The palaeoenvironmental history of Palawan is uncertain. Based on the distribution of animal species (Heaney, 1985; Reis & Garong, 2001), and sea-level reconstructions (Vorisi, 2000) it appears that there has been no Late Pleistocene connection between Borneo and Palawan, although Cranbrook (2000) maintains that Palawan was connected with northern Borneo during the LGM and only became separated at *c.* 14 Ka. Most evidence, however, suggests that Palawan remained an island during the Late Pleistocene and the presence of forest-dependent species on Palawan and its surrounding islands indicate the continued presence of closed forest during the LGM. This is also supported by the presence of several forest-dependent

species, endemic to Palawan (and therefore having been separated from their closest relatives for long enough to become distinct species), like *Hylopetes nigripes* (Thomas), *Palawanomys furvus* (Musser and Newcomb), *Sundasciurus rabori* (Heaney), *S. steerii* (Günther), *Maxomys panglima* (Robinson), and *Hystrix pumila* (Günther). Several of these species are also known from the Late Pleistocene fossil record of Palawan (see Reis & Garong, 2001), which suggests that at least parts of Palawan remained forest-covered during the LGM.

Bunguran and the North Natuna Islands

Bunguran in the northern South China Sea is located at the edge of the continental shelf, with a maximum sea depth of *c.* 75 m separating it from the mainland, and would have been one of the first islands to become isolated when sea levels started to rise. The presence of forest-dependent species such as *Arctogalidia trivirgata* (Gray), *Chiropodomys gliroides*, *Hylopetes lepidus* (Horsfield), *H. spadiceus* (Blyth), *Leopoldamys sabanus* (Thomas), *Maxomys rajah* (Thomas), *Nycticebus coucang* (Boddaert), *Petaurista elegans* (Müller), *Presbytis melalophos* (Raffles) (recently raised to species level as *P. natunae*, see Groves, 2001), *Ratufa affinis* (Raffles), *Sundamys muelleri* (Jentink), and two mouse-deer species (*Tragulus* sp.) indicates that the island was covered in forest when it became isolated. Pelejero *et al.* (1999) found evidence for the beginning of the inundation of the Sunda Shelf at 14.9 Ka, and the 75-m mark was probably crossed slightly later (at *c.* 13.5 Ka, also see Hanebuth *et al.*, 2000); sea levels at that time rose *c.* 24 m in 500 years (Hanebuth *et al.*, 2000). As this happened shortly after the first climatic reversal, it is difficult to judge to what extent the vegetation on Bunguran had adapted to the wetter conditions before rising sea levels isolated the island. Still, it appears unlikely that, during the LGM, Bunguran was devoid of forest vegetation, as this would require rapid re-establishment of closed forest on the island in the short time-span between the initiation of a sea temperature increase and related increased precipitation, and the isolation of the island. Also, this would mean that in the same short time-span Bunguran was reinvaded by numerous forest-dependent species. A more likely conclusion is that Bunguran remained forest covered during the LGM and that forest-dependent species were present during all of the LGM. This conclusion is supported by pollen spectra from the southern South China Sea (around the mouth of the Pleistocene Molengraaff River, see Fig. 5) indicating that during the last glaciation, the lowland area of the exposed Sunda Shelf was covered by tropical lowland rain forest, and mangroves grew along the river mouths and the coasts (Sun *et al.*, 2000). It is unclear to what extent these pollen spectra have been influenced by pollen from riverine vegetation. Tropical moist forest species could have survived in riparian habitats that acted as forest refugia in times of reduced precipitation (e.g. Meave *et al.*, 1991), and pollen from these refugia may give the impression that much larger areas were covered in tropical moist forest. These linear habitats could have provided dispersal opportunities for

Figure 5 Overview of areas where the data from this and other researches suggest closed forest vegetation during the LGM, and where the data indicate that more open vegetation types may have existed. Also shown is the Late Pleistocene area of seasonality and low rainfall as suggested by Heaney (1991). Area in light grey is the exposed land during times of lowest sea levels; darker grey depicts present-day land areas.



tropical forest species from and to present-day island areas, although this does not affect the assumption that forest-dependent species required the continuous presence of forest to survive on islands.

Other islands on the northern Sunda Shelf and off west Borneo

A similar scenario to the one in Bunguran can be developed for islands slightly higher up the continental shelf in this area, including Sirhassen, Matak and Siantan, all of which have forest-dependent species. However, because of their closer proximity to mainland Malaysia and Borneo and associated lower sea levels separating them from the mainland, it would have taken several thousand years, after rainfall started to increase, before the islands became isolated (see Voris, 2000). On these islands it cannot be excluded that forest became re-established in former areas of more open vegetation types. Such open environments have been suggested by Thomas (1987) for the early LGM, and by Majid (1982) who suggested that at the height of the LGM, the Niah area in Sarawak was covered by deciduous monsoon forest. More recent data, however, suggest that wetter conditions prevailed in western Borneo, where, during the LGM rain forest existed, very similar to that found during the mid-Holocene (Anshari *et al.*, 2000; Kershaw *et al.*, 2001).

Tioman, Bangka and Belitung

Tioman, Bangka and Belitung are all separated from the mainland by relatively shallow seas and probably became isolated only at *c.* 10 Ka, or even later. Recovery of forest

vegetation could easily have taken place and the presence of forest-dependent species can therefore tell us little about palaeoenvironmental conditions during the LGM.

Java Sea and Sunda Strait

The absence of forest-dependent species from the islands in the Java Sea, those off the east coast of eastern Borneo, most islands in the Sunda Strait, and on all islands off the west coast of the Malay/Thai Peninsula and in the Gulf of Thailand hints at climatic conditions during the LGM in these regions that were too dry for closed forest conditions. Especially the situation of Bawean, which is presently covered by semi-evergreen forest (MacKinnon, 1997), suggests that this island may have been covered by a more open vegetation type during the LGM. This island is separated from mainland Java by a maximum sea depth of *c.* 63 m and would only have become isolated at *c.* 10 Ka. The absence of species such as mouse-deer (*Tragulus* spp.), that occur on almost all large-sized islands in the region, suggests that suitable forest habitat was absent at the end of the LGM. This can similarly be argued for other islands in the Java Sea (Karimun Jawa), those in the Sunda Strait (apart from Krakatau which is of very recent origin), on either side of the Malay/Thai/Burmese Peninsula, and off the east coast of Borneo. All of these are presently covered in forest (or where so until deforested by logging), are close to the mainland and separated from the mainland by sea depths of 60–70 m, but lack the forest-dependent species. Palynological evidence from the Java Sea is scarce, but Late Pleistocene black alkaline clays (presumably vertisols) in East Java (Smit-Sibinga, 1947), indicate a pronounced seasonal, dry monsoon

climate, which may also have existed in the eastern Java Sea. On the contrary, the presence of Early Holocene peat at 30 m below sea level in the eastern Java Sea between Madura and Kalimantan suggests that peat lands occurred before the Java Sea was inundated after the LGM (Situmorang *et al.*, 1993). The evidence suggests that evergreen forests reinvaded the exposed Java Sea, but probably for too short a time to allow mammals to reach the Bawean and Karimun Jawa Islands. Wetter conditions probably also prevailed further north in south Borneo, where peat datings showed that peat had started to develop at 18.3 ± 0.05 Ka, and had continued to do so until *c.* 7 Ka, after which no peat was formed until it started again at 1.3 Ka (Page *et al.*, 1999).

In western Java and the adjacent Sunda Straits, a clear indication of cooler and drier climates in the lowlands is provided by a lowering of the montane forest vegetation boundaries by 1200 m, associated with changes from closed freshwater swamp forest to open herbaceous swamp dominated by Poaceae and Cyperaceae (van der Kaars, 1998 in Sun *et al.*, 2000). Data by van der Kaars *et al.* (2001) show that between 16.3 and 15 Ka, open herbaceous swamp vegetation dominated by grasses existed, with low counts of Pteridophytes and high values for charcoal suggesting relatively dry conditions. After 15 Ka, the forest cover in the area increased strongly, indicating a change to wetter conditions.

Islands off the Malay/Thai Peninsula

Forest-dependent species on islands in the Mergui Archipelago do not give much information about the vegetation of these islands during the last glacial, because all are separated from the mainland by seas < 20 m deep. Similarly, the absence of forest-dependent species from many of the other small islands off the Thai/Malay Peninsula does not necessarily mean that drier conditions prevailed during the LGM, because most of them are not in deep waters. Two islands, Rawi and Butang, are in slightly deeper waters, but the species that occur there do not exclusively occur in forests. Note that *Tragulus javanicus* (Osbeck), the mouse-deer species on these islands, is generally considered to be better adapted to open forest types than *T. napu* (F. Cuvier) (van Dort, 1986) and its presence may support the conclusion that these islands were not necessarily covered by closed forest during the LGM. Drier conditions during the last glacial are generally supported by other palaeoenvironmental data from that region. For instance, Morley (1999) suggested that *Pinus* savanna was probably widespread on the Malay Peninsula at 22 Ka. Also, geomorphological research by De Dapper (1985) on land forms in the Malay Peninsular uplands suggested dry climatic conditions with a fairly open vegetation (tree or grass savanna), although it could not be proved whether the conditions occurred during the LGM or at *c.* 80 Ka ago. In apparent contrast to this, Geyh *et al.* (1979) provided evidence for per-humid climatic conditions in the southern Malacca Strait before the sea level rise following the LGM. Between 50 and 10 Ka ago dry land conditions with peats and mangroves prevailed. Also,

Emmel & Curray (1982) suggested abundant vegetation in the emergent Malacca Strait, probably resembling the lowland vegetation of tropical regions, with mangroves in the low-lying areas and Nipah palm along the banks of muddy creeks. Tropical rain forest would cover the higher drier parts of this area. It is therefore possible that wet conditions and tropical, closed forest prevailed to the west of the Malay Peninsula, while on the Peninsula itself, and possibly to the east, drier conditions existed.

Islands of the Sulu Sea

The islands in the Sulu Sea (e.g. Tawi-Tawi and Jolo) also lack forest-dependent species, but these islands are surrounded by deep seas and would not have been connected with mainland Borneo during the LGM; the species characteristics can therefore not give an indication of the palaeoenvironments during the LGM.

East Borneo

No forest-dependent species occur on the islands off east Borneo, but because of their small size these island faunas are impoverished and little can be said about the palaeoenvironmental signal of their species compositions. Still, a pollen diagram from east Borneo shows an increase in savanna at *c.* 20 Ka, which might serve as an indicator of a drier climate than at present (Flenley, 1998) (note that Flenley pointed out that the dating for this diagram was poor). Also, Caratini *et al.* (1988) suggested that during the LGM the hinterland of the Mahakam Delta probably consisted of grassland or savanna.

CONCLUSIONS

The results of this research suggest that during the LGM the following areas had a climate that was wet enough to retain a closed forest vegetation: the areas off the west coast of Sumatra, Palawan and the Natuna Islands (Bunguran and Laut). The following areas may have been covered in forest during the LGM, but the data are inconclusive: the Riau and Lingga Archipelagos, and islands in the South China Sea [Anambas (Matak, Siantan)], South Natuna Islands (Sirhassen), and also Tioman, Bangka and Belitung. The following areas probably had more open vegetation types during the LGM: islands in the Java Sea (Bawean and Karimun Jawa) and Sunda Strait, and possibly those on and to the east of the Thai/Malay Peninsula, and those east of Borneo. The data from this and other researches therefore suggest that drier areas with more open vegetation types existed during the Late Pleistocene, but that large areas of wet forest areas also survived (see Fig. 5 for an overview). The data do not correspond well with the regional overview provided by Heaney (1991); a large area of seasonal climate that runs across the Sundashelf and the Java Sea coincides with several drier areas identified in this research, but several others (Sunda Straits and east Borneo) are not included. It is possible that localized geographical features, such as the

higher altitude islands, may have created their own climatic conditions, overriding patterns on a more regional scale.

This overview only provides a snapshot in time of palaeoenvironmental conditions at the end of the LGM, and the predicted palaeoenvironmental patterns may only have existed for a relatively brief period. Also, the boundaries of vegetation types, as depicted in Fig. 5, should be thought of as dynamic rather than static.

More data are needed to gain a more complete understanding of the complex interactions between climate, sea levels, substrate, flora and fauna. Research addressing this issue could include the analysis of molecular phylogenies of species that occur on any of the named islands and the relationships with their closest relatives on Java, Borneo, Sumatra and the Malay Peninsula. Such research, when combined with a molecular clock assumption, may reveal when island taxa became separated and from where they dispersed to their present island habitat. Also, the present research could be repeated for other forest-dependent species, including plants, invertebrates, fish, amphibians, reptiles and poorly dispersing birds.

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BIOSKETCH

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APPENDIX I

Species recorded on small islands in south-east Asia. Numbers behind the species names refer to those listed below in the island list.

- Aeromys tephromelas*, 135, 171; *Aonyx cinerea*, 14, 22, 26, 42, 55, 68, 69, 70, 92, 93, 95, 124, 162, 168, 175; *Arctictis binturong*, 14, 17, 26, 82, 119, 124, 132, 201, 210; *Arctogalidia trivirgata*, 14, 17, 22, 26, 30, 31, 55, 82, 89, 95, 144, 175, 176, 190, 201, 206, 210; *Atherurus macrourus*, 4, 206, 210; *Axis kuhlii*, 20; *Callosciurus caniceps*, 24, 35, 36, 45, 49, 56, 57, 75, 76, 89, 114, 135, 142, 157, 179, 185, 186, 192, 198, 199, 206; *C. finlaysonii*, 37, 41, 83, 87, 139, 141, 169; *C. melanogaster*, 117, 154, 171, 177; *Chirodomys calamanensis*, 10, 34, 42, 124; *C. gliroides*, 12, 31, 119, 178, 213; *C. karlkoopmani*, 117, 171; *Crocodyrus beccarii*, 14; *C. fuliginosa*, 4, 41, 45, 102, 129, 151, 157, 178, 210; *C. malayana*, (= *fuliginosa* ?), 102; *C. palawanensis*, (= *fuliginosa* ?), 10, 124; *Cynocephalus variegatus*, 4, 8, 13, 14, 17, 26, 31, 38, 52, 55, 68, 70, 82, 92, 93, 116, 127, 133, 137, 138, 139, 144, 153, 162, 165, 170, 175, 176, 178, 188, 190, 196, 204, 206, 208, 210, 212; *Dendrogale murina*, 41; *Echinosorex gymnura*, 84, 201; *Exilisciurus exilis*, 13; *Helarctos malayanus*, 14, 23, 123, 153; *Hemigalus derbyanus*, 154, 177; *Herpestes brachyurus*, 42, 124; *H. javanicus*, 125; *Hylobates klossi*, 117, 154, 171, 177; *Hylomys suillus*, 210; *Hylopetes lepidus*, 14, 31, 206; *H. nigripes*, 16, 124; *H. sipora*, 177; *H. spadiceus*, 31, 82; *Hystrix brachyura*, 110; *H. javanica*, 12, 20, 97; *H. pumila*, 10, 34, 42, 124; *Iomys horsfieldi*, 135, 175, 210; *I. sipora*, 117, 177; *Lariscus insignis*, 26, 117, 135, 170, 175, 196, 210; *L. obscurus*, 154, 171, 177; *Lenothrix canus*, 212; *Leopoldamys edwardsi*, 177; *L. sabanus*, 15, 24, 31, 39, 63, 89, 92, 93, 95, 116, 121, 127, 135, 143, 170, 176, 185, 186, 196, 197, 206, 210, 212; *L. siporanus*, 117, 154, 171, 177; *Lutra sumatrana*, 14, 29, 92; *Manis javanica*, 12, 14, 17, 20, 22, 26, 30, 31, 42, 55, 68, 82, 84, 95, 117, 119, 124, 135, 137, 154, 161, 175, 176; *Martes flavigula*, 14; *Maxomys pagensis*, 117, 154, 171, 177, 215; *M. panglima*, 10, 11, 13, 34, 42, 99, 124; *M. rajah*, 8, 11, 15, 17, 26, 31, 38, 41, 44, 52, 70, 71, 81, 82, 84, 85, 86, 95, 102, 112, 124, 137, 162, 176, 177, 178, 190, 212; *M. surifer*, 11, 13, 15, 31, 36, 37, 63, 68, 77, 80, 83, 85, 92, 93, 98, 99, 112, 116, 121, 127, 133, 135, 139, 144, 148, 150, 151, 157, 165, 167, 170, 178, 196, 197, 210, 212; *M. whiteheadi*, 11, 13, 14, 17, 22, 26, 99, 111, 119, 123, 144, 153, 165, 168, 178, 196, 197, 212; *Menetes berdmorei*, 37, 49, 83; *Muntiacus muntjak*, 12, 14, 19, 22, 26, 37, 55, 67, 69, 95, 105, 110, 119, 125, 128, 175; *Mus caroli*, 97; *Mydaus javanensis*, 31, 82, 86; *M. marchei*, 34, 42, 124; *Nannosciurus melanotis*, 14, 22, 127, 176; *Nasalis larvatus*, 29, 60; *Niviventer bukit*, 12, 37, 41, 83, 157; *N. cremoriventer*, 11, 12, 13, 14, 22, 26, 63, 70, 86, 89, 99, 119, 121, 135, 192, 206, 210; *N. lepturus*, 12; *Nycticebus coucang*, 14, 17, 28, 31, 55, 63, 68, 75, 125, 128, 135, 160, 170, 174, 175, 200, 201, 210; *Palawanomys furvus*, 124; *Panthera pardus*, 12, 67, 97; *P. tigris*, 12, 26, 168; *Petaurista elegans*, 31, 121, 153; *P. petaurista*, 26, 31, 84, 135, 144, 153, 175, 177, 196, 197, 206, 210; *P. philippensis*, 75, 152, 192; *Petinomys genibarbis*, 14, 135; *P. hageni*, 117, 171, 177; *P. vordermanni*, 22, 55; *Pithecheir melanurus*, 121; *Presbytis melalophos/femoralis*, 17, 26, 31, 55, 78, 82, 144, 153, 175, 196, 197; *P. potenziani*, 117, 154, 171, 177; *P. rubicunda*, 68; *Prionailurus bengalensis*, 12, 29, 68, 69, 119, 124, 125, 201; *P. viverrinus*, 12; *Prionodon linsang*, 14, 22; *Pteromyscus pulverulentus*, 135; *Ptilocercus lowii*, 14, 70, 84, 95, 144, 171, 178; *Rattus adustus*, 53; *R. anandalei*, 123, 153; *R. enganus*, 53; *R. lugens*, 117, 154, 171, 177; *R. remotus*, 77, 80, 142, 157, 198; *Ratufa affinis*, 13, 14, 17, 22, 26, 30, 31, 68, 70, 82, 84, 92, 93, 95, 116, 127, 144, 165, 175, 176, 178, 190, 193, 196, 197, 212; *R. bicolor*, 12, 22, 23, 40, 41, 49, 63, 83, 85, 89, 96, 108, 120, 125, 135, 142, 157, 196, 197, 203, 206, 210, 212; *Rhinosciurus laticaudatus*, 17, 18, 26, 31, 70, 82, 95, 170, 175, 178, 210, 212; *Rhizomys sum atrensis*, 173; *Simias concolor*, 117, 154, 171, 172, 177; *Suncus palawanensis*, 124; *Sundamys muelleri*, 8, 10, 11, 13, 14, 15, 17, 31, 34, 38, 42, 52, 63, 70, 71, 82, 84, 85, 86, 95, 102, 111, 115, 116, 124, 144, 162, 165, 168, 170, 178, 190, 191, 196, 197, 212;

Sundasciurus hoogstraali, 34; *S. lowii*, 13, 31, 82, 84, 85, 92, 96, 117, 144, 154, 171, 177, 178, 196; *S. moellendorffi*, 34, 42, 58, 94, 195; *S. rabori*, 124; *S. steerii*, 10, 124; *S. tenuis*, 15, 17, 31, 63, 84, 95, 113, 116, 151, 170, 175, 196, 197, 210; *Sus barbatus*, 10, 14, 17, 26, 29, 33, 34, 42, 52, 55, 60, 65, 82, 102, 124, 127, 133, 190, 201; *S. verrucosus*, 20, 97; *Tarsius bancanus*, 14, 22, 68, 178; *Trachypithecus cristata*, 8, 14, 17, 22, 26, 30, 37, 55, 67, 95, 162, 178, 190; *T. obscurus*, 89, 135, 138, 139, 150, 206; *Tragulus javanicus*, 14, 15, 17, 23, 26, 31, 32, 68, 70, 71, 75, 76, 84, 89, 92, 93, 95, 104, 108, 123, 125, 127, 135, 136, 137, 143, 144, 145, 149, 150, 151, 153, 170, 175, 176, 192, 194, 196, 197, 201, 212; *T. napu*, 8, 10, 13, 14, 17, 22, 26, 30, 31, 52, 55, 59, 63, 70, 71, 82, 89, 93, 95, 104, 115, 116, 119, 137, 162, 163, 165, 168, 170, 176, 178, 188, 190, 191, 196, 197, 210; *Tupaia belangeri*, 37, 56, 75, 76, 152, 192, 199; *T. glis*, 2, 4, 10, 14, 17, 26, 41, 63, 89, 95, 102, 117, 129, 134, 135, 138, 139, 150, 151, 154, 157, 170, 171, 175, 176, 177, 196, 198, 203, 206, 210; *T. gracilis*, 13, 14, 22, 68; *T. javanica*, 12, 14, 22, 119, 124; *T. minor*, 11, 13, 14, 22, 68, 92, 93, 95, 176; *T. palawanensis*, 10, 34, 42, 43, 124; *T. splendidula*, 31, 68, 92; *T. tana*, 13, 15, 26, 32, 84, 95, 178, 194, 196, 197, 212; *Viverra megaspila*, 135, 175; *V. tangalunga*, 14, 22, 26, 31, 34, 42, 68, 82, 89, 92, 93, 95, 124, 127, 153, 175; *V. zibetha*, 175; *Viverricula indica*, 12, 20, 26, 67, 120, 125, 135, 175.

1 = Adang (SW Thailand); 2 = Airabu (Anamba Isl.); 3 = Alange Isl. (off E. Borneo); 4 = Aor; 5 = Arends (=Keramian); 6 = Atas (=Badas?) Isl, S. China Sea; 7 = Babi Isl. (Simeulue); 8 = Bakong (Lingga Isl.); 9 = Bakungan (Derawan Isl.); 10 = Balabac; 11 = Balemangan; 12 = Bali; 13 = Banggi; 14 = Bangka; 15 = Bangkaru; 16 = Bangkalan (nr Balabak); 17 = Batam; 18 = Batan (Riau Isl.); 19 = Bawal (off Borneo); 20 = Bawean; 21 = Bedung, south of Redang Isl.; 22 = Belitung; 23 = Bengkalis; 24 = Bentinck (Mergui Isl.); 25 = Berhala; 26 = Bintan; 27 = Birah-birahan; 28 = Bongao (Sulu Isl.); 29 = Bruit; 30 = Bulan (Riau Isl.); 31 = Bunguran (=Natuna Besar); 32 = Bunoa (Tambelan Isl.); 33 = Burung; 34 = Busuanga (Calamian Isl.); 35 = Butang (near Terutau); 36 = Chance (Mergui Isl.); 37 = Chang (Thailand); 38 = Chombol (Riau Isl.); 39 = Clara; 40 = Con Dao; 41 = Con Son; 42 = Culion (Calamian Isl.); 43 = Cuyo (Cuyo Isl.); 44 = Datuk (W. Borneo); 45 = Dayang Bunting; 46 = Deli; 47 = Derawan (off E. Borneo); 48 = Direction (S. China Sea); 49 = Domel (=Letsok-aw Kyun); 50 = Dua (W. Java coast); 51 = Dua (near Enggano); 52 = Durian; 53 = Enggano; 54 = Eraban (off E. Borneo); 55 = Galang; 56 = Hastings; 57 = High; 58 = Iloc; 59 = Iyan (Riau Isl.); 60 = Jambongan; 61 = Jarak (Malacca Str.); 62 = Jemur (=Jemor), Aroa Isl (Malacca Str.); 63 = Jimaja (=Letong); 64 = Jolo (Sulu Isl.); 65 = Juanta; 66 = Kaban, Johore Is.; 67 = Kangean; 68 = Karimata; 69 = Karimum Jawa; 70 = Karimon (Riau Isl.); 71 = Karimon Kecil (Riau Isl.); 72 = Kateman; 73 = Kemudi (S. China Sea); 74 = Ketam (Klang Isl.); 75 = King (=Kadan Kyun); 76 = Kissaraing; 77 = Klum; 78 = Kompei; 79 = Krakatau; 80 = Kra; 81 = Kram (Thailand); 82 = Kundur; 83 = Kut; 84 = Lab-

Labuan; 85 = Lagong (Natuna Isl.); 86 = Lamukotan (off W. Borneo); 87 = Lan (Thailand); 88 = Lang (Krakatau Isl.); 89 = Langkawi; 90 = Lang Tengah; 91 = Lasia/Reusam; 92 = Laut (Natuna Isl.); 93 = Laut (SE Borneo); 94 = Lin-Linapacan; 95 = Lingga; 96 = Lungung (N. Natuna Isl.); 97 = Madura; 98 = Mak; 99 = Malawali (N. Borneo); 100 = Mangalum (NW Borneo); 101 = Mankotan (S. China Sea); 102 = Mapor (Riau Isl.); 103 = Maratua; 104 = M-Matak (Anamba Isl.); 105 = Mata Siri; 106 = Mataha (off E. Borneo); 107 = Mehsi; 108 = Mendanau; 109 = Merah (SW of Karimon Isl.); 110 = Mesan (Thailand); 111 = Miang Besar; 112 = Midai (Natuna Isl.); 113 = Mobur (Anamba Isl.); 114 = Mohea (near. Terutau); 115 = Moro Kecil (Riau Isl.); 116 = Musala Isl (off W. Sumatra); 117 = N. Pagai; 118 = Nguwal (Riau Isl.); 119 = Nias; 120 = Nusa Barung (off S. Java); 121 = Nusa Kembangan; 122 = Nusa Penida; 123 = Padang I (off E. Sumatra); 124 = Palawan; 125 = Panaitan; 126 = Panau (=Atas Isl., S. China Sea); 127 = Panebangan; 128 = Pangkor; 129 = Panjang (S. Natuna Isl.); 130 = Panjang (off E. Borneo); 131 = Paya (Malacca Str.); 132 = Payong; 133 = Pelapis; 134 = Pemanggil (Malaya); 135 = Penang; 136 = Penjalei (=Mendol); 137 = Penuba; 138 = Perhenerhentian, west; 139 = Perhentian, east; 140 = Peucang; 141 = Phai (Thailand); 142 = Phangan (Thailand); 143 = Phuket (=Junk Seylon); 144 = Pinie; 145 = Pipidon (=Phi Phi Don); 146 = Pisang (Malacca Str.); 147 = Rabu Rabu (off E. Borneo); 148 = Rang; 149 = Ransang; 150 = Rawi; 151 = Redang; 152 = Ross (Mergui Isl.); 153 = Rupert; 154 = S. Pagai; 155 = Sedanau (Natuna Isl.); 156 = Saddle (Tambelan Isl.); 157 = Samui; 158 = Sanga-Sangalan (Derawan Isl.); 159 = Sangka Laki (=Sangalaki, E. Borneo); 160 = Sanga Sanga (Sulu Isl.); 161 = Sanglar (=Sanglang?); 162 = Sebangka (Lingga Isl.); 163 = Sebatik (off E. Borneo); 164 = Sebesi (Sunda Strait); 165 = Sebuku (SE Borneo); 166 = Seraia (Natuna Isl.); 167 = Serutu (Karimata Isl.); 168 = Setoko; 169 = Si Chang (Thailand); 170 = Siantan (Anamba Isl.); 171 = Siberut; 172 = Simaleimalegu; 173 = Simeulue; 174 = Siminul (Sulu Isl.); 175 = Singapore; 176 = Singkep; 177 = Sipura; 178 = Sirhassen (Serasen); 179 = Sir John Malcolm; 180 = Siumat; 181 = Siuncal; 182 = Solombo (midway between Madura and Borneo); 183 = St Barbe (=Pedjan-edjantan = Pengiki, Tambelan Isl.); 184 = St Julian (=Pengibu) (Tambelan Isl.); 185 = St Luke (Mergui Isl.); 186 = St Matthew (=Zedetkyi Kyun, Mergui Isl.); 187 = Sribuat (Pahang, Malaya); 188 = Subi (S. Natuna Isl.); 189 = Subi Kecil; 190 = Sugi; 191 = Sugi Bawa; 192 = Sullivan (=Lampi = Lanbi Kyun, Mergui Isl.); 193 = Talang; 194 = Tambelan Besar; 195 = Tampil; 196 = Tana Bala; 197 = Tana Masa; 198 = Tao (near Samui); 199 = Tavoy; 200 = Tawitawi (Sulu Isl.); 201 = Tebing Tinggi (E. Sum.); 202 = Teibeianbesar; 203 = Telibon; 204 = Tello (Batu Isl.); 205 = Temaju; 206 = Terutau; 207 = Tiga (Sabah); 208 = Tinggi; 209 = Timbun Mata; 210 = Tioman; 211 = Tong Tutup (Derawan Isl.); 212 = Tuangku; 213 = Tujuh Isl. (E. Sum.); 214 = Wai (=Uwi?), Tambelan Isl.; 215 = Weh.