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BIODIVERSITY AND ENDEMIC CENTRES OF INDONESIAN TERRESTRIAL VERTEBRATES

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To my late parents
Jaja Amali and T. Rosita Amali

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Inar Rosmayati Natus

Abstract

This study investigates the endemic centres of Indonesian animals and the biodiversity across geographical gradients. At the same time, it also evaluated different lines suggested for separating the Oriental and Australian faunal region in the Indonesian region. The analyses have mainly used the present-day distribution of terrestrial vertebrates, especially the smallest ranges of species and subspecies.

The results show that faunal migration of Oriental and Australian lineages to the Indonesian Archipelago may have been happening since the Palaeocene period and more importantly, island drifts might have facilitated such migration. These events caused major reorganisation of island positions and island forms, which in turn resulted in faunal extinction around the mid-Pliocene. Some islands, especially in the Wallacea region, emerged very late and as a result nowadays they are lacking endemic forms.

There are currently at least seven endemic centres, which can be recognised, i.e. Borneo, Java, Sumatra, Sulawesi, North Moluccas, New Guinea and the Lesser Sundas/Banda Arcs. The affinities between these endemic centres revealed that there are two clusters of islands in the Indonesian Archipelago.

The first cluster separated Indonesia in the past into three regions:

1. Borneo, Java, Sumatra, Sulawesi and the Lesser Sundas as far as Flores Island;
2. Talaud Island and Sangihe Island, Northern Moluccas, Sanana Island, the Outer Banda Arc as far west as Timor and New Guinea;
3. Wallacea region.

The second cluster has today similarly divided Indonesia into three regions, but the island elements are different. They are:

1. The Great Sundas (Borneo, Java, Sumatra) and Bali;
2. New Guinea, including Waigeo and Batanta to the northwest;
3. Wallacea region.

These different clusters suggest in turn the shifts of biogeographical lines in the Indonesian Archipelago.

Furthermore, oscillation in climate, eustatic sea level changes and fluctuations in vegetation in the Quaternary period had much affected the distribution pattern of animals. There was a phase of expansion for montane oak forests, grasslands and woodlands during the period 18,000-14,000 years ago in East Indonesia and 16,500-12,000 years ago in West Indonesia. Such an expansion led to the increased isolation of rainforests and of the faunas adapted to them. These periods are also indicated by the lowering of the tree line which facilitated montane fauna to disperse across lower elevations. At 8,000-9,000 years ago, the climate became warmer and slightly wetter. The mid- to upper montane forests expanded to their full altitudinal range, while montane oak forest, grassland, and woodland areas had contracted.

The oscillation in climate, eustatic sea level changes and fluctuations in vegetation in turn determines much the formation of numerous sub endemic centres, which today can be found within the mainland. Recently, there are 14 sub endemic centres on Borneo, 8 on Java, 16 on Sumatra, 14 on Sulawesi and 14 on New Guinea. From the conservation management point of view, the identification of such sub endemic centres would generate valuable information for the protection effort.

Zusammenfassung

Diese Arbeit analysiert die Lage der Endemitenzentren Indonesiens und damit der Biodiversität. Gleichzeitig evaluiert sie unterschiedliche „Linien", die die Trennung zwischen orientalischen und australischen Faunenregionen in Indonesien markieren. Die Analyse bezieht sich hauptsächlich auf die Verbreitung von terrestrischen Vertebraten, in erster Linie auf Kleinareale von Spezies und Subspezies.

Das Ergebnis zeigt, dass die Faunenmigration orientalischer und australischer Verwandschaftsgruppen in den indonesischen Archipel schon seit dem Paläozän stattgefunden hat. Dabei spielen Insel-Verdriftungen eine große Rolle. Dadurch veränderten sich die Insel-Positionen und die Formen, wobei im mittleren Pliozän deutliche Extinktionen auftraten. Einige Inseln, vor allem die in der Wallacea Region liegen, entstanden sehr spät, so dass sie endemitenarm sind.

Sieben Endemitenzentren lassen sich eindeutig abgrenzen, und zwar Borneo, Java, Sumatra, Sulawesi, Nord-Molukken, Neuguinea und die Kleinen Sunda-Inseln/Banda Arc. Die Verwandschaft zwischen diesen Endemitenzentren beweist, dass es zwei Gruppen von Inseln im indonesischen Archipel gibt.

Die erste Gruppe teilte früher Indonesien in drei Regionen:
1. Borneo, Java, Sumatra, Sulawesi und die Kleinen Sunda-Inseln ostlich bis zur Flores Insel;
2. Talaud Inseln, Sangihe Inseln., Nord-Molukken, Sanana Insel, die äußere Banda Arc westlich bis Timor und Neuguinea;
3. Wallacea Region.

Die zweite Gruppe teilt Indonesien heute ebenfalls in drei Regionen, ähnlich wie die erste, aber die Insel-Zuordnung ist eine andere. Es sind:
1. die Großen Sunda Inseln (Borneo, Java, Sumatra) und Bali;
2. Neuguinea, einschließlich Waigeo und Batanta; und
3. Wallacea Region.

Schließlich deuten diese unterschiedlichen Gruppen auf Verschiebungen der biogeographischen Linien im indonesischen Archipel hin.

Weiterhin beeinflussten die Oszillation des Klimas, eustatische Meerespiegelschwankungen und die Fluktuation der Vegetation im Quartär stark das Verbreitungsmuster der Tiere. Eine Expansionsphase der Trockenwälder und der Savannen lässt sich nachweisen während der Periode vor 18.000-14.000-Jahres in Ost-Indonesien und vor 16.500-12.000-Jahren in West-Indonesien. Diese Expansionen führten zu einer zunehmenden Isolation der Tieflandregenwälder und der dazu gehörenden Fauna. Diese Periode wurde auch von einer fallenden Baumgrenze gezeichnet, welche die montanen Faunen basimontan verschob. Vor 8.000-9.000 Jahren kam es zu einer Klimaerwärmung und es wurde etwas feuchter. Die Montanwälder expandierte während die Trockenwälder und Savannen kontrahierten.

Die Oszillation des Klimas, eustatische Meerespiegelschwankungen und Fluktuation der Vegetation determinierten schließlich die Formation von zahlreichen sub-Endemitenzentren, die innerhalb einer Insel vorkommen. Gegenwärtig gibt es 14 sub-Endemitenzentren auf Borneo, 8 auf Java, 16 auf Sumatra, 14 auf Sulawesi und 14 auf Neuguinea. Aus der Sicht des Naturschutz-Managements liefert die Identifikation solcher sub-Endemitenzentren wesentliche Informationen für Arten-Schutzmaßnahmen.

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Chapter 1

Introduction

For the principal goal of conservation activity, the concept of “Mega-diversity Countries” has been introduced (Mittermeier 1988; Mittermeier & Werner 1990; cited in Groombridge 1992) for which Indonesia is recognised as one of the 12 known countries, based on the lists of vertebrates, swallowtail butterflies, and higher plants (McNeely et al. 1990 in Groombridge 1992). Since then, Indonesian biodiversity is mostly concerned with species richness. For animals, Indonesia, which covers only 1.3% of the earth’s land surface, is recognised as harboring 6% of the world’s amphibian species and 7 %, 10% and 16% respectively of its reptile, mammal and bird species (FWI/GWF, 2002). It ranks first in the world for species richness of terrestrial mammals (515 species) and breeding birds (929 species), third for reptiles (745 species) and ninth for amphibians (278 species) (UNEP-WCMC, 2004).

Nevertheless, the geographic dimension of Indonesian biodiversity, especially endemicity across geographical gradients, is not as well accounted for. The term endemic itself, simply means occurring nowhere else. Organisms can be endemic to a location for two different reasons: either they originated in that place and never dispersed, or they now survive in only a small part of their former range. Organisms can be endemic to a geographic location on a variety of spatial scales and at different taxonomic levels. The lower the taxonomic categories, the narrower the geographic ranges are (Brown & Lomolino 1998).

The use of “endemic” or “restricted-range” species already begins to show the drawback to the approach of using species richness as it shows that it fails to take into account the *uniqueness* of the fauna and flora of a country or region (Groombridge, 1992). However, apart from the goal of each activity, most attempts to recognise Indonesian biogeography have mostly been based primarily upon the distribution of a single biota groups and in relatively higher taxonomical levels. As a result of this, Myers (1988, 1990 in Groombridge 1992) recognised only one “hotspot” (cf. “endemic centre” in this work) based on endemic plant species, in the Indonesian Archipelago, i.e. North Borneo. Meanwhile, Bibly *et al.* (1992) recognised 24 Endemic Bird Areas (EBAs) based upon the restricted ranged birds whose distribution are less than 50,000 km^2. Despite these high number of EBAs found, the geographical dimension of most lowlands, especially in the Great Sundas, are less clarified.

These two examples show that such analyses resulting in biogeographical units are valid only for a certain group; they have no general significance.

Similar to the proposals for delimiting Indonesian biogeography is the attempt to divide the Indonesian Archipelago into two faunal realms, i.e. Asiatic and Australian assemblages. Alfred Russel Wallace is the first scientist who drew a red line on the map passing down the Makassar Strait in 1863. To the west, he wrote "Indo-Malayan Region" and to the east, he wrote "Austro-Malayan Region" (Whitten, 1981). By the early twentieth century, other lines, shown on Fig. 1.1, had appeared among the islands, based on the distribution of one group of animals or another (George 1964 and Simpson 1977 in Whitmore, 1981). Of these lines, Wallace's line (1863-1880) and Lydekker's line (1896) concur with the Sunda and Sahul shelves. The attempts to precisely place such a "border line" continued until recently (cf. How & Kitchener 1997).

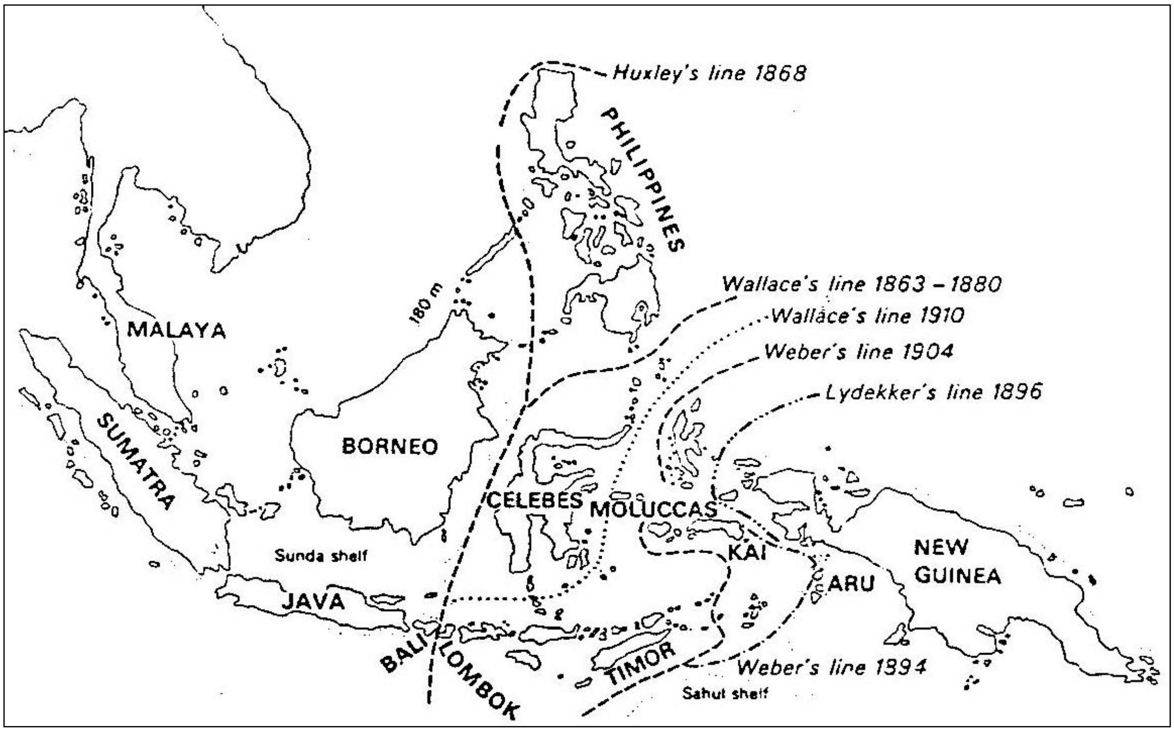


Figure 1.1 Different lines suggested for separating the Oriental and Australian faunal region, 1868-1910 (After George 1964 in George 1981).

While many scientists concentrated on two shallow water lines marking the Wallace and Lydekker lines, which represent a delineated ancient continent, other scientists have taken an ecological approach to boundaries. They are for example Salomon Müller in 1846, Zolinger in 1857, Lincoln in 1975 and van Steenis in 1979. The later approach defined regional faunas in terms of what they are, not what they were. However, like the first of all evolutionary zoogeographers, Wallace himself believe that regional zoogeography should reflect the geological, floral and faunal history of the area as well as present day distribution (Whitmore, 1981).

Closer relationships of zoogeographical distributions with abiotic factors were shown by Müller (1973), in his work on dispersal centres in the neo-tropical realm. The analysis of dispersal centres offers a more satisfactory approach. The importance of such centres was already recognised by De Lattin for the Holarctic realm (1957, 1967). The analysis of such centres begins from a comparative study of animal and plant distribution. It differs from the regional concept in being based entirely on the geographical ranges of species and subspecies ("Arealsysteme") representing real systematic units (Mayr, 1917).

Further, he shows that the results got by analysing dispersal centres are not only important for biogeography. They also help us to understand how species arose, and throw light on earth and climatic history and present-day landscape relationships. Dispersal centre are as important for the study of evolution as for geography.

Therefore the analysis of restricted-range taxa offers a more satisfactory approach in delimiting biogeography of a certain region. In regard to the well-known evidence of two faunal assemblages found on islands of the Indonesian Archipelago, I shall attempt to establish first the existence of Indonesian endemic centres (cf. "dispersal centres" of Müller, 1973) among the islands. Furthermore, the differentiation within the mainland is explained to clarify the existence of sub-endemic centres there. In this way, I hope to contribute to the correct geographical subdivision of Indonesia for the better understanding of Indonesian biogeography.

Chapter 2

Material and Methods

The systematics of Indonesian terrestrial vertebrates is comparatively well documented and information on their distribution on the islands of Indonesia is available in numerous published studies. Marine species are excluded. Bats are also excluded due to their flight capability. As a result of this, only birds are considered as representing a volant-group.

As explained under "Introduction", dispersal centres of Müller (1973) could be more or less compared to the endemic centre that I use in this work. Therefore I follow his work and work out the endemic centres by plotting the breeding ranges of species and subspecies on a map of the region under investigation. The individual ranges overlap in "areas of congruence" or "nuclear areas" ("Arealkerne" of Reinig 1937, 1950 in Müller 1973; hotspots in the US-Publication). It is the first task to ascertain regions where an unusually large number of ranges overlap, for these are what we call "endemic centres" or "dispersal centres" in term of Müller (1973).

It should not be assumed at the outset that dispersal centres represent "centres where faunas and floras were preserved during regressive phase" (De Lattin 1957 in Müller 1973), nor even that their origin is connected with the Pleistocene. It also is not to imply, *a priori*, that dispersal centre of particular taxa represent their centres or origin. To avoid misunderstanding, two ideas must be kept quite separate.

Every species possesses, or used to possess, at least one dispersal centre that was its centre of origin. During the evolution of a taxon, however, the centre of origin and the centre of dispersal can become widely separated from each other (Müller 1972 in Müller 1973).

Faunal elements of an endemic centre are species and subspecies, which resemble each other in their geographical distribution and which can be ascribed to that centre (De Lattin 1957 in Müller 1973). They are monocentric if monotypic species are related to only a single endemic centre. Contrastly, species related to several different endemic centres are polycentric. In regard to this, it assumes that the species or subspecies ranges plotted on the map of a region are relatively small compared with the region itself. On the other hand, the limits of range must be known with certainty and that the validity of the species and subspecies is not in dispute.

The limits of the ranges of species and subspecies sometime can only be worked out with greater or lesser probability unless they happen to be stabilised by natural barriers such as water or mountains. As concerns the ranges of subspecies, working out the limits of the ranges of subspecies is much easier due to the fact that populations differentiated to a subspecific degree must have allopatric distributions or non-overlapping ranges for reasons of evolutionary genetics (Müller 1973, 1980; Brown & Lomolino 1998).

Chapter 3

Investigation Area

The areas investigated in this work (Figure 3.1) are broader than the ranges of the Indonesian Region. This is because animals do not recognise political borders, for them physical barriers such as mountains or rivers are much more effective to limit their ranges. Therefore, Bornean fauna are regarded as occurring throughout all islands, including on the Indonesian Kalimantan, on Sarawak and Sabah on East Malaysia and on Brunei Darussalam. The same can be said for New Guinean fauna. These include fauna confined to Indonesian Irian Jaya on the western part and those confined to Papua New Guinea on the eastern part. Finally, fauna of Timor Island are also considered, as they are found on West Timor and on the recently independent East Timor. Except for ranges across political borders on some islands, the limits of investigation areas are relatively simple to define. Marine barriers are regarded as effective ones for most terrestrial vertebrates. Hence, the Malacca Strait is considered as a limit to Southeast Asia; Balabac Strait, Sibutu passage, and Celebes Sea to the Palawan Group, Sulu Archipelago and the East Philippines respectively; Vitiaz Strait to the New Britain of Bismarck Archipelago; and Arafura as well as Torres Strait to Australia.

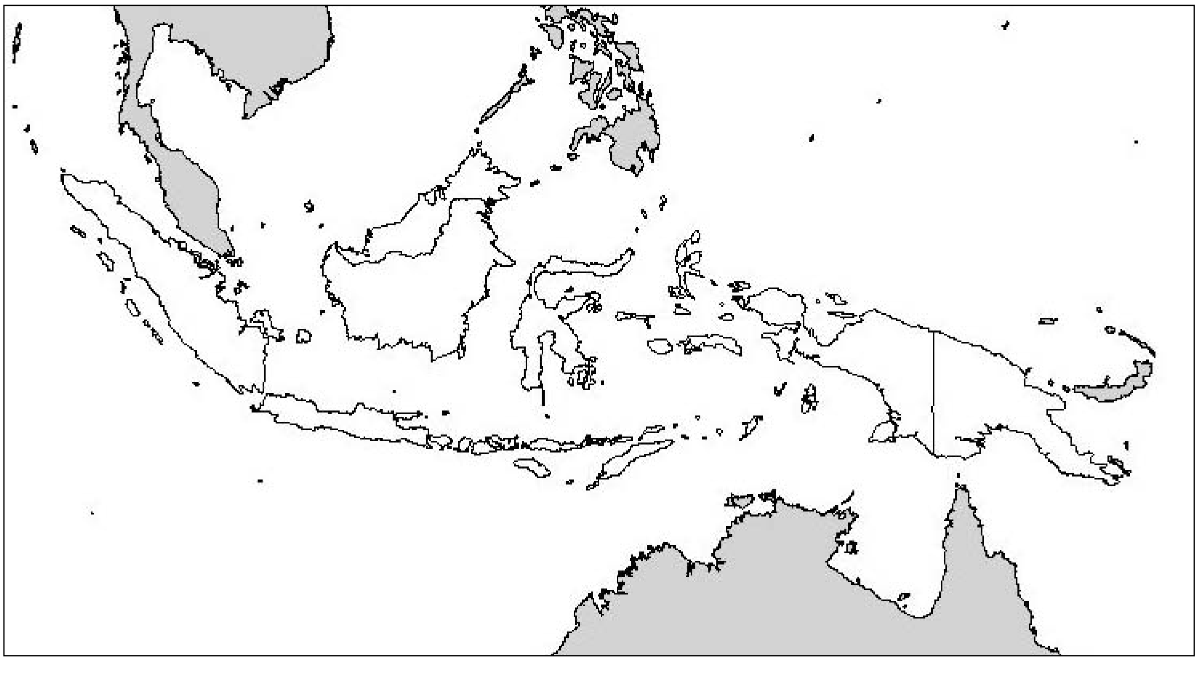


Figure 3.1 The investigation area (unshaded) including the Indonesian Republic, Papua New Guinea, Eastern Malaysia and Brunei, and East Timor.

Within the region itself, there are many terms used for island groups found there. The important island group names are derived from Whitmore (1981). They are as follows: **Greater Sunda Islands** includes Borneo, Java and Sumatra; **Lesser Sunda Islands** (Nusa Tenggara) is the geographical term for the islands east of Java from Bali and Lombok eastwards to Damar and Babar; **Banda Arc** is the geological term for the double arc of islands from Flores East through to Alor and Wetar and north to Banda (Inner Banda Arc) and from Raijua through Timor and the Tanimbar islands then north through the Kai Islands and west to Ceram and Buru (Outer Banda Arc); **Moluccas** is the geographical term for the islands which occupy the region between Celebes (Sulawesi) plus the Talaud and Sula Islands, Butung and the Tukangbesi Islands, the Lesser Sunda Islands, Aru and New Guinea (plus Misool and Waigeo). The biggest Moluccan Islands are Halmahera, Ceram, Buru and Tanimbar; **Wallacea** is the island region, which lies between Wallacea's line and Weber's line (see Fig. 1.1).

Chapter 4

The Endemic Centres of Terrestrial Vertebrates in the Indonesian Archipelago

4.1 Geographic Position and Faunal Elements of The Indonesian Endemic Centres

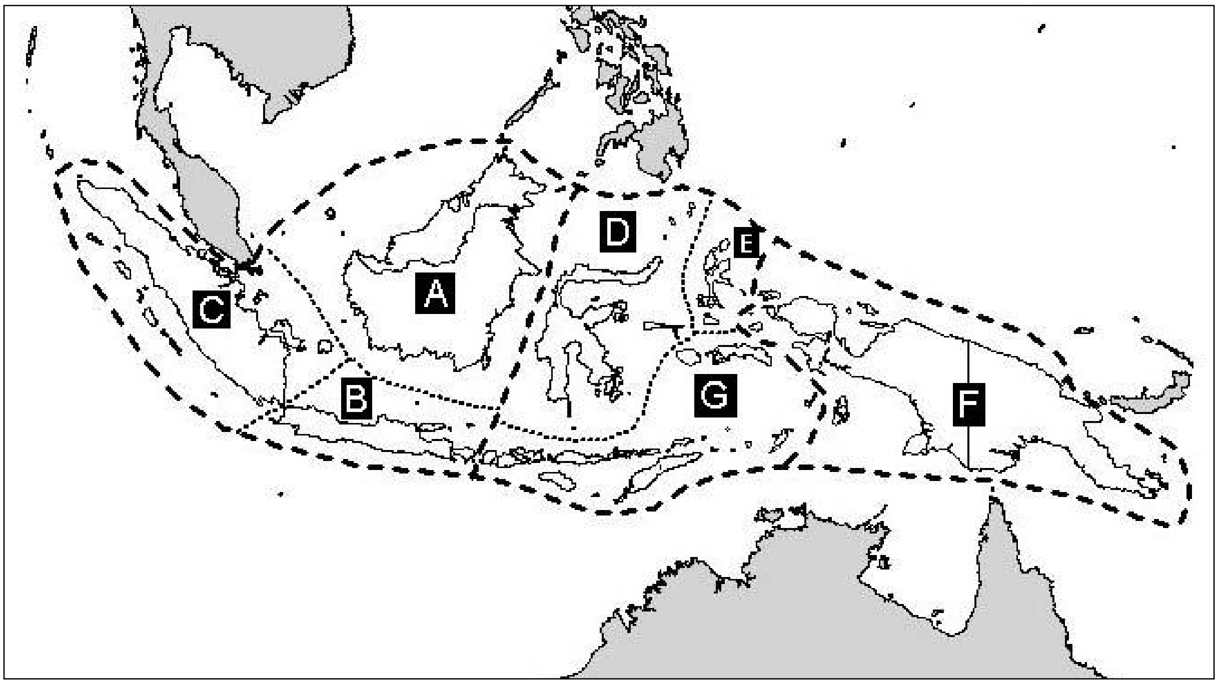


Figure 4.1 The geographic position of endemic centres in Indonesian Archipelago. A= Bornean Endemic Centre, B= Javan Endemic Centre, C= Sumatran Endemic Centre, D= Sulawesian Endemic Centre, E= North Moluccas Endemic Centre, F= New Guinean Endemic Centre and G= Lesser Sundas/Banda Arcs Endemic Centre.

4.1.1 The Bornean Endemic Centre

This endemic centre includes the mainland and the nearby Natuna and Anambas Islands to the northwest; Tambelan, Panembangan, Karimata and numerous other small islands to the west; Laut and Sebuku islands as well as Laut Kecil Island to the southeast; Panjang, Maratau, and Derawan Islands as well as Maratua Islands to the east; and Balembangan, Banggi and Malewali Islands to the north (see Figure 4.2).

Borneo is bigger than Sumatra and Java; therefore it is not surprising to note the higher numbers of Bornean amphibians, than on Sumatra and Java. Nonetheless, the endemism, which indicates the isolation level of taxa on a certain region, is also much higher for Bornean amphibians. This feature is rather odd, as islands of the Great Sundas are well known to have connected to each other in the last Glacial Maxima so that their faunal elements are expected to reflect the same pattern. Thus, the much higher endemism among Bornean amphibians compared to endemism in other Great Sunda Islands is interesting.

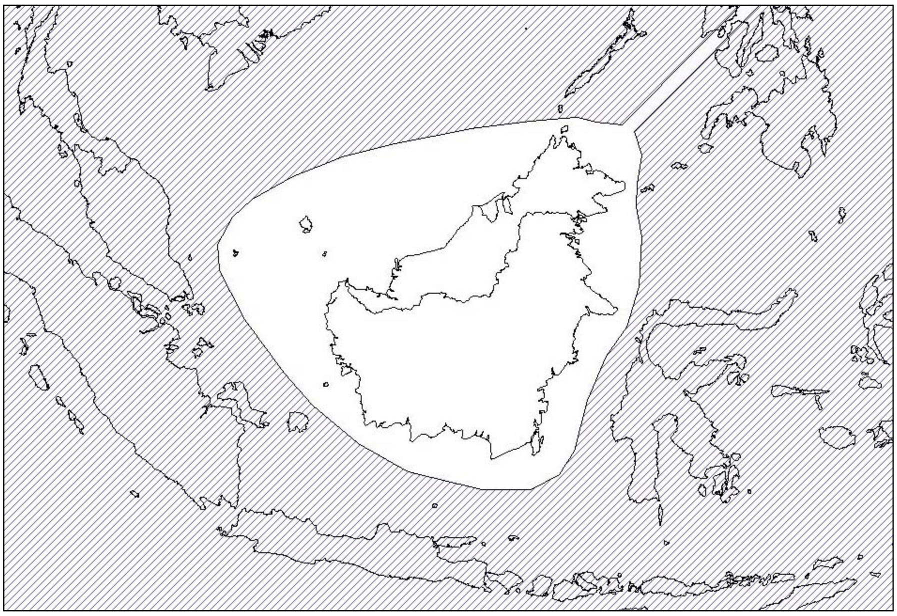


Figure 4.2 The Bornean endemic centre, comprising of the mainland and its satellite islands and including the Anambas Islands off Northwest Borneo, which provincially belongs to Sumatra.

The endemic forms on Borneo are represented by 97 taxa out of 157 taxa recorded (61.8%) (see Table 4.1). (This statement is based on data from Inger 1956, 1960, Matsui 1986, Dring 1987, Inger & Stuebing 1991, 1992, Yang Da-Tong 1991, Emerson & Berrigan 1993, Inger *et al.* 1995, Inger & Lian 1996, Malkmus & Riede 1996, Manthey & Grossmann 1997, Duellman 1999, Dubois & Ohler 2000, Emerson *et al.* 2000, Iskandar & Colijn 2000, Veith *et al.* 2001, Frost 2002). This endemism is even higher than that of the well known isolated Sulawesian amphibians, which accounts for only 51.7%.

Table 4.1 Endemic amphibians of Borneo and its nearby islands. An asterisk marks the monotypic genera.

Family	Genera with number of endemic species
Bombinatoridae	Barbourula 1
Bufonidae	Ansonia 11, Pedostibes 3, Pelophryne 5
Megophryidae	Leptobrachella 7, Leptobrachium 3, Leptolalax 5, Megophrys 2, Xenophrys 2
Microhylidae - Dyscophinae	Calluella 3
Microhylidae – Microhylinae	Gastrophrynoides* 1, Kalophrynus 6, Metaphrynella 1, Microhyla 3
Ranidae	Fejervarya 1, Huia 1, Ingerana 2, Limnonectes 6, Meristogenys 8, Occidozyga 1, Rana 1, Staurois 2
Rhacophoridae – Rhacophorinae	Philautus 16, Rhacophorus 6

In regard to the well known land bridge connected islands of the Great Sundas as already mentioned above, (which extended to Southeast Asia in the last Pleistocene Glacial Maxima), this feature is enigmatic as it shows not only that most Bornean amphibians experienced a long isolation, (obviously much longer since the Pleistocene Period), but it also suggests that most endemic forms did not reach the island by such a land bridge.

The distinction of Borneo has been indicated by the occurrence of a bombinatorid *Barbourula kalimantanensis*. Its only extant relative is *B. busuanga* on the Palawan and Busuanga Islands off Northeast Borneo, lying within the 200m isobath. While genus *Barbourula* is well restricted to these regions, its distant relative, genus *Bombina*, is found in Europe, Turkey, the former western Soviet Republic and disjuncted in the former Eastern Soviet Republic, China, Korea and Vietnam. In regard to the well-known amphibian ranges that are limited by marine barriers, it is probable that only tectonic movement brought an ancestor of *Barbourula* to Borneo and the nearby islands.

The assumption of such tectonic movement is supported by the range of *Ansonia* (Bufonidae). This genus occurs from Southern India to Northern Thailand, on the Malay Peninsula and on Tioman Island to the east, Borneo and the East Philippines. It could simply be thought that the genus reached Borneo and the East Philippines through the Malay Peninsula, but this is not evidenced by the strongly differentiated Bornean *Ansonia* with 13 species confined to out of 21 extant species and also with the location of the East Philippines, which is currently separated from Borneo by deep trenches. High differentiation of Bornean *Ansonia* at specific levels definitely needs a long duration of isolation, certainly much longer than since the last Glacial Maxima. If the ancestor did not penetrate through the Malay Peninsula, there must have been another way to bring *Ansonia*'s ancestors to Borneo and to the East Philippines. The only plausible explanation is a tectonic movement. It seems that only later in the last Pleistocene Glacial Maxima did they first disperse out from Borneo and migrate to Sumatra, Java and nearby islands as well as to Southeast Asia, possibly as far as Southern Thailand.

Another example showing dispersal by such tectonic movements is illustrated by the range of *Polypedates colletti* (Rhacophoridae). This taxon is prevalent from Peninsular Thailand southwards to Sumatra and Borneo with a disjunct population in Vietnam. From such a range, it can be seen that Borneo received its population from Vietnam and those currently found from Sumatra up to Peninsular Thailand are likely to be recent immigrants from Borneo. Furthermore, the occurrence of other *Polypedates* confined to, i.e. *P. leucomystax*, on the East Philippines, Sulawesi and perhaps New Guinea even suggest that tectonic movements resulted in oriental lineages drifting not only to Borneo and to the East Philippines, but also farther east to Sulawesi and New Guinea. Its possible occurrence on New Guinea comes from one synonym of *P. leucomystax*, i.e. *Hyla wirzi* Roux, 1927. This has been recorded from the Sentani Lake region in Northern New Guinea. This record has been commented on, if it is correct, type locality is likely in error. Nonetheless, now it is clear that its occurrence there might be naturally as a result of such tectonic movements.

Numerous genera are strongly differentiated on Borneo, indicating their early arrival through island drifts driven by tectonic movements. Such examples are *Pelophryne*, *Pedostibes* (Bufonidae); *Leptobrachium*, *Leptolalax* (Megophryidae); *Calluella* (Microhylidae – Dyschopinae); *Kalophrynus*, *Microhyla* (Microhylidae – Microhylinae); *Staurois* (Ranidae); *Rhacophorus* and *Philautus* (Rhacophoridae). Even genus Meristogenys (Ranidae) is endemic to Borneo. Also genus *Leptobrachella* (Megophryidae) is endemic to Borneo and the nearby South Natuna Islands off the northwestern coast of Borneo. Genus *Megophrys* and *Xenophrys* (Megophryidae) each are only represented by two species, but their ranges suggest that they also drifted to Borneo. Also the ranges of *Fejervarya* and *Huia* (Ranidae), some genera of *Limnonectes* (Ranidae), *Occidozyga* (Ranidae), *Nyctixalus* (Rhacophoridae), and *Polypedates* (Rhacophoridae) suggest that they arrived early on Borneo through island drifts.

On the other hand, the ranges of most monotypic genera suggest that they had their origin on Borneo. They are for example *Pseudobufo subasper* (Bufonidae), *Chaperina fusca* and *Gastrophrynoides borneensis* (Microhylidae – Microhylinae). The first taxon, *P. subasper*, is found on the Malay Peninsula, Sumatra and Borneo; *C. fusca* on Malay Peninsula, Borneo, Palawan, Mindanao, and Jolo in the Sulu Archipelago, Philippines; and *G. borneensis* on Sarawak. Also *Metaphrynella* (Microhylidae – Microhylinae) seems to have its origin on Borneo. The species that occurs on Borneo, *M. sundana*, ranges from Sabah and Sarawak to Western Kalimantan at low elevations. The only other extant species is *M. pollicaris* on the Malay Peninsula.

The high number of taxa sharing their ranges with the East Philippines supports the assumption of tectonic movements, drifting oriental lineages further east from Borneo as already mentioned above. They are *Pelophryne brevipes* (Bufonidae); monotypic *Chaperina fusca*, *Kalophrynus pleurostigma*, *Microhyla annectens* (Microhylidae – Microhylinae); *Fejerfarya limnocharis*, *Staurois natator* (Ranidae); *Nyctixalus pictus*, *Polypedates macrotis*, *Rhacophorus appendiculatus* and *R. pardalis* (Rhacophoridae – Rhacophorinae). Contrastly, only a few taxa also include Sulawesi within their ranges, i.e. *Kaloula pulchra pulchra*

(Microhylidae – Microhylinae); *Rana erythraea* (Ranidae); and *Polypedates leucomystax* (Rhacophoridae – Rhacophorinae). This evidence suggests that Bornean lineages apparently used the East Philippines as a stepping-stone in order to reach Sulawesi. On the other hand, the only species that possibly shares its range just with Sulawesi is *Limnonectes finschi* (Ranidae). This taxon is definitely confined to the eastern half of Sabah in Northern Borneo, but Iskandar (2000) reported a possible occurrence in Northern Sulawesi. Supposing this taxon does occur in Northern Sulawesi, this would suggest possibly another migration route for faunal exchange between Borneo and Sulawesi.

Other than to Sulawesi, early migration from Borneo to Java has been indicated by some species for example: *Bufo melanostictus* (Bufonidae); *Fejervarya limnocharis*, *F. nicobariensis*, *O. sumatrana*, *Rana chalconota*, *R. erythraea* (Ranidae); *Kaloula baleata baleata* (Microhylidae – Microhylinae); and *Polypedates leucomystax* (Rhacoporidae – Rhacophorinae). Their early existence on Java is mostly indicated by the occurrence of their disjunct populations either on Nicobar Island off Northwest Sumatra and/or on Sulawesi and the Lesser Sundas, which are today separated from Sumatra and Java respectively by deep marine barriers. Also *Occidozyga lima* which is recently absent on Borneo, seems to represent an early emigrant to Java.

While early emigration to Java can be well detected, this is not the case for Sumatra or the Malay Peninsula. Bornean lineages found on Sumatra and the Malay Peninsula are detected as recent immigrants from Borneo in the Pleistocene Period. On the other hand, Borneo also received numerous immigrants from Southeast Asia at this time. Those which migrated from Southeast Asia are easily detected by their ranges, which are restricted to the Great Sundas and the nearby islands within the 200m isobath or in other words, restricted to islands occurring on the Sunda Shelf. In contrast, Bornean lineages, which dispersed in this period, might have disjunct populations on islands situated outside the 200m isobath, as a result of their early dispersal. Additionally, those that migrated from Borneo to Southeast Asia have in common the northernmost limit on the Peninsular Thailand, below the Isthmus Kra.

In contrast to Sumatra and the Malay Peninsula, there is no indication of direct faunal exchanges between Borneo and Java in the Pleistocene Period. There are no taxa sharing their ranges with Java without also sharing with Sumatra. The only probable Bornean species, which possibly shares its range just with Java, is *Limnonectes hascheanus* (Ranidae). Manthey (1997), Iskandar (2000) and Frost (2002) recorded it from Malay Peninsula with disjunct populations either only on Natuna Islands off Northwest Borneo (Iskandar), or only on Java (Frost), or possibly on both Natuna and Java (Manthey). Additionally, this species also occurs from India to Vietnam. Through knowledge of early emigration of Bornean taxa to Java, such a range seems to have resulted from this kind of migration. The occurrence of disjunct populations on the Malay Peninsula, apart from that in the Indochina, clearly suggest that this taxon might have drifted early on to Borneo, extending further south to Java, and only later dispersed to the Malay Peninsula. Its absence on Borneo and its questionable record for the Natuna Islands and Java might be the result of its extinction in most parts of its range. Thus, it seems that there are absolutely no direct gene flow between Bornean and Javan amphibians in the Pleistocene Period.

Different to amphibians, endemism among Bornean mammals only accounts for i.e. 80 endemic forms out of 150 taxa (53.3%) (see Table 4.2) (Corbet & Hill 1992, Wilson & Reeder 1993, Yanuar *et al*. 1993, Suyanto *et al*. 1998, Nowak 1999).

Table 4.2 Endemic mammals of Borneo and its nearby islands. An asterisk marks the monotypic genera

Family	**Genera with number of endemic species (and endemic subspecies)**
Cercopithecidae	Nasalis *1, Presbytis (10)
Cervidae	Muntiacus 1
Erinaceidae	Echinosorex* (1), Hylomys* (1)
Felidae	Felis (Catopuma) 1
Hylobatidae	Hylobates (3)
Hystricidae	Hystrix 1
Muridae – Murinae	Chiropodomys 3, Haeromys 1, Maxomys 3, Pithecheirops *1, Rattus 1
Mustelidae	Melogale 1
Pongidae	Pongo (1)
Sciuridae	Aeromys 1, Callosciurus 2(16), Dremomys 1, Exilisciurus 2, Glyphotes *1, Lariscus 1, Petaurillus 2, Petaurista (1), Petinomys (1), Rheithrosciurus *1, Sundasciurus 2(4)
Soricidae	Suncus 2
Tupaiidae	Dendrogale 1, Tupaia 4(5)
Viverridae	Diplogale *1, Paguma *(1)

This excludes *Cuon alpinus* (Canidae) that possibly occurred there in the Pleistocene Period. Such an endemism is obviously higher than between Sumatran and Javan mammals, but much lower than in mammals of Sulawesi, Northern Moluccas and New Guinea. This in turn suggests that Bornean mammals also experienced long isolation as did the amphibians, but their better ability to disperse has likely strongly reduced their endemism. Positive evidence comes from the higher number of shared taxa in mammals than in amphibians with Sumatra. Shared taxa in mammals reach 68 taxa (44%), while in amphibian's only 36 taxa (26.3%).

The number of mammals, which presumably reached Borneo by way of tectonic movements, is surprisingly high. This gives us a clue that landmasses, which drifted by tectonic movements, must have been big enough, so that they could transport a number of mammals, which are generally bigger and heavier than amphibians. This is found to be true when we see that some of the mammals transported in this manner are quite large in size. The mammals, which likely arrived on Borneo through such a migration way, are listed in Table 4.3. Further comprehensive genetic analysis is needed to support this assumption.

Table 4.3 Examples of mammals, which presumably drifted to Borneo from Asia

Family	Taxa
Bovidae	*Bubalus bubalis*
Cercopithecidae	*Macaca fascicularis, M. nemestrina, Presbytis hosei sabana, Trachypithecus cristatus*
Cervidae	*Axis kuhlii, Cervus timorensis, Muntiacus muntjak*
Elephantidae	*Elephas maximus*
Hystricidae	*Hytrix brachyura brachyura*
Muridae - Murinae	*Bandicota bengalensis, B. indica, Chiropodomys gliroides, Leopoldamys edwardsi, Maxomys surifer, Mus caroli, M. cervicolor, M. terricolor, Rattus argentiventer, R. exulans, R. tanezumi*
Mustelidae	*Melogale everetti, Mustela nudipes*
Pongidae	*Pongo pygmaeus pygmaeus*
Sciuridae	*Callosciurus nigrovittatus, Dremomys everetti, Hylopetes spadiceus, Petaurista elegans banksi, Petinomys setosus, Pteromyscus pulverulentus, Sundasciurus hippurus pryeri.*
Soricidae	*Crocidura attenuata, C. fuliginosa, Suncus hosei, S. murinus*
Suidae	*Sus barbatus*
Tupaiidae	*Dendrogale melanura, Tupaia montana*
Viverridae	*Cynogale bennettii, Viverra tangalunga*

Regarding the readiness of mammals to disperse in comparison to amphibians, some mammals, which drifted early on to Borneo and dispersed later to Southeast Asia, have distribution ranges that are similar to those which migrated recently from Southeast Asia. An example of it is the range of *M. muntjak* (see Figure 4.3), simply leading to the thought that this species is a recent immigrant from Southeast Asia. This species ranges throughout India, marginally in Northeast Pakistan and east to South China, continuously south to Malaya; Sumatra, Java, Borneo; Sri Lanka; Hainan; and on the smaller islands of Middle Andaman (possibly introduced), Pangkor (Malaya), Singapore (extinct).

Nevertheless, the occurrence of an endemic *M. atherodes* on Borneo suggests that this species might have originated on Borneo, being derived from an ancestor that reached Borneo very early. Wurster-Hill & Atkins (1972 in Corbet and Hill, 1992) was able to show karyological differences between the Sunda animals (*M. m. muntjak*) and those further north (*M. m. vaginalis*) that might support their recognition as separate species. In regard to this, it seems that *M. muntjak* is the ancestor of *M. atherodes*. *M. atherodes* itself was for long known as a subspecies of *M. muntjak* (Corbet and Hill, 1992). The early arrival of *M. muntjak* on Borneo is indicated by its success in colonising Lombok Island in the Lesser

Sunda, lying outside the Sunda Shelf. A land bridge, which existed in the last Pleistocene Glacial Maxima, had apparently united the broken gene flow, which had existed until the time that the Bornean form drifted away from Asia.

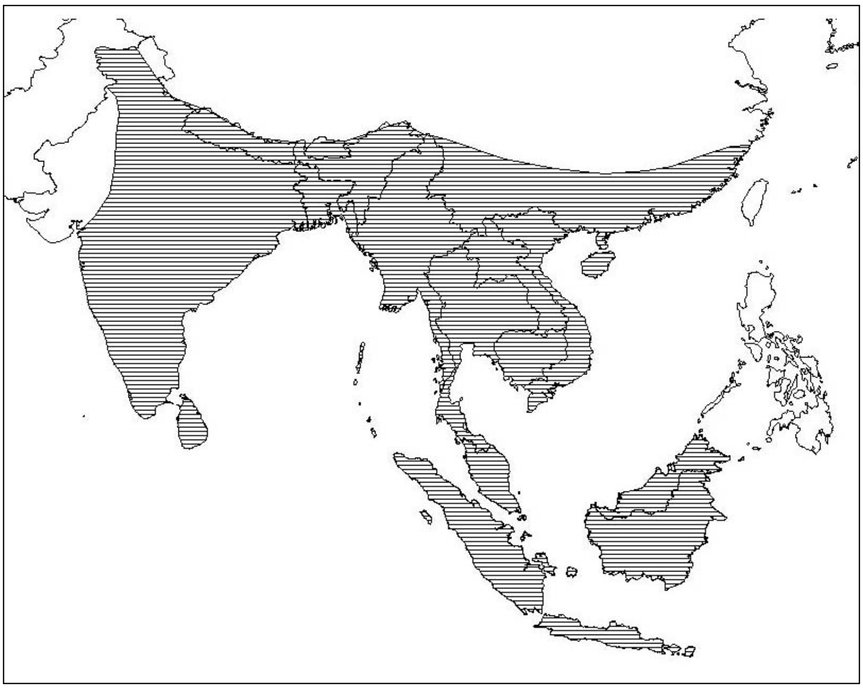


Figure 4.3 The distribution range of *Muntiacus muntjak* (horizontal hatching) (From Corbet & Hill, 1992). Its continuous distribution from Southeast Asia to the Great Sundas leads to the thought that it migrated in the Pleistocene Glacial Maxima from Southeast Asia through a land bridge. This study shows that the population on the Great Sundas may have been derived from lineages, which drifted early on to Borneo from Asia much earlier than the Pleistocene Period.

It seems that Corbet and Hill (1992) were correct to keep *Chiropodomys pusillus* (Muridae – Murinae) within *C. gliroides* although Nowak (1999) treated both of them as two separate species. The occurrence of a disjunct population of *C. gliroides* on the Malay Peninsula in the south of the Isthmus of Kra (see Figure 4.4) may indicate that this population was derived from the Bornean lineage, which has migrated there in the Pleistocene Period, and not from the South Asian lineage, which is disjuncted far to the north. In regard to this, I follow Corbet and Hill in considering *C. pusillus* of Borneo in this work as *C. gliroides*.

Similar to amphibians, there are a lot of indications of early migration to Sulawesi and Java by some mammals. Those that migrated to Sulawesi mostly resemble amphibians in that they drifted first to the East Philippines. Such species, whose ranges still include Borneo, are for example *Paradoxurus hermaphroditus*, *Viverra tangalunga* (Viverridae); *Suncus murinus* (Soricidae); and *Rattus argentiventer* (Muridae – Murinae). Their ranges beyond the 200m isobath, i.e. beyond the Sunda Shelf, are mostly regarded as a result of human introduction, but they are likely to naturally have come about as a result of tectonic movements. In contrast to amphibians, there is positive evidence showing another migration route for faunal exchange between Borneo and Sulawesi, which is not through the East Philippines. A macaque confined to Borneo, i.e. *Macaca nemestrina*, is closely related to Sulawesian macaques. They all belong to the silenus group. While Sulawesian macaques are restricted to the Sulawesian mainland and its nearby islands, *M. nemestrina* occurs on Assam, Burma, Southern Yunnan, Thailand, Indochina, Malay Peninsula, Sumatra, Bangka, Borneo and some small nearby islands. There are no populations of the silenus group that are found on the Philippines or Java. Thus, Sulawesian macaques seem to have been derived from Bornean lineages, which directly drifted to Sulawesi.

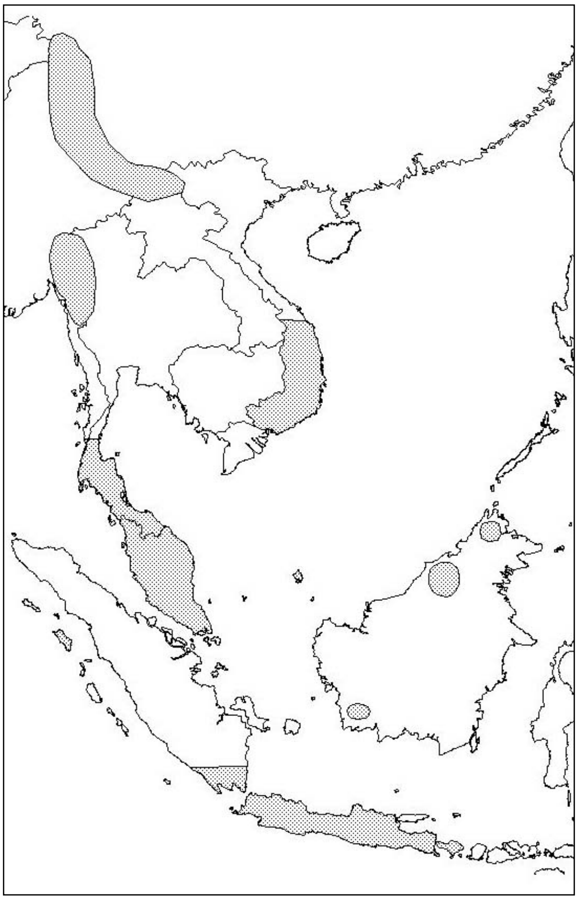


Figure 4.4 The range of *Chiropodomys gliroides* (grey-shaded). The occurrence of disjunct populations on the Malay Peninsula, apart from population in the north of the Isthmus of Kra, apparently resulted from migration from Borneo in the Pleistocene Period.

Early migration to Java is well indicated by the ranges of some taxa, for example *Macaca fascicularis*, *Trachypithecus cristatus* (Cercopithecidae); *Rattus tanezumi*, *R. tiomanicus*, *R. argentiventer*, *Chiropodomys gliroides*, *Niviventer cremoriventer* (Muridae – Murinae); possibly *Felis (Prionailurus) bengalensis* (Felidae); possibly *Paradoxurus hermaphroditus* (Viverridae); *Crocidura fuliginosa*, possibly *C. monticola*, *Suncus murinus*

(Soricidae); and *Manis javanica* (Manidae). Some of them, i.e. *M. fascicularis*, *R. tanezumi* and *R. tiomanicus*, have disjunct populations on Nicobar Island. All records for outside the 200m isobath are mostly regarded as a result of human introduction. In contrast to amphibians, there is positive evidence from taxa whose ranges are shared between Borneo and Java but not Sumatra, showing a possible early migration from Borneo to Java. Such taxa are for example the wild *Bos javanicus* (Bovidae) and *Crocidura monticola* (Soricidae). Populations of wild *B. javanicus* occur from Myanmar, Thailand and Vietnam to the Northern Malay Peninsula with disjunct populations on Borneo and Java (see Figure 4.5). Populations on Enggano Island off Southwest Sumatra and on Sangihe Island off Northeast Sulawesi are regarded as a result of probable feral domestic introduction.

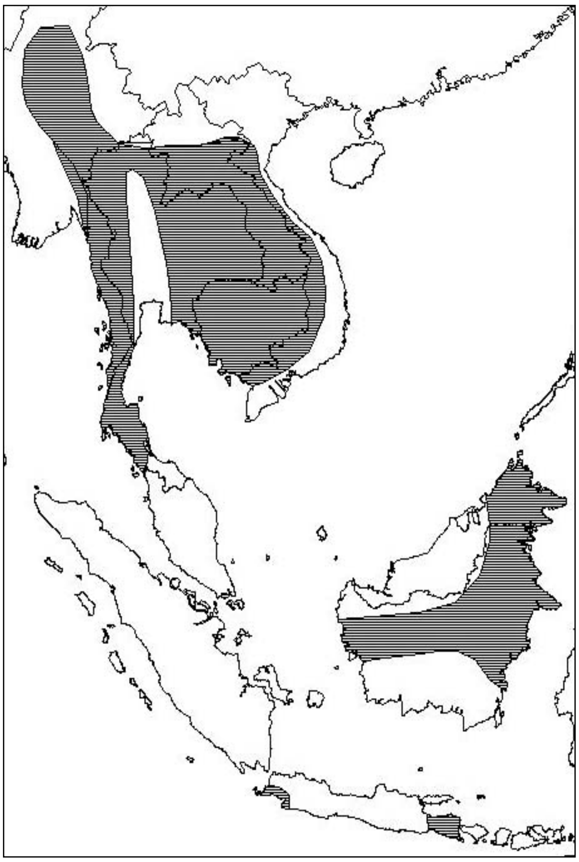


Figure 4.5 The distribution range of the wild *Bos javanicus* (horizontal hatching) (After Corbet & Hill, 1992). Population on Borneo might have resulted from an early migration from Asia through an island drift. It presumably migrated later to Java through a land bridge, which once existed in the Pliocene period about 6.6 Ma years ago.

On the other hand, *C. monticola* is found on the Malay Peninsula, on Borneo and on Java, and its close relative, *C. maxi*, is found from Java eastwards to Obi, Ambon, Timor and Aru Island. Most of its ranges in the East Indies are considered as being introduced. It is very difficult to find out whether these represent early migrants from Borneo to Java or recent migrants from Southeast Asia, which are extinct on Sumatra. This would lead us to believe that there was possibly human introduction. Nonetheless, the fact that their ranges do not match with Pleistocene dry relicts in spite of their preferred habitats on drier and open areas, suggest that they are not Pleistocene migrants.

Of the 268 reptiles confined to Borneo, 97 (36.2%) are endemic forms (see Table 4.4) (Uetz 2005, Schulz 1996, Das 1998, McDiarmid *et al.* 1999, Iskandar 2000). This endemism is higher than between Sumatran and Javan reptiles, but much lower than among Bornean amphibians and mammals. Such lower endemism indicates a much better ability of reptiles to disperse than amphibians and mammals, despite their long isolation on Borneo. This assumption is supported by a lot more taxa of reptiles with disjunct populations outside the 200m isobath, such as on the Indochina and Philippines, in comparison to the level of taxa of amphibians and mammals. Furthermore, most of them have broad distribution ranges, extending far eastwards to Sulawesi, Moluccas and to New Guinea and even further east to the Pacific Islands. All these features support the theory that reptiles are the best group to disperse broadly by island drifts.

Table 4.4 Endemic reptiles of Borneo and its nearby islands. An asterisk marks the monotypic genera

Family	Genera with number of endemic species (and endemic subspecies)
Agamidae	Aphaniotis 1, Calotes 1, Draco 2(1), Gonocephalus 1, Harpesaurus 2, Hypsicalotes* 1, Phoxophrys 4, Pseudocalotes 1
Anguidae	Ophisaurus 1
Anomochilidae	Anomochilus 1
Colubridae	Amphiesma 2, Boiga (1), Calamaria 10(1), Enhydris 1, Hydrablabes 2, Oligodon 3(2), Oreocalamus* 1, Pareas 1, Pseudorabdion 3, Psedoxenodon 1(1), Rhabdophis 1, Stegonotus 1, Stoliczkaia 1
Crocodylidae	Crocodylus 1
Cylindrophiidae	Cylindrophis 2
Elapidae	Bungarus (1), Maticora (3)
Gekkonidae	Cnemaspis 1, Cyrtodactylus 7, Lepidodactylus 1, Luperosaurus 1, Ptychozoon 1
Lanthanotidae	Lanthanotus* 1
Scincidae	Apterygodon* 1, Brachymeles 1, Lamprolepis 2, Sphenomorphus 14, Tropidophorus 6
Tropidophiidae	Xenophidion* 1
Typhlopidae	Ramphotyphlops 1, Typhlops 1
Viperidae	Ovophis 1, Trimeresurus 1(1)

Of early migrants to Java, at least six taxa did not extend further west to Sumatra. They are *Harpesaurus tricintus* (Agamidae); *Python molurus bivittatus* (Boidae); *Calamaria bicolor*, *C. lateralis*, *C. lowii* (Colubridae); and *Crocodylus siamensis* (Crocodylidae). Frost (2002) proposed the possible extinction of *C. siamensis* in many areas, e.g. on Malaysia and Indonesia, in order to explain their absence there. Early migration to Java would however more easily and plausibly explain such ranges.

The endemism among Bornean birds is also higher than between Sumatran and Javan birds. With 241 endemic forms (see Table 4.5) out of 501 birds recorded (48.1%) (Andrew 1992, MacKinnon & Phillipps 1993, Jones *et al.* 1995, Laman *et al.* 1996, Stattersfield *et al.* 1998, Clements 2000). This in turn also indicates a long evolution of most Bornean birds. The restriction of birds on isolated islands has long concerned scientists.

Table 4.5 Endemic birds of Borneo and its nearby islands. An asterisk marks the monotypic genera

Family	Genera with number of endemic species (and endemic subspecies)
Accipitridae	Accipiter (1), Aviceda (1), Spilornis 1(2)
Aegithinidae	Aegithina (2)
Alcedinidae	Actenoides (1), Ceyx (1), Pelargopsis (1)
Apodidae	Aerodramus (6)
Bucerotidae	Buceros (1)
Campephagidae	Coracina (2), Pericrocotus (2)
Capitonidae	Calorhamphus* (2), Megalaima (4)
Chloropseidae	Chloropsis (2)
Cinclosomatidae	Eupetes* (1)
Cisticolidae	Prinia (1)
Columbidae	Macropygia (2), Treron (2)
Corvidae	Cissa (1), Dendrocitta 1, Platysmurus (1)
Cuculidae	Carpococcyx 1, Chrysococcyx (1), Phaenicophaeus (2)
Dicaeidae	Prionochilus 1(1)
Dicruridae	Dicrurus (4)
Estrildidae	Erythrura (2), Lonchura 1(5)
Eurylaimidae	Calyptomena 1, Corydon* (1), Cymbirhynchus* (1), Eurylaimus (2)
Falconidae	Microhierax 1
Monarchidae	Hypothymis (4), Terpsiphone (1)
Muscicapidae	Aethopyga (1), Anthreptes (3), Arachnothera (6), Cyornis 1(7), Copsychus (8), Enicurus (1), Eumyias (1), Ficedula (1), Rhinomyias (1)
Nectariniidae	Chalcoparia* (2), Hypogramma* (1), Leptocoma (2)
Oriolidae	Oriolus 1(2)
Pachycephalidae	Pachycephala (2)
Paramythiidae	Dicaeum 1(4)
Paridae	Parus (1)
Phasianidae	Arborophila (3), Argusianus* (1), Caloperdix* (1), Haematortyx* 1, Lophura 1(2), Melanoperdix* (1), Polyplectron 1, Rhizothera* (1)
Pycnonotidae	Alophoixus (5), Hemixos (1), Pycnonotus (2),
Picidae	Celeus (1), Chryocolaptes (1), Dendrocopos (1), Dinopium (1), Meiglyptes (2)
Pittidae	Pitta 2(3)
Pityriaseidae	Pityriasis* 1
Podargidae	Batrachostomus 1(1)
Prionopidae	Philentoma (1), Tephrodornis (1)
Psittacidae	Psittacula (1)
Pycnonotidae	Alophoixus (6), Hemixos (1), Pycnonotus (13), Tricolestes* (1)
Rallidae	Porzana (1)
Rhipiduridae	Rhipidura (2)
Sittidae	Sitta (1)
Strigidae	Glaucidium (1), Ketupa (1), Ninox (1), Otus (3), Strix (2)
Sturnidae	Aplonis (2)
Sylviidae	Abroscopus (1), Cettia (2), Orthotomus (6), Seicercus (1)
Timaliidae	Alcippe (1), Garrulax (5), Macronous (7), Malacocincla (4), Malacopteron (5), Napothera 1(1), Pellorneum (5), Pomatorhinus (1), Pteruthius (1), Ptilocichla 1, Stachyris (7), Trichastoma (1), Yuhina (1)
Trogonidae	Harpactes (3)
Turdidae	Brachypteryx (1), Myophonus (1), Turdus (1), Zoothera (1)
Tytonidae	Pholidus (1)
Zosteropidae	Chlorocharis* (4), Oculocincta* 1

Currently, the most widely accepted explanation for the evolution of flightlessness in birds involves selective pressures associated with the absence of predators and limited resources on islands (McNab 1994; Diamond 1991 in Brown and Lomolino 1998). Thus, most oriental lineages from Asia seem to have drifted early on to Borneo, as have the other non-volant groups. Some taxa, which drifted to Borneo, are for example *Eurostopodus temminckii* (Caprimulgidae); *Irediparra gallinacea gallinacea* (Jacanidae); *Ficedula dumetoria muelleri*, *Ficedula hyperythra sumatrana*, *Ficedula westermanni westermanni* (Muscicapidae); *Coturnix chinensis lineata* (Phasianidae); and *Gallirallus striatus striatus* (Rallidae).

On the other hand, it is easy for birds, which do not lose their flight capability, to colonise remote islands that are hard to reach by other non-volant group. We gained greatly from this because they show possible migration routes that are rarely shown by non-volant groups. The range of *Ducula pickeringii ssp.* (Columbidae), for example, on small islands off Northeastern Borneo, Sulu Archipelago, and Northern Sulawesi show one such migration route, which connected Borneo with Sulawesi via the Sulu Archipelago.

An interesting phenomenon observed for birds is the restriction of some taxa to the northern Bornean region, though their close relatives are widely found on other islands. These are for example *Turdus poliocephalus seebohmi* (Turdidae), *Aerodramus linchi dodgei* (Apodidae) and *Macropygia emiliana borneensis* (Columbidae). While these taxa occur on high elevations in the mountains of Northern Borneo, their relatives from other regions surprisingly have been recorded mostly in lower elevations.

Differentiation within the Bornean mainland

Differentiation among Bornean fauna within the mainland is considerably high. Numerous taxa have determined the existence of sub-endemic centres on the mainland. There are at least fourteen sub-endemic centres (Figure 4.6) based mainly on the distribution of *Hylobatus agilis* and *H. Mueller* (Hylobatidae)*i; Presbytis frontata, P. hosei, P. femoralis,* and *P. Rubicunda* (Cercopithecidae)*; Callosciurus prevostii* (Sciuridae) an*d Tupaia tana* (Tupaiidae) (data derived from Payne *et al*. 1985 and Swindler & Erwin 1986 in MacKinnon *et al*. 1997).

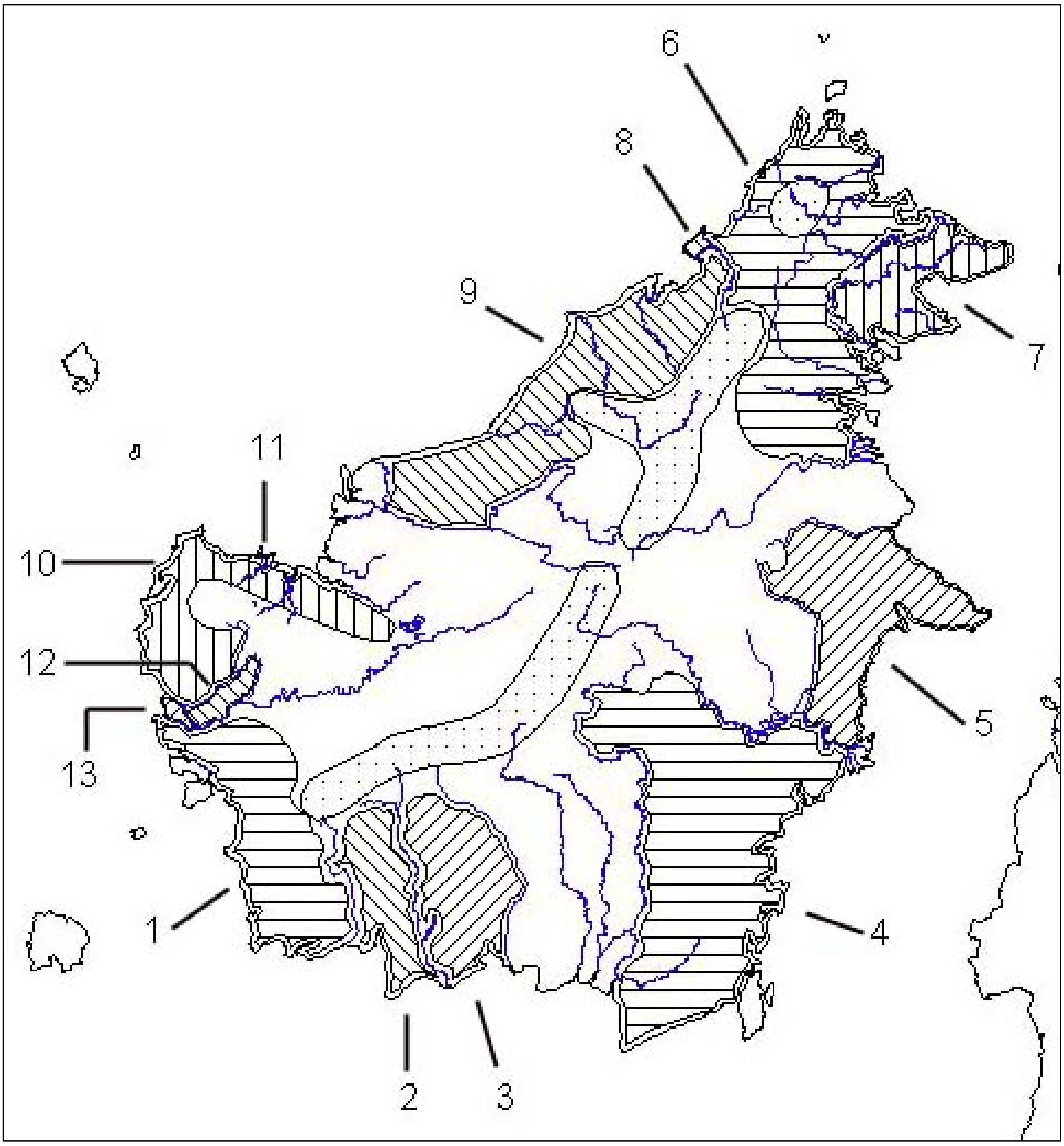


Figure 4.6 The fourteen sub-endemic centres on the Bornean mainland: 1) Kapuas-Arut 2) Arut-Seruyan 3) Seruyan-Katingan 4) Southeast Borneo 5) Mahakam-Berau 6) Kayan-Kalupis 7) Brassey-Kinabatangan 8) Lower Padas 9) Padas-Rajang 10) Lupar-Landak 11) Teluk Datu 12) Landak-Kapuas 13) Lower Kapuas and 14) Central Highlands (stipples)

1. Kapuas – Arut

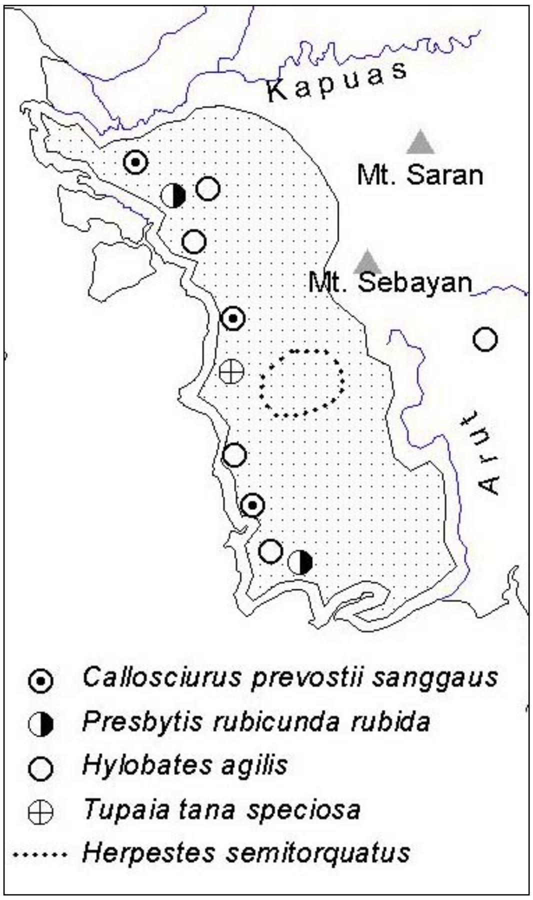


Figure 4.7
Distribution faunal elements of the Kapuas-Arut sub-endemic centre (stipples). The Kapuas River to the north is a strong barrier, in contrast to the mountain barrier to the east. *Hylobates agilis*, *Tupaia tana speciosa*, and *Herpestes semitorquatus* are examples of taxa that extend farther east.

This sub-endemic centre (Fig. 4.6 No.1; Fig. 4.7) is mainly made up of lowlands and mangroves with scattered hills in between. It is bordered on the north by the Kapuas River and in the east by of Mt. Saran (1,758m), and Mt. Sebayan (1,377m), as well as the Arut River. Its existence is defined by the ranges of the endemic forms *Presbytis rubicunda rubida* (Cercopithecidae) and *Callosciurus prevostii sanggaus* (Sciuridae). Dense forest inhabitant, whose altitudinal ranges attained mid-montane altitudes, such as *Tupaia tana speciosa* (Tupaiidae), is apparently isolated to the Mt. Palung area. In contrast to this, its disjunct populations in Eastern Borneo have obviously broader ranges. Additionally, also to be found here are *Hylobates agilis* (Hylobatidae) and *Herpestes semitorquatus* (Herpestidae). The first extends as far east as the sub-endemic centre of Seruyan-Katingan and the latter also occurs in Sabah and Sarawak in Northern Borneo as well as in the sub-endemic centre of Seruyan – Katingan.

2. Arut – Seruyan

This sub-endemic centre (Fig. 4.6 No.2; Fig. 4.8) can be defined by the range of the endemic *Callosciurus prevostii waringensis* (Sciuridae). It is only a narrow area between the Arut and Seruyan rivers. To the north, a West-East tributary of Seruyan River limits it. The only migration lying on the upper river was relatively easily blocked by the low tree line in the Last Glacial Maxima. Disjunct populations of other faunal element, *H. agilis ssp.*, are found on Kapuas – Arut to the west and on lower drainage areas of the Mendawai and Kahayan rivers to the east.

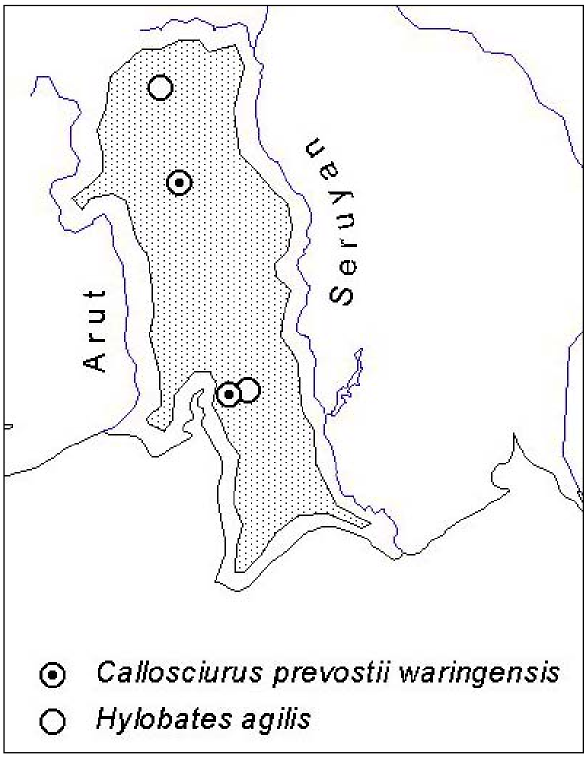


Figure 4.8

Sub-endemic centre of Arut – Seruyan (stipples). The only migration way on the upper river is susceptible to the isolation by the lowered tree line in the Last Glacial Maxima.

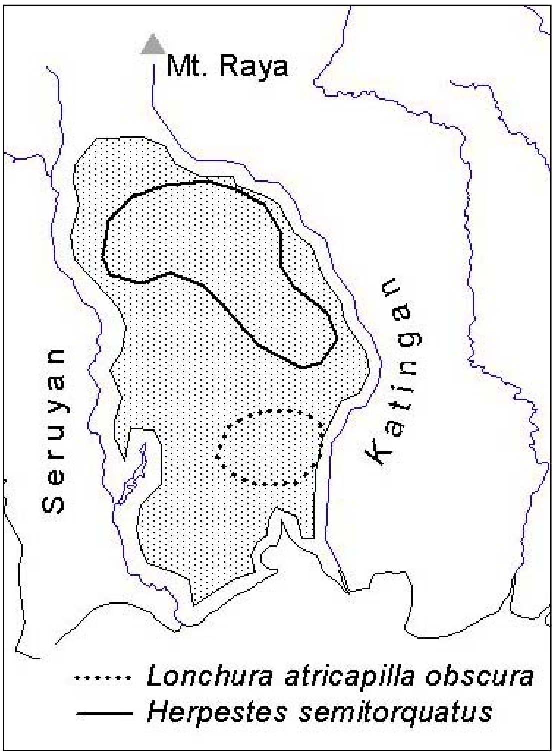


Figure 4.9
The sub-endemic centre of Seruyan-Katingan (stipples). It resembles much the Arut-Seruyan sub-endemic centre in having the only migration way on the upper river to the north. Close relative of *L. a. obscura* occurs as a faunal element of Kapuas Delta sub-endemic centre in West Borneo.

3. Seruyan – Katingan

The position of this sub-endemic centre (Fig. 4.6 No.3; Fig. 4.9) can be defined by the range of the endemic *Lonchura atricapilla obscura* (Estrildidae). This area is limited by the Seruyan River to the west and by the Katingan River to the east, which arise from Mt. Raya (2,278m). To the north, it is bounded by the Schwaner Mts. Also to be found here is *Herpestes semitorquatus*, which also occurs in the Kapuas-Arut sub-endemic centre to the west. In regard to habitat preferences of its faunal elements to drier habitats, this region seems to represent one of the Pleistocene dry habitat relicts.

4. Southeast Borneo

This sub-endemic centre (Fig. 4.6 No.4; Fig. 4.10) is made up of mainly lowlands on the eastern side of the Meratus Range; being bordered on the west by the Barito River as well as its tributary the Negara River. The Mahakam River limits it to the north. The distinction of this region has been indicated by the occurrence of at least two endemic birds separated at species level, i.e. *Lonchura pallidiventer* (Estrildidae) and *Zosterops flavus* (Zosteropidae). Some other faunal elements suggest close affinities with those confined to the Southern Philippines, Java or other islands eastwards instead of to the other regions within the Bornean mainland. For example *Chrysococcyx minutillus aheneus* (Cuculidae); *Dicaeum trochileum trochileum* (Paramythiidae); *Gallinula tenebrosa frontata* (Rallidae) and *Acrocephalus stentoreus lentecaptus* (Sylviidae).

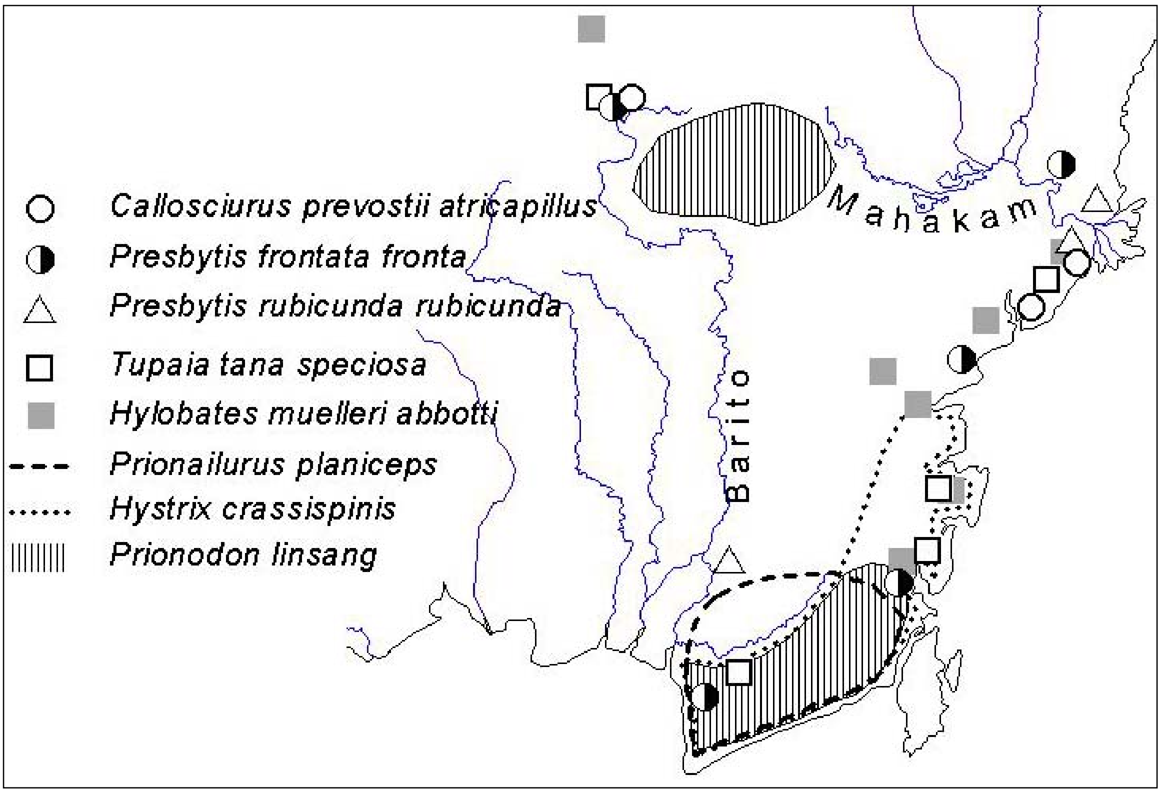


Figure 4.10 The distribution of faunal elements in the sub-endemic centre of Southeast Borneo. *C. p. atricapillus*, *P. planiceps, H. crassispinis* and *P. linsang* shared their ranges with northern Borneo, crossing over the highlands of Central Borneo.

Mammals such as, *Tupaia tana speciosa* (Tupaiidae), which are rarely found in the Kapuas-Arut region, has a broader range in this region, where it has been continuously recorded in the rainforests along coastal areas. Also to be found in this region are for example *Hylobates muelleri abbotti* (Hylobatidae), *Presbytis frontata fronta*, *P. rubicunda rubicunda* (Cercopithecidae), and *Callosciurus prevostii atricapillus*. While most faunal elements show close affinities to those on the Mahakam-Berau sub-endemic centre to the north, *C. p. atricapillus* remarkably crosses over the upper rivers of Mahakam and Kapuas to Northwest Borneo. Also these taxa show close affinities to North Borneo, i.e. *Prionodon linsang* (Viverridae), *Prionailurus planiceps* (Felidae) and *Hystrix crassispinis* (Hystricidae).

5. Mahakam - Berau

The position of this sub-endemic centre (Fig. 4.6 No.5; Fig. 4.11) can be defined by the range of the endemic *Presbytis hosei canicrus* (Cercopithecidae). It is bordered by the Mahakam River in the south, the Telen River in the west, and the Berau River in the north. This division is dominated by a mountainous region in the northern part, the Sambaliung Range. Its physiography gradually changed southwards to extensive lowlands of the lower Telen and Mahakam rivers. For *H. m. abbotti* (Hylobatidae) and *Tupaia tana speciosa* (Tupaiidae), this division is their northernmost range. On the other hand, *Callosciurus pluto atrox* (Sciuridae) has replaced *C. p. atricapillus* here. Additionally, some faunal elements, such as *Presbytis frontata fronta* and *Callosciurus pluto atrox*, extend as far northward as the Kayan River.

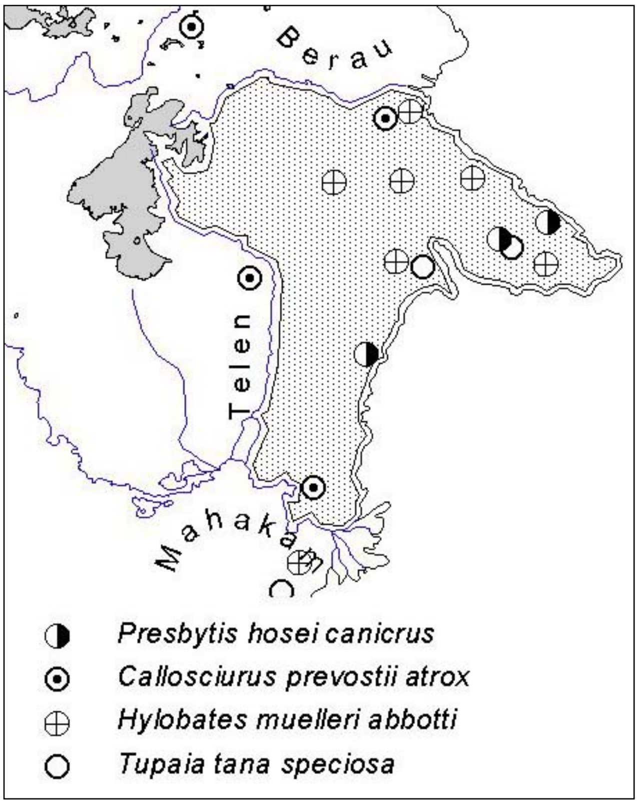


Figure 4.11 Types of distribution of Mahakam–Berau faunal elements.

6. Northeast Borneo

The existence of this sub-endemic centre (Fig. 4.6 No.6; Fig. 4.12) is mainly indicated by the ranges of *Callosciurus prevostii pluto* (Sciuridae). Also to be found here are for example *Tupaia tana paitana* (Tupaiidae) and *Presbytis hosei sabana* (Cercopithecidae). It is bordered to the south by the Kayan River and to the west by the Kalupis River (Northeast Borneo). Higher elevations of mountainous region stretching from Northeast to Southwest Borneo limit it inland. Additionally, the Brassey Range and the West-East Kinabatangan River to the west borders it to other biogeographic unit, i.e. the Brassey – Kinabatangan, which is situated in the intermediate area between Kayan and Kalupis. The existence of this other biogeographic units has disjuncted perfect populations of, for example, *T. t. paitana*, but some others, such as *C. p. pluto* and *P. h. sabana*, have also been recorded from the Brassey–Kinabatangan sub-endemic centre.

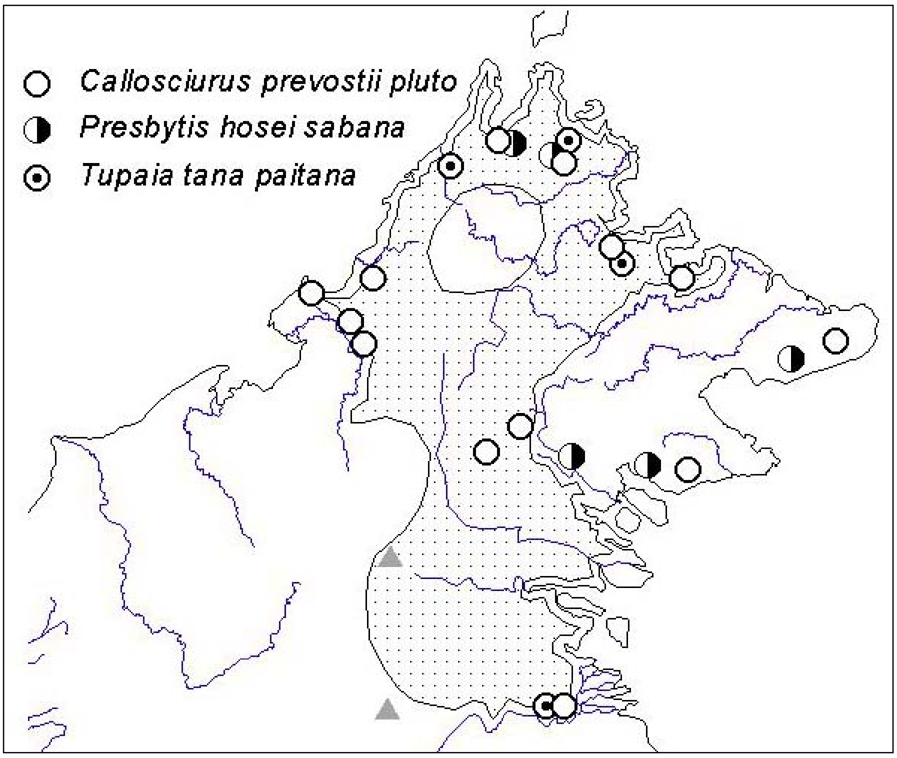


Figure 4.12 The sub-endemic centre of Kayan – Kalupis (stipples)

7. Brassey – Kinabatangan

This sub-endemic centre (Fig. 4.6 No.7; Fig. 4.13) is limited to the west and north respectively by the Brassey Range and the Kinabatangan River. Its distinction is indicated by the occurrence of the endemic forms *Tupaia tana kretami* (Tupaiidae) and *Presbytis rubicunda chrysea* (Cercopithecidae). Regarding the existence of the Brassey Range on the west, the low tree line in the Last Glacial Maxima issuspected to be the cause for their separation from their relatives.

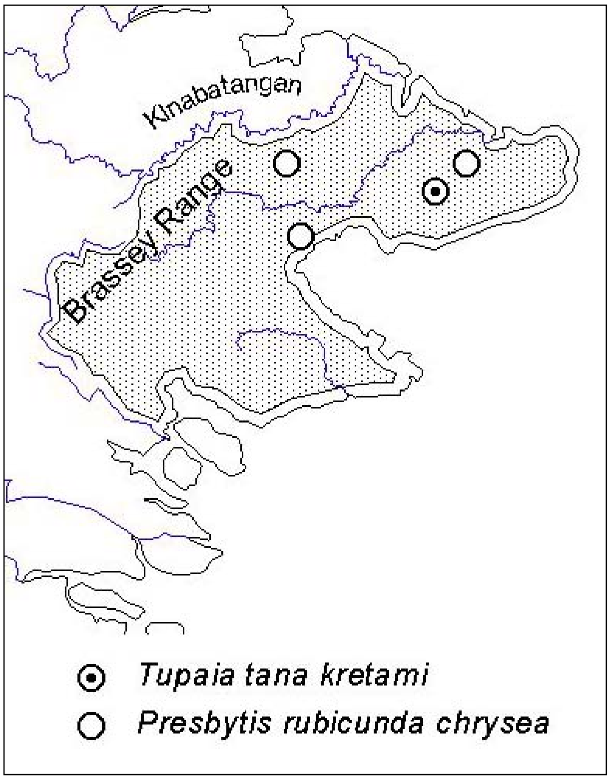


Figure 4.13
The sub-endemic area of Brassey-Kinabatangan (stipples).

8. Padas Delta

The distinction of this sub-endemic centre (Fig. 4.6 No.8; Fig. 4.14) is indicated by the occurrence of endemic *Tupaia tana chrysura* (Tupaiidae). This sub-endemic centre is situated on the delta of the Padas River. Its isolation occurred as sea levels rose during the warm period in the Holocene about 6,000 years ago. Endemic areas, which existed as a result of such isolation, are mostly found on western Borneo, which is drier than other parts of Borneo.

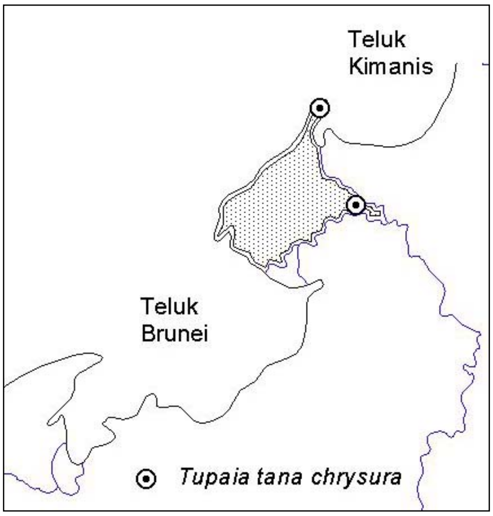
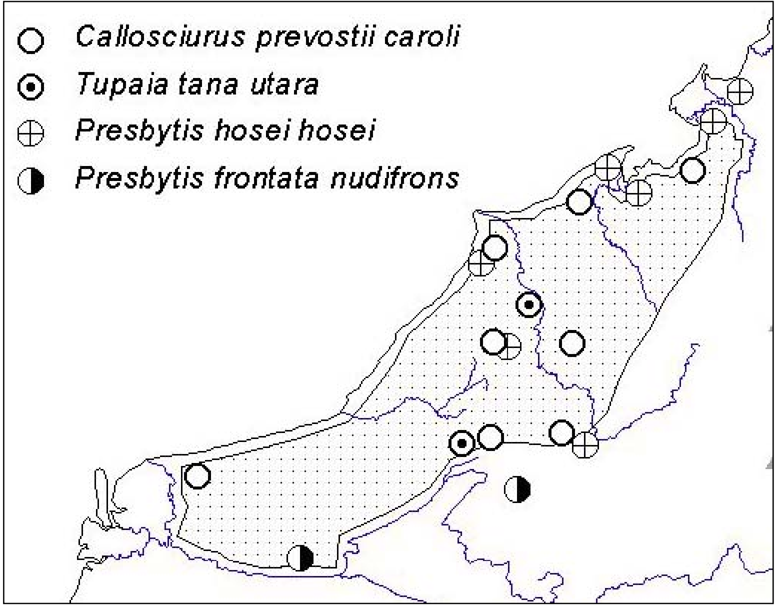


Figure 4.14 The sub-endemic centre of Padas Delta sub-endemic area (stipples) in the opposite of Labuan Island.

9. Padas – Rajang

Figure 4.15 The sub-endemic centre of Padas-Rajang (stipples)



This sub-endemic centre (Fig. 4.6 No.9; Fig. 4.15) can be defined by the range of *Callosciurus prevostii caroli* (Sciuridae). It is situated between the Padas and Rajang rivers in the east and west respectively. To the south, the high altitudes of Penambo Range border it. While *C. p. caroli* occurs broadly throughout this region, the typical dense rainforest inhabitant *Tupaia tana utara* (Tupaiidae) is restricted to the Mt. Mulu and Mt. Dulit areas only. On the other hand, the existence of the Northwest-Southeast Dulit Range in the middle region has separated the ranges of two cercopithecids, i.e. *Presbytis hosei* and *P. frontata*, which are mostly found on hill forests.

10. Lupar – Landak

This sub-endemic centre (Fig. 4.6 No.10; Fig. 4.16) is low lying along the northwestern coast of Borneo being bordered by the Lupas River in the north and by the Landak River in the south. Inland, the high altitudes of Mt. Niut limit this region. While lowland form such as *Callosciurus prevostii borneoensis* (Sciuridae) is more or less found throughout, taxa adapted to higher altitudes such as *Hylobates muelleri muelleri* (Hylobatidae) are more restricted to the eastern side and apparently penetrated this sub-endemic area through the eastern side of Mt. Niut.

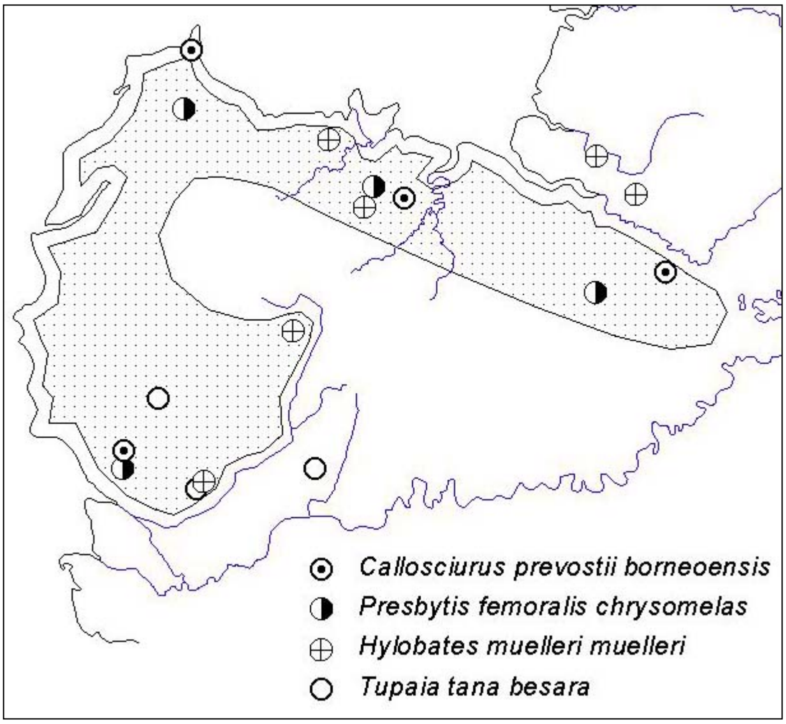


Figure 4.16 The sub-endemic centre of Lupar-Landak.

11. Teluk Datu

This sub-endemic centre (Fig. 4.6 No.11; Fig. 4.17) occupies only a small area, lying on a delta in Teluk Datu, Western Sarawak. Its existence has been determined by the occurrence of the endemic *Tupaia tana nitida* (Tupaiidae). This taxon is undoubtedly isolated there as the sea levels rose during the warm period in the Holocene period. Other endemic taxon found here is a typical dry inhabitant *Lonchura leucogastra smythiesi* (Estrildidae).

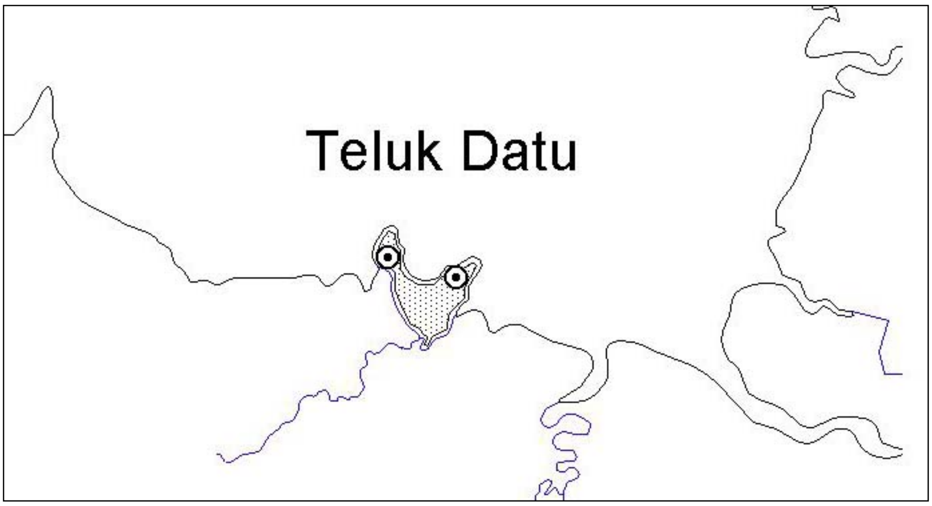


Figure 4.17 The sub-endemic centre of Teluk Datu.

12. Landak – Kapuas

South of Landak River, *Callosciurus prevostii borneoensis* (Sciuridae) is replaced by its close relative, *C. p. palustris*. Its range lies basically between the Landak and Kapuas rivers as well as a tributary, which drains to the Kapuas River in the Sanggau area. Although lowlands can be found far inland along the north of Kapuas bank, *C. p. palustris* is restricted only to lowlands nearby the coastal areas. Meanwhile, the hills are occupied, for example, by *Tupaia tana besara* (Tupaiidae) and *Hylobates muelleri muelleri* (Hylobatidae) (see Figure 4.18).

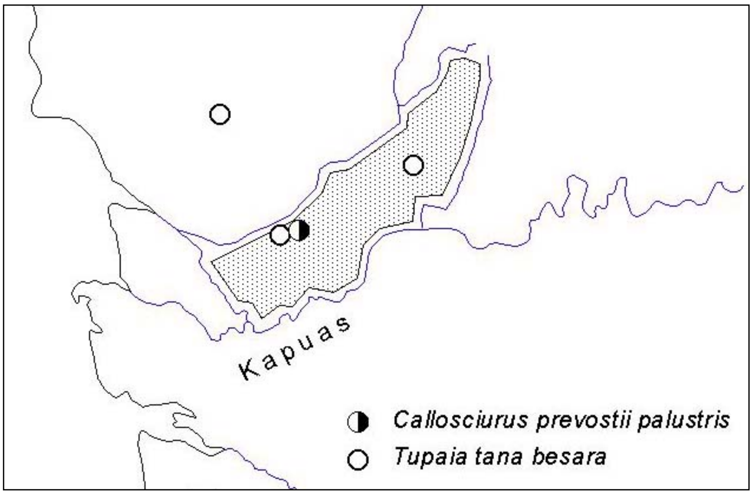


Figure 4.18 The sub-endemic centre of Landak – Kapuas.

13. Kapuas Delta

Similar to the sub-endemic centre of Teluk Datu, this sub-endemic centre (Fig. 4.6 No.13, Fig. 4.19) existed as the result of the isolation during the warm period in the Holocene about 6,000 years ago. It existence has been defined by the ranges of *Callosciurus prevostii coomansi* (Sciuridae) and *Lonchura atricapilla selimbaue* (Estrildidae). Both are typical dry inhabitants and thus show that the natural habitat of this sub-endemic centre, are dry habitats. *Petinomys hageni ouwensi* (Sciuridae) is known only from a single specimen. Its close relative, *P. h. hageni* occurs in Tanjung Morawa, Deli-Serdang and Northeast Sumatra.

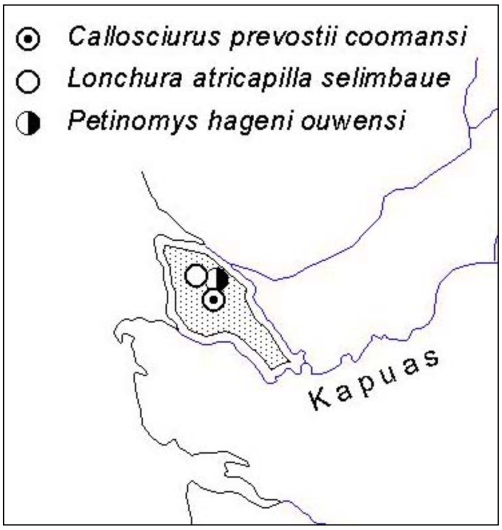


Figure 4.19 The sub-endemic area of Kapuas Delta (stipples).

14. Mountains of Central Borneo

This sub-endemic area (Fig. 4.6 No. 14, Fig. 4.20) can be defined by, the ranges of *Garrulax mitratus* (Timaliidae). It includes mountainous areas from the Schwaner Mountains in the southwest to Mt. Kinabalu in the northeast. At the higher elevations, it can be divided into three subdivisions, as suggested by the range of its subspecies. Of the four subspecies recognised, three of them are confined to this biogeographic division. They are *G. m. griswoldi* (highlands of Schwaner and Mueller mountains), *G. m. damnatus* (mountains of east Sarawak, i.e. Dulit, Derian and Kelabit Plateau) and *G. m. treacheri* (Mt. Kinabalu) (see Figure 4.18). The occurrence of the last subspecies, i.e. *G. m. mitratus* on the highlands of western Sumatra, suggests a close affinity of its faunal elements with those occuring on this region. Among subdivisions, Mt. Kinabalu region harbours incredible high diversity and endemism of all faunal groups. Most taxa which drifted on to Borneo early in the past from Asia are still restricted to this region.

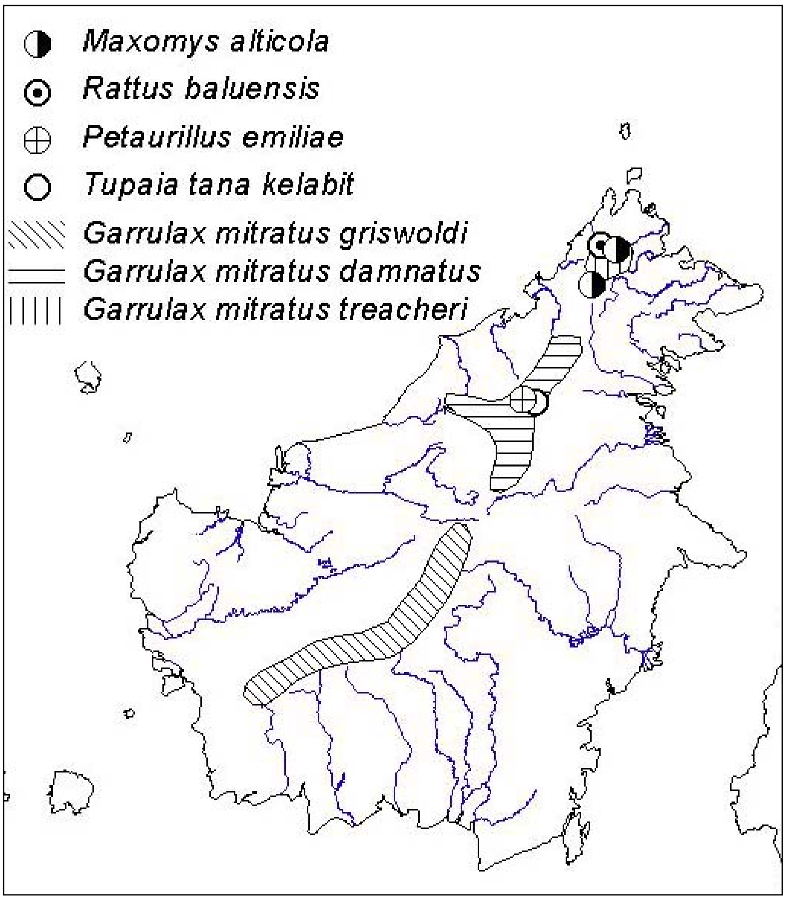


Figure 4.20 The sub-endemic area of mountains of Central Borneo (stipples)

4.1.2 Javan Endemic Centre

This endemic centre includes the mainland and its offshore islands, for example Bawean, Madura and Kangean islands to the north, Nusa Kambangan to the south, and Bali Island as well as its offshore Nusa Penida Island to the east (see Figure 4.21). Bali Island is the westernmost island in the Lesser Sundas. It differs from other islands of the Lesser Sundas in its location, lying on the Sunda Shelf and thus, was connected to the Java mainland by lowered sea level in the glacial time. Hence, its faunal elements are not surprisingly more closely related to the Javan faunal elements found to the west rather than to Lombok and the other Lesser Sunda islands to the east. In regard to this, this island is included within the Javan endemic centre.

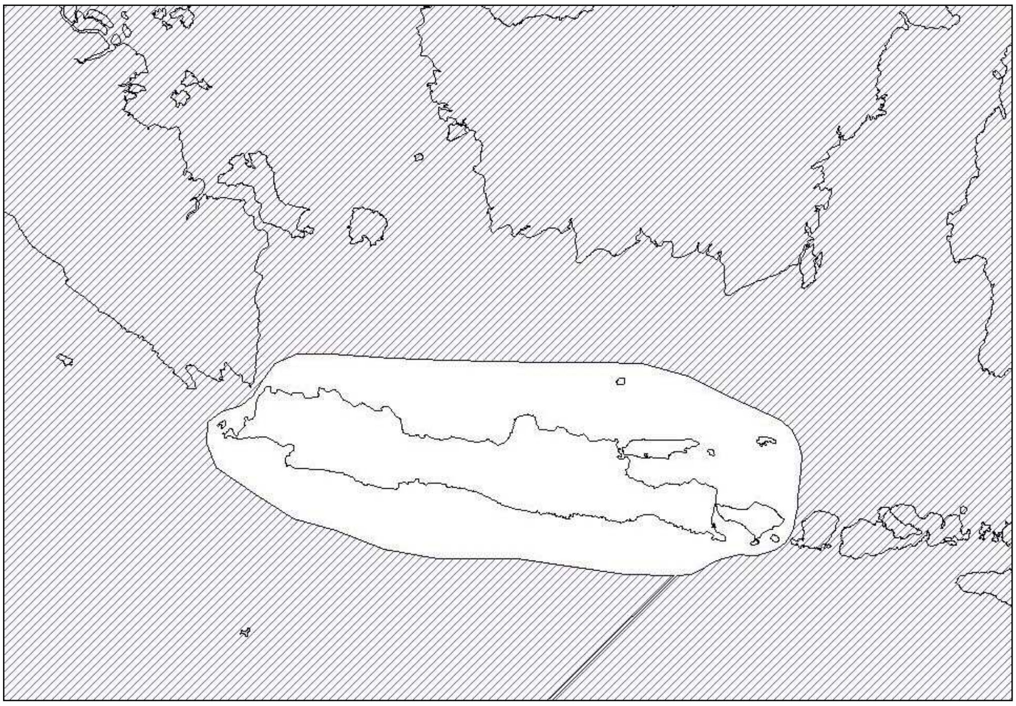


Figure 4.21 The Javan Endemic Centre. Bali Island, lying to the east and a part of the Lesser Sundas, is included within this endemic centre regarding the close affinity of its faunal elements to Java.

In general, Java and Bali among all islands of the Great Sundas support the fewest number of taxa. Also the level of endemism is the lowest, except for the endemism in amphibians. Of the amphibians found on Java and Bali, there are in total only 39 taxa, but the endemism of 28.2% surpasses that of Sumatran amphibians with 20.9%. (This statement is based on data from Yang 1991, Iskandar 1998, Emerson & Berrigan 1993, Duellman 1999, Dubois and Ohler 2000, Emerson *et al.* 2000, Veith *et al.* 2001, Frost 2002, Harvey *et al.* 2002). The endemic forms are listed in Table 4.6. While many genera and numerous taxa confined to Borneo and Sumatra are absent from this island, those confined to Java and Bali are not more than 16 genera, i.e. *Bufo* and *Leptophryne* (Bufonidae); *Leptobrachium* (Megophryidae); *Kalophrynus*, *Kaloula*, and *Microhyla* (Microhylidae – Microhylinae); *Oreophryne* (Microhylidae – Genyophryninae), *Fejervarya*, *Huia*, *Limnonectes*, *Occidozyga* and *Rana* (Ranidae); *Nyctixalus*, *Philautus*, *Polypedates*, and *Rhacophorus* (Rhacophoridae – Rhacophorinae). Genus *Oreophryne* recorded from Bali is the only member of this genus whose range is found within the Sunda Shelf.

Table 4.6 Endemic amphibians of Java and Bali

Family	Taxa
Bufonidae	*Leptophryne cruentata*
Microhylidae – Microhylinae	*Microhyla achatina*
Ranidae	*Fejervarya iskandari, Huia masonii, Limnonectes kuhlii, L. microdiscus*
Rhacophoridae	*Nyctixalus margaritifer, Philautus jacobsoni, P. pallidipes, P. vittiger, Rhacophorus margaritifer*

Its higher endemism than among Sumatran amphibians is mainly as a result of Bornean lineages, which migrated directly to Java early on, long before the Pleistocene Period. *Limnonectes kuhlii* (Ranidae) is one of the endemic forms, which migrated early from Borneo. This *L. kuhlii* is formerly known as being widely distributed in Southeast Asia as far as China and India, but it is split into more than a dozen species. This nominal form is now restricted to Java (Iskandar, 1998). Based on a molecular study, Emerson et al. (2000) was able to show that this species was separated early on from populations related to and hence formerly considered as *L. kuhlii* on Taiwan and Northern Borneo (Sabah & Brunei). Such a range can be simply reconstructed as follows: after its ancestors arrived on Borneo through an island drift from Taiwan, they dispersed further south to Java and became isolated there. Also *L. microdiscus*, which is currently restricted to the forested region of Java at 0–1,400m elevations, with a possible extension to Southern Sumatra as reported by Iskandar (1988 & 2000), is likely to be an early immigrant from Borneo. A number of its former subspecies are now considered independent species, i.e. *L. dammermani* of Lombok to Flores in the Lesser Sundas, *L. finchi* of the eastern half of Sabah and possibly also including populations in North Sulawesi, *L. palavanensis* of Palawan Island in the Southwest Philippines, and *L. parva* of Mindanao I. in Southeast Philippines.

Furthermore, the occurrence of widely differentiated genus *Philautus* (Rhacophoridae – Rhacophorinae) on Java indicates also its early arrival there. These are *P. aurifasciatus*, *P. pallidipes*, *P. vittiger* and *P. jacobsoni*. The previously widespread *P. aurifasciatus* is recently split into several nominal forms, such as *P. acutirostris* (Mindanao and Basilan), *P. petersi* (Borneo, Natuna Is., Malay Peninsula), and *P. mjobergi* (Borneo). Dring (1987) removed several taxa from synonymy and restricted this name to the Javan population. It is recorded throughout the mountainous region of Java in contrast to the other three species that are all restricted to only narrow areas. *P. pallidipes* is found only in Mt. Pangrango in West Java; *P. vittiger* from Pangalengan, Situ Lembang and Mt. Burangrang also in West Java, and *P. jacobsoni* from Mt. Ungaran in Central Java.

Most other endemic species are also likely to be early immigrants from Borneo for example these three rhacophorids, i.e. *Nyctixalus margaritifer*, *Megophrys montana* and possibly *Rhacophorus margaritifer*. On the other hand, endemic forms, which evolved in the Pleistocene Period, are among others *Leptophryne cruentata* (Bufonidae), possibly *Microhyla achatina* (Microhylidae – Microhylinae) and *Huia masonii* (Ranidae). Meanwhile, the non-endemic forms, which presumably migrated early from Borneo are for example *Fejervarya cancrivora, F. limnocharis*, *F. nicobariensis,* possibly *Occidozyga lima, O. sumatrana, Rana erythraea* and perhaps *Rana chaconota* and *Bufo melanostictus* (Bufonidae); possibly *Polypedates leucomystax* (Rhacophoridae). An indication of their early arrival is the occurrence of their disjunct populations both on Nicobar Islands off Northwest Sumatra and/or on the Lesser Sundas and Sulawesi, that are all situated outside the 200m isobath.

Except for those early immigrants from Borneo, Java also received immigrants from Sulawesi and Lombok. A species, which migrated from Sulawesi, is *Limnonectes grunniens* (Ranidae); its range involved Java, Sulawesi, Northern Moluccas, Seram and the nearby Ambon, Haruku, and Saparua, as well as New Guinea. Its ability to arrive on Java suggests that the migration time occurred before the Pleistocene Period but its absence on Borneo indicates that its arrival on Java is much later than a period when Bornean lineages migrated to Java, because any contact between Borneo and Java had disappeared at that time. On the other hand, *Oreophryne monticola* (Microhylidae – Genyophryninae) is known only from Bali and Lombok. Regarding numerous *Oreophryne* found on Sulawesi, it seems that this species was derived from ancestors, which migrated from this island to Lombok and Bali. Furthermore, it is remarkable that this species does not extend further west to the Javan mainland considering that a land bridge connected Bali and Java in the last Pleistocene Glacial Maxima.

In contrast to early immigrants from Borneo and Sulawesi, those that migrated from Sumatra are thought to be more recent immigrants, which obviously came in the Pleistocene Period. The ranges of such migrants are normally restricted to the Great Sundas and the nearby islands connected with the 200m isobath. They are for example *Leptophryne borbonica* (Bufonidae); *Kalophrynus pleurostigma* (Microhylidae – Microhylinae); and *Rhacophorus reinwardtii* (Rhacophorus – rhacophoridae).

Different to amphibians, mammals of Java and Bali have the lowest endemism among islands of the Great Sundas, with 28 endemic forms out of 88 taxa (31.8%) (see Table 4.7) (Corbet & Hill 1992, Wilson & Reeder 1993, Suyanto *et al.* 1998, Nowak 1999, Nijman 2000). This includes the probable occurrence of *Bubalus bubalis* (Bovidae) and *Tarsius bancanus* (Tarsiidae) as well as the occurrence of *Rattus exulans*, *R. tanezumi* and *R. tiomanicus* (Muridae – Murinae), which are mostly considered as the result of human introduction. Nonetheless, this lower percentage does not mean that Java received no early lineages from Borneo. The ranges of some mammals do show that several of them presumably did arrive early on this island from Borneo, for example *Sus verrucosus* (Suidae); possibly *Tragulus napu* (Tragulidae); *Melogale orientalis*, *Mustela lutreolina* (Mustelidae); *Crocidura monticola* (Soricidae); *Lepus nigricollis* (Leporidae); *Hystrix javanica* (Hystricidae); monotypic genus *Kadarsanomys sodyi*, *Mus vulcani*, *Niviventer lepturus*, *Pithecheir melanurus*, *Sundamys maxi* (Muridae – Murinae); *Lariscus insignis*, *Petinomys genibarbis* (Sciuridae); and *Tupaia javanica* (Tupaiidae). Also *Hystrix javanica* (Hystricidae), which is currently confined to Java, Madura, Bali, Lombok, Sumbawa, Rinca, Flores and to the nearby islands of Tanah Jampea as well as to Southwest Sulawesi (which is considered as human introduction), is also obviously an early migrant, apparently derived from its close relative *H. brachyura brachyura* which is found on Borneo, Sumatra and on the Malay Peninsula. Additionally, descendants from these early lineages are for example *Mus caroli* and *M. cervicolor* (Muridae – Murinae).

Table 4.7 Endemic mammals of Java and Bali. An asterisk marks the monotypic genera

Family	Genera with number of endemic species (and endemic subspecies)
Cercopithecidae	Presbytis (2)
Cervidae	Axis 1
Hylobatidae	Hylobates 1
Lorisidae	Nycticebus (1)
Murinae – Murinae	Kadarsanomys* 1, Maxomys 1, Mus 1, Niviventer 1, Pithecheir 1, Sundamys 1
Sciuridae	Callosciurus (11), Hylopetes 1, Petaurista (1)
Soricidae	Crocidura 2
Suidae	Sus 1
Viverridae	Arctogalidia* (1)

Also the occurrence of the endemic *Axis kuhlii* (Cervidae) on the Bawean Islands off Northern Java is likely to be the result of early migration from Borneo southwards. Its close relatives are found on the Calamian Islands in Southwest Philippines (*A. calamianensis*) and on Pakistan and Northern India as far as to Indochina (*A. porcinus*). Some authors proposed the possibility of ancient human introduction and the others suggested that the species, along with *A. calamianensis*, are survivors of widespread Pleistocene populations of their close relative *A. porcinus*. This last assumption is obviously based on a common preference of *A.*

deer to grasslands and open forests, although Blouch and Atmosoedirdjo (1987 in Nowak 1999) found *A. kuhlii* depends on dense cover in favorable secondary forest habitats. Nonetheless, supposing population of *A. kuhlii* on Bawean Island represents Pleistocene relicts, it is rather odd for its absence in other drier regions, for example on Eastern Java. In regard to this, it seems that it represents populations, which formerly existed on Borneo and extended southwards but not as far as Java.

Rather similar to the range of *A. kuhlii* is that of *Panthera pardus* (Felidae). In historical times, it occurred throughout the mainland of South Asia and on Sri Lanka, Singapore, Java and nearby Kangean Islands to the northeast. The last is considered to be perhaps introduced (Helvoort et al., 1985 in Corbet and Hill, 1992). Nowadays, it is probably still distributed sparsely throughout the less densely populated parts of its former range, but extinct on Singapore. Such a range obviously represents an early immigrant from Borneo. Meanwhile, another *Panthera* occurs on Indonesia is *P. tigris*, whose current range is also endangered. In contrast to *P. pardus*, this species is recognised as a recent immigrant from Southeast Asia. Three subspecies occur in the region, i.e. *P. t. sumatrae* (Sumatra), *P. t. sondaica* (Java), and *P. t. balica* (Bali). A single subfossil tooth suggests the former presence of *P. tigris* on Borneo. *P.t. sondaica* and *P. t. balica* are probably extinct now (Corbet & Hill, 1992; Nowak, 1999).

Bawean Island is one of the three offshore islands, which is inhabited by endemic forms. Another island is Madura Island to the northeast and Bali Island to the east where the endemic *Callosciurus notatus madurae* and *C. n. stresemanni* (Sciuridae) occur respectively. The poor insular forms among mammals are found not only in the endemic forms, but also in the non-endemic forms. There are so few mammals which moved to offshore islands although they are found on the mainland. The few taxa, which can be found, are for example *Sus verrucosus* (Suidae) on Madura and Bawean, *Paradoxurus hermaphroditus* and *Viverricula indica* (Viverridae) on Kangean Island, *Hystrix javanica* (Hystricidae) and *Mus caroli* (Muridae) on Madura I., and *Petaurista elegans elegans* (Sciuridae) on Nusa Kambangan Island. This evidence shows that only a few non-volant fauna could migrate to these satellite islands although most of these islands are well-known to have been connected to the mainland through a land bridge, which existed in the last Pleistocene Glacial Maxima. A certain ecological barrier is suspected to have existed between these islands and the mainland.

The lesser endemism among Javan mammals in comparison to that among Sumatran mammals is due to the fact that a lot more Javan mammals migrated early on from Borneo further to Sumatra. This shows a better ability of mammals to disperse than amphibians. These taxa were then isolated and evolved into endemic forms on Sumatra. It is not rare that taxa derived as Sumatran endemic forms, are themselves represented by non-endemic forms on Java. They are for example *Lepus nigricollis* (Leporidae); *Rattus tiomanicus* (Muridae – Murinae); and *Paradoxurus hermaphroditus* (Viverridae) and their derivatives today, which are endemic to Sumatra such as *Nesolagus netscheri*, *R. adustus* and *P. lignicolor* respectively (see accounts thereof).

The origin of *L. nigricollis* on Java is confusing. This taxon currently ranges from East Pakistan and Peninsular India, east through South Nepal to West Bengal, Bangladesh and Tripura (Agrawal & Bhattacharyya, 1977 in Corbet & Hill, 1992). Its occurrence on Java is considered as introduction, but this has been queried on the basis of sub fossil finds dating from the Neolithic period (Dawson, 1971 in Corbet & Hill, 1992). I would consider this taxon to be an early migrant from Borneo, while today it is extinct there and in most other intermediate regions, perhaps being replaced by *L. peguensis* of Southeast Burma, Thailand, Indochina and Hainan Island. Due to its early arrival on Java, it could possibly have migrated early on to Sumatra and had enough time to evolve into monotypic genus *Nesolagus netscheri* that today is endemic to montane habitats of Sumatra. The restriction of *N. netscheri* to the montane habitats suggests its early arrival on Sumatra, as this island was much lower than it is today.

Endemic species *Rattus adustus* of Enggano Island has likely been derived from the Javan population of *R. tiomanicus*. The present-day distribution ranges of *R. tiomanicus* show that it dispersed early on to Sumatra and thereafter, moved to Nicobar Island off Northwest Sumatra, which is today separated from the mainland by a deep marine barrier. Enggano Island off Southwest Sumatra resembles Nicobar Island in its position outside the 200m isobath and hence only tectonic movements are plausible as an explanation of the occurrence of *R. adustus* there. Human introduction seems less plausible due to its absence on other nearby islands, which were visited by man. Close affinity of *R. adustus* to *R. tiomanicus* has been mentioned by Musser (1986 in Corbet & Hill, 1992) and both species, along with *R. lugens* of Mentawai Island, are ordered into the *Rattus* Group by Musser and Carleton in (Nowak 1999). From this evidence, we can assume that another Sumatran endemic form, *R. enganus*, which was also restricted to Enggano Island is undoubtedly also derived from an early migrant from Java. Its affinity to other *Rattus* found on the Great Sundas is unsure, making it difficult to find out its possible ancestors. However, these three species, i.e. *R.*

argentiventer, *R. exulans*, or *R. tanezumi* are likely the candidates due to their early arrival on Java.

Also the endemic *P. lignicolor* on the Mentawai Islands has been derived from a widely distributed *P. hermaphroditus*, which migrated from Java to Sumatra very early on. The occurrence of disjunct populations of *P. hermaphroditus* on Simeuleu and Enggano islands show that their arrival there was the result of tectonic movement, which came about before the lowering of the sea level in the Pleistocene Period. This suggests that there must have been at least two invasions of *P. hermaphroditus* from Java to Sumatra. The first invasion left only a population on the Mentawai Islands, which later evolved into *P. lignicolor*. The second invasion brought the current populations of *P. hermaphroditus* to the mainland and its offshore islands, except Mentawai Island. In regard to this, it is clear that something broke off the gene flow between populations on Java and Mentawai Islands in the period between the two invasions mentioned above.

The low endemism among mammals of Java and Bali is also as a result of the less endemic forms derived from recent migrants either from Borneo or Southeast Asia, which migrated to Java and Bali through Sumatra in the Pleistocene Period. The few endemic forms, which derived from recent migrants, are for example *Presbytis comata comata* and *P. c. fredericae* (Cercopithecidae); *Hylobates moloch* (Hylobatidae); *Maxomys bartelsii*, *Niviventer lepturus* and *Sundamys maxi (*Muridae – Murinae); *Hylopetes bartelsi* (Sciuridae); and *Arctogalidia trivirgata trilineata* (Viverridae). Meanwhile, some of their relatives represented as endemic forms in Sumatra are much greater in number. The *Presbytis* are represented by 11 endemic forms, *Maxomys* by three, and *Hylobates* as well as *Hylopetes* each by two endemic forms.

Of reptiles, there are about 146 taxa, which can be named in this endemic centre, of which only 11 of them are endemic forms (7.5%) (see Table 4.8) (Uetz 2005, Schulz 1996, McDiarmid *et al.* 1999, Iskandar 2000).

Table 4.8 Endemic reptiles of Java and Bali

Family	Endemic Taxa
Colubridae	*Boiga dendrophila dendrophila, Pseudoxenodon inornatus inornatus, Tetralepis fruhstorferi**
Elapidae	*Maticora bivirgata bivirgata*
Scincidae	*Lamprolepis leucosticta, Mabuya macrophthalma, Sphenomorphus necopinatus,* *S. puncticentralis, S. vanheurni*
Typhlopidae	*Typhlops bisubocularis, T. fuscus*

This very poor endemism is obviously the result of a much better ability of reptiles to disperse, even better than mammals. An indication of early migration from Borneo is well illustrated by the ranges of genus *Sphenomorphus* (Scincidae). This genus has the most diversified endemic forms among other reptiles confined to Java. Of the six species, three of them are strongly differentiated as endemic forms, i.e. *S. necopinatus*, *S. puncticentralis*, and *S. vanheurni*. Such a strong differentiation can only be the result of long isolation on this island, after their early arrival from Borneo. Also numerous taxa, whose ranges are shared between Java and Borneo, but not Sumatra, indicate such early migration from Borneo to Java. Those taxa are for example *Harpesaurus tricinctus* (Agamidae); *Python molurus bivittatus* (Boidae); *Calamaria bicolor*, *C. lateralis*, and *C. lowii* (Colubridae); as well as *Crocodylus siamensis* (Crocodylidae).

The possibility of early migration from Java to Enggano Island as indicated by some mammals can also be seen among reptiles such as on *Lipinia relicta* (Scincidae). Currently disjunct populations of this taxon can be found among others on islands off the west coast of Sumatra.

Birds of Java and Bali have also the lowest endemism among islands on the Great Sundas, with 153 endemic forms out of 422 taxa (36.26%) (see Table 4.9) (Andrew 1992, del Hoyo *et al.* 1992, 1994, 1996, 1997, 1999, 2001, MacKinnon & Phillipps 1993, Jones *et al.* 1995, Mees 1996, Stattersfield *et al.* 1998, Clements 2000). However, this endemism is higher than that in mammals, which is more sedentary and less ready to disperse. The higher endemism among birds than among mammals has been contributed to by the greater number of endemic insular forms with 22% of the total endemic forms. Meanwhile, the number of endemic insular forms in mammals only accounts for 11% of the total endemic forms. This means that the higher endemism in birds is as a result of the much better ability of birds to colonise offshore islands, which is followed by their restriction there as they lose their flight capability.

At least three species are widely differentiated as endemic forms, i.e. *Arborophila javanica* (Phasianidae); *Stachyris melanothorax* (Timalidae) and *Turdus poliocephalus* (Turdidae). The three subspecies of *A. javanica* confined here are all restricted to the upper montane zone of Java (above ca. 1,000m), i.e. *A. j. javanica* to mountains of West Java; *A. j. bartelsi* to mountains of West central Java; and *A. j. lawuana* to mountains of East central Java. Eastward of this, it is replaced by its congener, *A. orientalis orientalis*, whose relatives are surprisingly all found on the mountains of Sumatra and on the mountains of the Malay Peninsula. By considering *A. javanica* as a first invasion southwards from Borneo and *A. orientalis orientalis* as a much later invasion from Borneo, it is much simpler to explain the ranges of this mountain partridge from Java and Sumatra. This concurs with one of two opinions proposed by Mees (1996) for the existence of two separate invasions, but not with his migration route. He proposed that *A. javanica* is the relict of a first invasion southwards into the Sunda sub region, while *A. orientalis* is considered to originate from a much later invasion from Southeast Asia. Using this theory, he could not however explain why nominate *A. orientalis* could have reached East Java without touching the populations of *A. javanica* in West and Central Java.

Table 4.9 Endemic birds of Java and Bali. An asterisk marks the monotypic genera

Family	Genera with number of endemic species (and endemic subspecies)
Accipitridae	Pernis (1), Spilornis (1), Spizaetus 1
Aegithalidae	Psaltria* 1
Alcedinidae	Alcedo (1), Pelargopsis (1)
Apodidae	Aerodramus 1
Bucerotidae	Buceros (1)
Cacatuidae	Cacatua (1)
Campephagidae	Coracina (2)
Capitonidae	Megalaima 1(3)
Caprimulgidae	Caprimulgus (1)
Chloropseidae	Chloropsis (2)
Cisticolidae	Prinia (1)
Columbidae	Ducula (1), Macropygia (1), Ptilinopus (1), Treron (1)
Corvidae	Cissa (1), Platylophus (1)
Cuculidae	Cacomantis (1), Centropus 1(1), Phaenicophaeus (2)
Dicaeidae	Prionochillus (1)
Dicruridae	Dicrurus (1)
Estrildidae	Erythrura (1), Lonchura (1)
Eurylaimidae	Eurylaimus (1)
Fringillidae	Serinus (2)
Irenidae	Irena (1)
Monarchidae	Hypothymis (1)
Muscicapidae	Cinclidium (1), Cochoa 1, Copsychus (5), Cyornis (4), Enicurus (2)
Nectariniidae	Aethopyga 1(1), Arachnotera (2), Chalcoparia* (2)
Oriolidae	Oriolus (2)
Paramythiidae	Dicaeum (1)
Phasianidae	Arborophila (4), Pavo (1)
Picidae	Celeus (1), Chrysocolaptes (1), Hemicircus (1), Meiglyptes (1), Picus (3), Reinwardtipicus* (1)
Pittidae	Pitta (2)
Podargidae	Batrachostomus (2)
Podicepididae	Tachybaptus (1)
Prionopidae	Philentoma (1)
Psittacidae	Psittacula (2)
Pycnonotidae	Alophoxius (1), Hypsipetes (1), Pycnonotus (4)
Rhipidura	Rhipidura 2
Sittidae	Sitta (3)
Strigidae	Ninox (1), Otus 1(1), Strix (2)
Sturnidae	Acridotheres (2), Aplonis (1), Leucopsar* 1
Sylviidae	Abroscopus (1), Acrocephalus (1), Bradypterus (1), Orthotomus (5), Tesia 1
Timaliidae	Alcippe 1, Crocias* 1, Garrulax (2), Macronous (3), Malacocincla (2), Malacopteron (1), Napothera (2), Pellorneum (3), Pnoepyga (1), Pomatorhinus (1), Pteruthius (2), Stachyris 1(6), Timalia* (1)
Trogonidae	Harpactes (2)
Turdidae	Brachypteryx (1), Myophonus (1), Turdus (5), Zoothera (1)
Turnicidae	Turnix (1)
Zosteropidae	Lophozosterops (2), Zosterops (2)

Also the consideration of *S. melanothorax* as an early migrant from Borneo would answer a long-unexplained question as to why this species shows a special attachment to extinct volcanoes on Java as noted by Mees (1996). Due to its early arrival on Java, it settled over a long period on this island. The current extinct volcanoes on Java today are nothing more than parts of Java, which were inhabited very early by this taxon. Also its early arrival resulted in *S. melanothorax* being strongly differentiated into four subspecies, i.e. *S. m. melanothorax* (Mt. Gede-Pangrango region in West Java); *S. m. albigula* (Mt. Papandayan region in West Java); *S. m. mendeni* (Mt. Ciremai region in West Java); and *S. m. intermedia* (Mt. Raung region in East Java). The only other extant subspecies is *S. m. baliensis*, which is restricted to the lowlands of Bali Island to the east. This geographical distribution was proposed first by Neumann (1935) and followed by Hoogerwerf (1947), but it was not accepted by Jany, (1953) who in contrast to this theory drew attention to the great vertical distribution of the species from sea level to ca. 2,500m above sea level. He proposed to retain in Java (he had no material from Bali) two subspecies, i.e. *S. m. melanothorax* for populations from the lower regions and *S. m. albigula* for populations from the higher levels (particularly in West Java). To the latter subspecies he could ascribe only two of his specimens, one from Mt. Ciremai (2,500m) and one from Telaga Warna near the Puncak Pass, Mt. Gede (1,400m). Further to the distribution, there is little doubt that *S. melanothorax*, with its huge vertical range, occurred throughout Java until recently (Mees, 1996). These in turn give us more additional important information. Huge vertical ranges resulted from its adaptation to the raise of mountains of Java, that were early in the past possibly mainly represented on Western Java. Their separation later into subspecies must have occurred much later as other mountains began to rise.

Still illustrating early migration from Borneo is the range of *T. poliocephalus*, but at a higher level than that of *Arborophila* and *S. melanothorax.* This species inhabits light woodland in the high mountains, generally above 2,000 m. The five subspecies recorded are *T. p. fumidus* (Mt. Gede region); *T. p. biesenbachi* (Mt. Papandayan region); *T. p. javanicus* (mountains in West-central Java from Mt. Ciremai to Mt. Sumbing); *T. p. stresemanni* (Mt. Lawu region in East-central Java); and *T. p. whiteheadi* (mountains of East Java).

Additionally, it is worth noting that Bali has a monotypic genus *Leucopsar rotschildi* (Sturnidae) indicating its long isolation on this island. This species was discovered only in 1911 (Stresemann 1912 in Whitten et al. 1996) and was declared as a globally endangered species by IUCN in 1977. Its entire distribution is confined to the western tip of the island. Contrastly, the other four, two of which are endemic forms recorded from Bali and Nusa

Penida to the southeast respectively are all separated at subspecies level, suggesting only their recent separation.

Sub-endemic areas on the mainland

On Java, sub-endemic centres can be mainly divided into two groups, i.e. highlands along the southern coasts and lowlands, predominantly on northern coasts. The total eight sub-endemic centres recognised (Fig. 4.20) are described below:

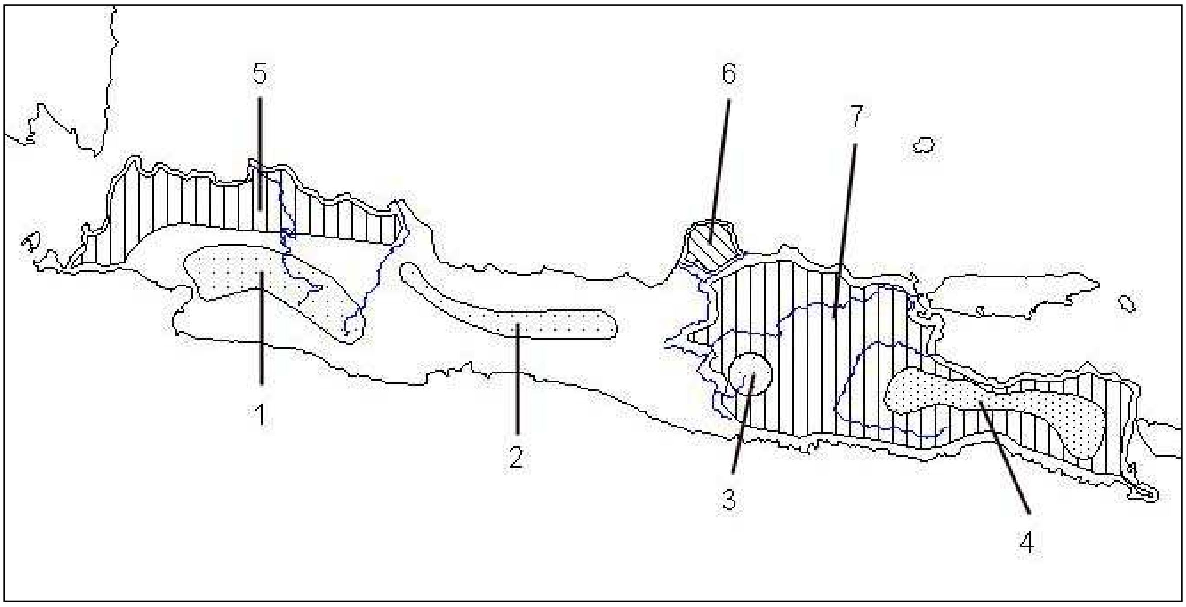


Figure 4.22 Eight sub-endemic centres on Java mainland: 1) West-Javan Mountains 2) Central-Javan Mountains 3) Mt. Lawu 4) East-Javan Mountains 5) West-Javan Lowlands 6) Mt. Muria 7) East-Javan Lowlands.

1. West-Javan Mountains

The distinction of this sub-endemic centre (No.1 in Fig. 4.22; Fig. 4.23) has been indicated by the most taxa from a different group. It is a mountainous region to the south of the West-Javan lowland sub-endemic centre. It includes among others the mountains of Halimun (1,929m), Salak (2,217m), Gede-Pangrango (3,019m), Patuha (2,434m), Malabar (2,321m), Papandayan (2,821m), Tangkuban Perahu (2,081m), and Burangrang. The drier Mt. Ciremai to the northeast is excluded from this biogeographic division through its different faunal elements. Three amphibians are certainly endemic to it, i.e. *Leptophryne cruentata* (Bufonidae), *Philautus pallidipes* and *P. vittiger* (Rhacophoridae). Of mammals, endemic taxa are for example the monotypic genus *Kadasonomys sodyi* (Muridae). Birds contribute to the highest endemic taxa of its faunal elements. One example is *Arborophila javanica* (Phasianidae). At higher elevations, two subdivisions can be recognised, i.e. Mt. Gede-Pangrango with *Turdus poliocephalus fumidus*

(Turdidae) and *Stachyris melanothorax melanothorax* (Timalidae) as its faunal elements and Mt. Papandayan with *T. p. biesenbachi* and *S. m. albigula* as its faunal elements.

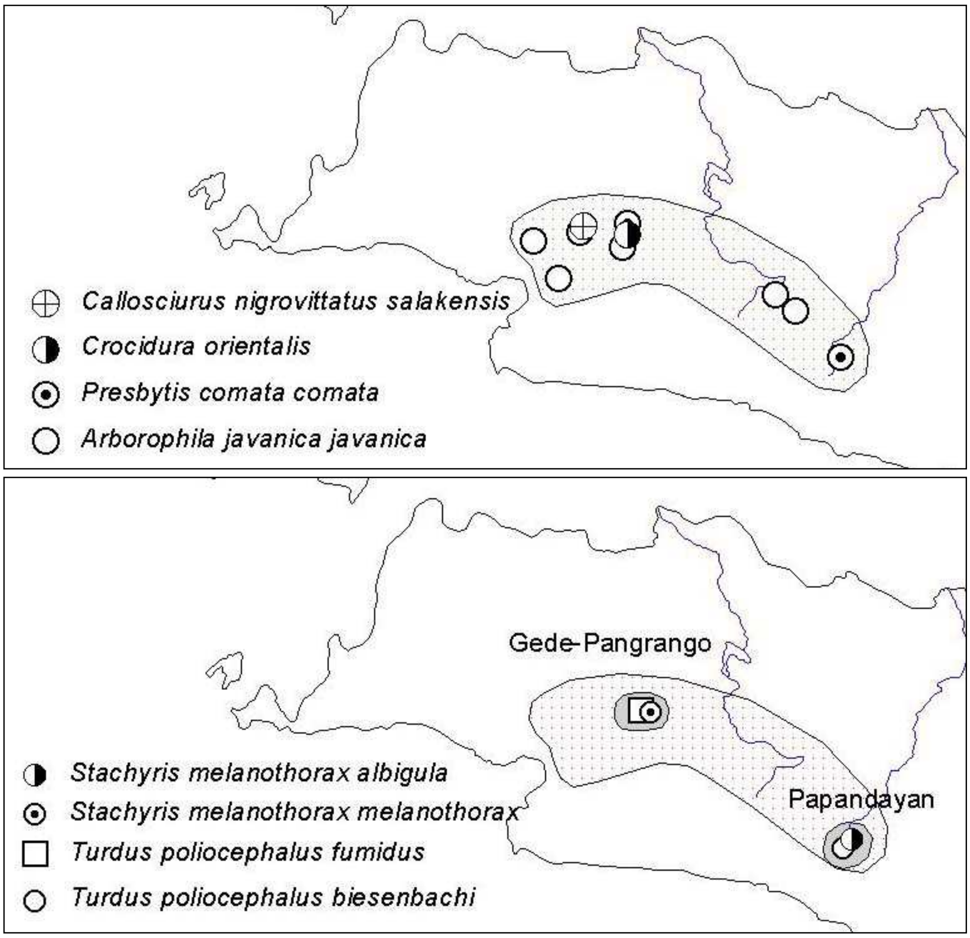


Figure 4.23 Sub-endemic centre of the West-Javan Mountains (stipples). Above: type distribution of faunal elements of West-Javan Mountain sub-endemic centre. Below: two subdivisions (grey-shaded) recognised in the higher elevations, i.e Mt. Gede-Pangrango division and Mt. Papandayan division.

2. Central-Javan Mountains

This sub-endemic centre (No. 2 in Fig. 4.22; Fig 4.24) has been indicated mainly by the ranges of *Philautus jacobsoni* (Rhacophoridae); *Presbytis comata fredericae* (Cercopithecidae); *Turdus poliocephalus javanicus* (Turdidae), *Arborophila javanica bartelsi*, *Garrulax rufifrons slamatensis* and *Stachyris melanothorax mendeni* (Timalidae). The mountains included within the region are for example Ciremai (3,078m), Slamet (3,428m), Perahu (2,565m), Sindoro (3,135m), Sumbing (3,371m) and the nearby Mt. Ungaran.

3. Mt. Lawu

This sub-endemic centre (No. 3 in Fig. 4.22; Fig. 4.25) is basically restricted to high elevations of Mt. Lawu (3,265m) region. The existence of this area has been indicated by the occurrence of the endemic *Turdus poliocephalus stresemanni* (Turdidae) and *Arborophila javanica lawuana* (Timalidae) there.

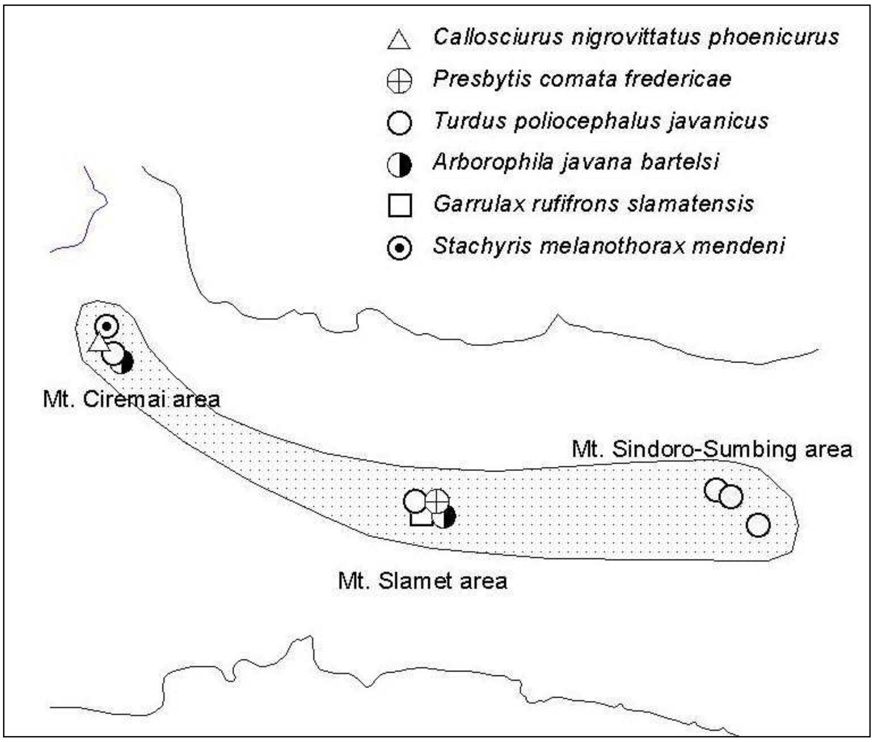


Figure 4.24 Distribution of six faunal elements of Mountains of Central-Java sub-endemic centre (stipples).

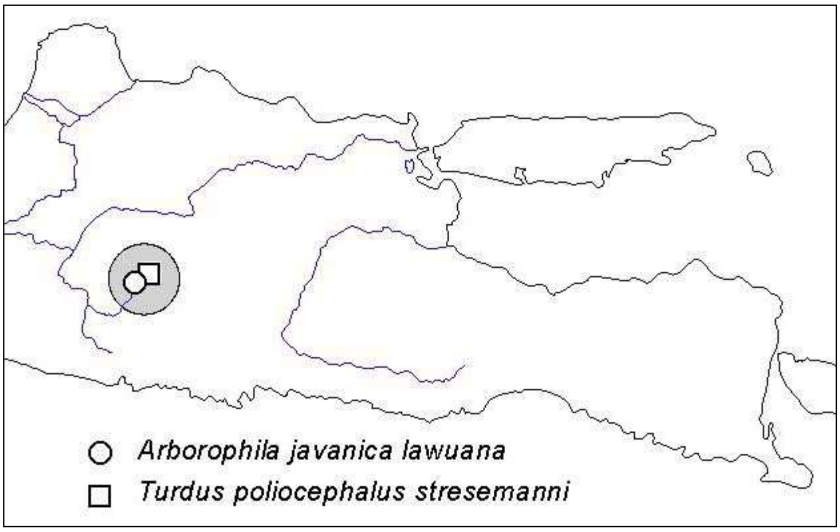


Figure 4.25 The sub-endemic centre in eastern Central-Java is restricted to Mt. Lawu region (grey-shaded)

4. Mountains of Eastern Java

This sub-endemic centre (No. 4 in Fig. 4.22; Fig. 4.26) coincides with the distribution of the montane forests in Eastern Java, from Mt. Arjuno (3,343m) and Mt. Kawi (2,874m) in the west to Meru Betiri and Ijen Highlands in the east. This shows that it is only significant for the montane fauna, such as *Turdus poliocephalus whiteheadi* (Turdidae) and *Arborophila orientalis orientalis* (Timalidae). Taxa found below 1,000m elevations thus must be regarded as lowland species. This indicates the existence of an independent lowland sub-endemic centre.

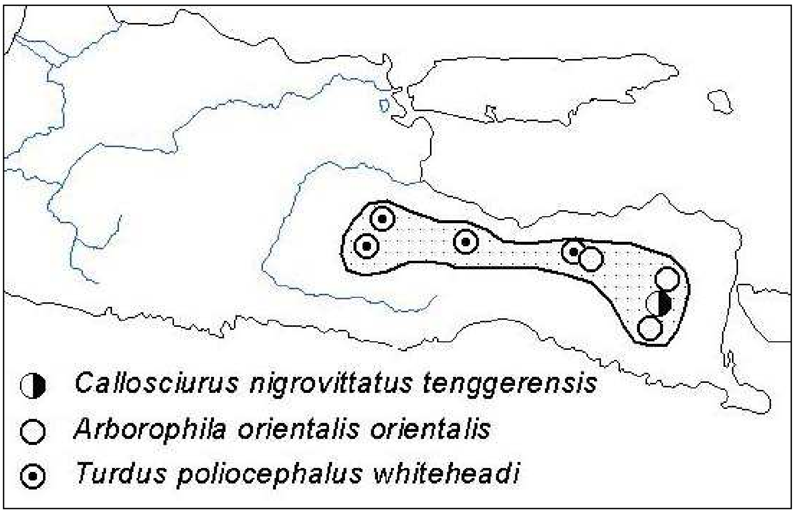


Figure 4.26 Distribution of three faunal elements of East-Javan mountain sub-endemic centre (stipples).

5. West-Javan Lowlands

Lowland forests in this sub-endemic centre (No. 4 in Fig. 4.22; Fig. 4.27) extend as far eastward as the flat northern coasts of the Indramayu district, being bounded on the east by Cimanuk River. High elevations of mountainous regions have limited it to the south. Its existence is determined by the range of the endemic *Callosciurus nigrovittatus bantamensis* (Sciuridae) and the easternmost range of the more widespread *Copsychus malabaricus tricolor* (Muscicapidae). The latter ranges to Sumatra, Bangka, Belitung and Karimata.

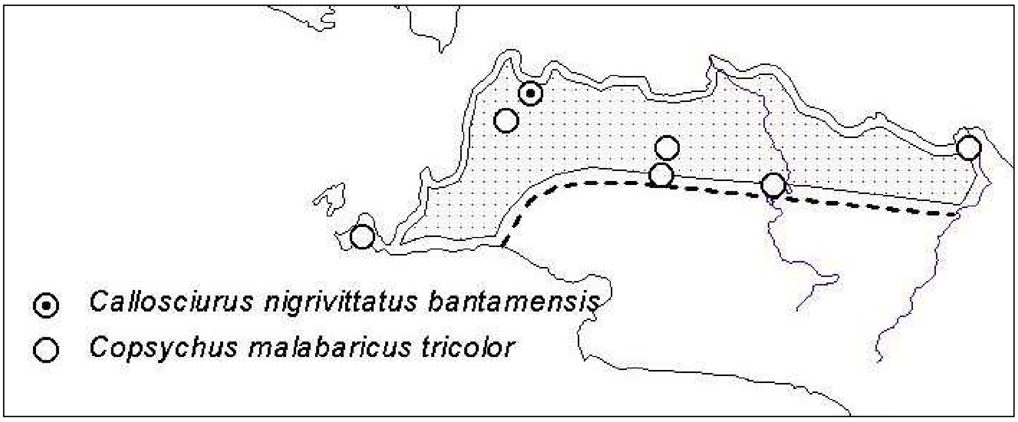


Figure 4.27 Type distribution of faunal elements of the West-Javan lowland sub-endemic centre (stipples). The broken lines are an arbitrary line, delimiting its border to the south.

6. Mt. Muria Region

The existence of this endemic centre (No. 5 in Fig. 4.22; Fig. 4.28) has been determined by the occurrence of the endemic *Callosciurus nigrovittatus madsoedi*. Geographic isolation to its faunal elements resulted from eustatic sea level changes during Pleistocene and Holocene period. It has been connected to the mainland to the south by the lowered sea levels in the last Pleistocene Glacial Maxima and isolated as sea levels rose in the Post Glacial Period.

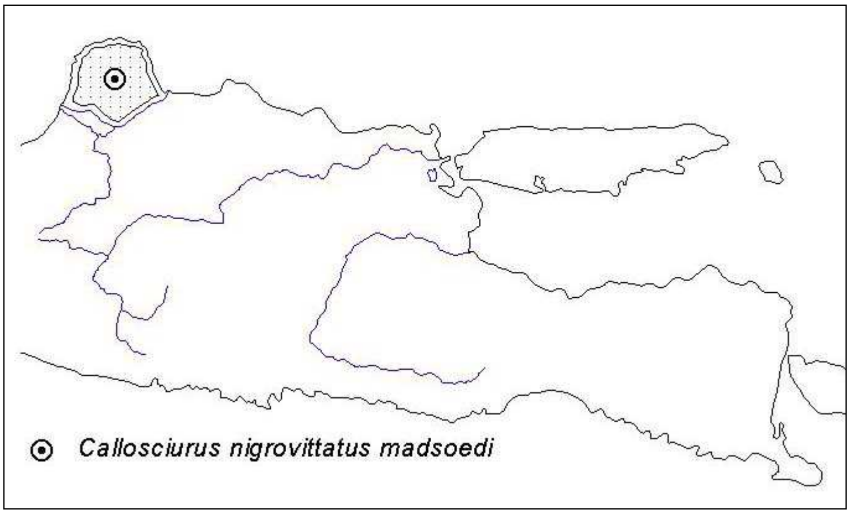


Figure 4.28 The sub-endemic centre of Mt. Muria region (stipples): a typical geographic isolation through eustatic sea level changes during Pleistocene and Holocene period.

7. East-Javan Lowlands

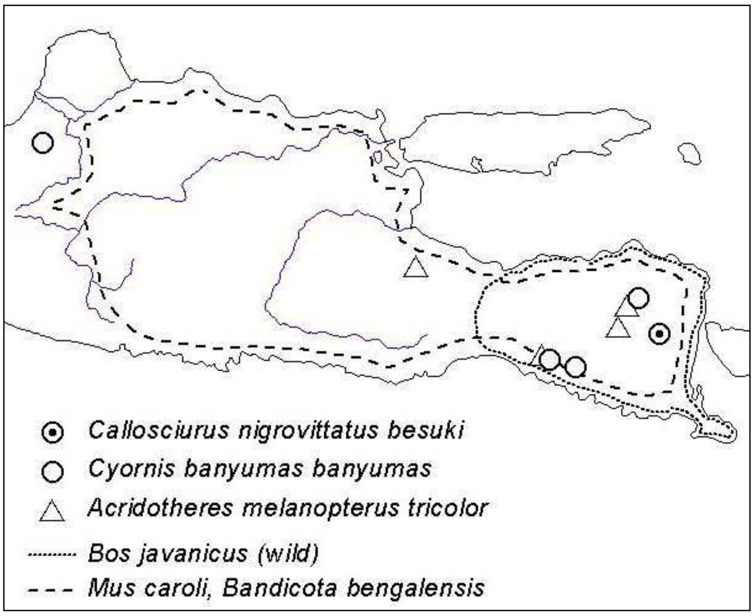


Figure 4.29 Ranges of the five faunal elements of the East-Javan lowlands. *Cyornis banyumas banyumas* (Muscicapidae) extends as far west as western Central-Java region.

This sub-endemic centre (No. 7 in Fig. 4.22; Fig 4.29) includes lower to middle elevations in Eastern Java, below the montane forest sub-endemic centre (Refer to no. 4). Its existence is mainly indicated by the ranges of two murids, i.e *Mus caroli* and *Bandicota bengalensis*. This sub-endemic centre is much drier than the lowlands in the western part of Java because it receives the dry southeasterly winds from Australia. This has also been indicated by the endemic *Acridotheres melanopterus tricolor* (Sturnidae) that is strickly adapted to open country with scattered trees in the lowlands and middle levels (Mees, 1996).

4.1.3 Sumatran Endemic Centre

The Sumatran endemic centre (Fig. 4.30) includes the mainland, islands off the western coast of Sumatra, i.e. Simeuleu, Banyak, Nias, Batu and Mentawai Islands, and Enggano as well as islands off the eastern coast of Sumatra such as Riau Islands, Lingga Islands, Bangka and Belitung. Also included within this hotspot is We Island off the northern coast of Sumatra. We Island, Simeuleu and Enggano Islands are separated from the mainland by deep marine barriers. Nias Island on the other hand is connected indirectly with the mainland through Banyak Islands to the north and Batu Islands to the south. Batu Island also seems to have been a "stepping-stone" for fauna, which migrated to Mentawai Island. Meanwhile, islands off the eastern coast of Sumatra are all lying on the shallow Sunda Shelf and were certainly connected to the mainland in the Pleistocene Glacial Maxima.

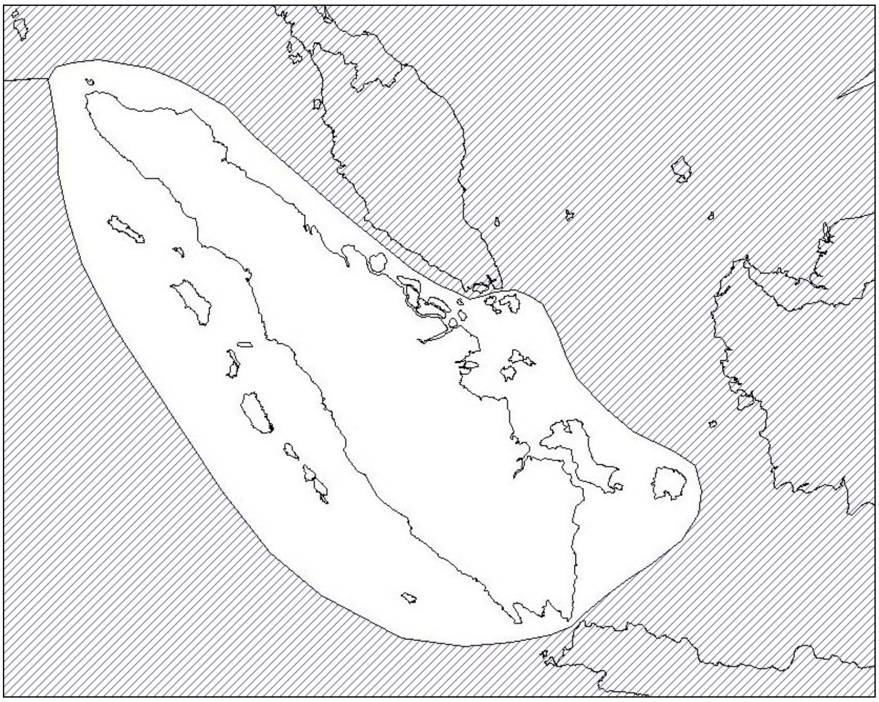


Figure 4.30 The Sumatran Endemic Centre, excluding Anambas Islands off the eastern coast.

Amphibians of Sumatra have the lowest endemicity among those of islands in the Great Sundas with only 20.9% of the total 67 taxa found there (Yang 1991, Emerson & Berrigan 1993, Manthey & Grossmann 1997, Duellman 1999, Dubois & Ohler 2000, Emerson *et al*. 2000, Iskandar & Colijn 2000, Veith *et al*. 2001, Frost 2002). The endemic forms are listed in Table 4.10. This falls far lower than that of Borneo (61.8%) and Java (29%). It occupies the second place in the number of taxa found above Java (34 taxa), but is still much lower than Borneo (137 taxa). Numerous taxa confined to Borneo (see accounts thereof) are absent from this island. Contrastly, only two genera found on Sumatra are absent either on Borneo or Java, i.e. *Micryletta* and the monotypic genus *Phrynella* (Microhylidae – Microhylinae). Additionally, Sumatra still supports five genera more than Java, i.e. *Pedostibes*, *Pelophryne*, and monotypic genus *Pseudobufo* (Bufonidae); *Calluella* (Microhylidae – Dyscophinae); and *Theloderma* (Rhacophoridae). On the other hand, the number of shared taxa with Borneo is relatively high (56.3%); despite the obvious difference in their endemicity, while shared taxa with Java reaches a level of only 35.9%.

Table 4.10 Endemic amphibians of Sumatra and its nearby islands

Family	Endemic taxa
Bufonidae	*Bufo claviger, B. sumatranus, B. valhallae*
Ranidae	*Huia modiglianii, H. sumatrana, Rana crassiovis, R. debussyi, R. kampeni, R. persimilis, R.siberu*
Rhacophoridae	*Philautus cornutus, P. similis, Rhacophorus modestus, R. poecilonotus*

The lower endemicity among Sumatran amphibians, than those of Borneo and Java shows that the Sumatran amphibians are much younger than those of Borneo and Java from an evolution point of view. It is likely that, in contrast to the numerous oriental lineages, which drifted to Borneo through tectonic movements, Sumatra did not receive oriental lineages in such a way. A direct migration of oriental lineages from Southeast Asia only occurs through a land bridge, which existed much later in the Pleistocene Period. The only immigrants coming earlier than the Pleistocene Period are possibly only those which migrated from Java, for example *Bufo sumatranus* (Bufonidae); *Fejervarya nicobariensis*, *Rana chalconota*, *R. erythraea* (Ranidae); and *Polypedates leucomystax* (Rhacophoridae - Rhacophorinae). Their early arrival on Sumatra has been indicated by the occurrence of their disjunct populations, except *B. sumatranus*, on the Nicobar Islands off Northwest Sumatra, which is situated outside the 200m isobath. The Nicobar Islands probably never had a land connection with the mainland and hence perhaps only tectonic movements could be responsible for the dispersal of those taxa found there. Such tectonic movements must also be responsible for the separation of *Bufo valhallae* (Bufonidae) currently endemic to We Island to the north. Also endemic forms of Sumatran rhacophorids, i.e. *Philautus cornutus*, *P. similis*, *Rhacophorus modestus* and *R. poecilonotus*, might be early migrants from Java.

In contrast to the later migrants on Sumatra, this island obviously received much more recent immigrants in the Pleistocene Period from Borneo and Southeast Asia of which only a few of them could extend further east to Java. This explains the high number of such taxa confined here in comparison to those found on Java and statistically supported by higher shared taxa with Borneo but still lower than with Java. Such recent immigrants from

Southeast Asia are for example *Bufo asper* (Bufonidae) and *Micryletta inornata* (Microhylidae – Microhylinae). Their ranges are in common restricted to the Great Sundas and the nearby islands connected by a land bridge in the Pleistocene Glacial Maxima. In Southeast Asia, their ranges encompass generally the region northward from the Isthmus Kra. In contrast, recent immigrants from Borneo have the northernmost limit in the south of the Isthmus Kra in common. Supposing that any populations occurred in the north, they are normally disjuncted from populations to the south. Such species are among other monotypic genera *Phrynella pulchra* (Microhylidae – Microhylinae), *Pelophryne brevipes* and *Pseudobufo asper* (Bufonidae).

In contrast to amphibians, the endemism among Sumatran mammals is slightly higher than that of Javan mammals. From the total of 163 taxa found there, including the probable occurrence of *Bubalus bubalis* (Bovidae) and *Viverra megaspila* (Viverridae), at least 60 of these are endemic forms (see Table 4.11) (Corbet & Hill 1992, Wilson & Reeder 1993, Yanuar *et al*. 1993, Suyanto *et al*. 1998, Nowak 1999). This corresponds to 36.8% of the total and as mentioned above, this is slightly higher than the Javan level that accounts for only 31%. As already mentioned in the section on Javan endemic centre, this is mainly as a result of the earlier migrants from Java, in contrast to amphibians, which became isolated and evolved into endemic forms and were accentuated by those derived from recent migrants from Borneo and Southeast Asia.

Table 4.11 Endemic mammals of Sumatra and its nearby islands. An asterisk marks the monotypic genera

Family	Genera with number of species (and endemic subspecies)
Cercopithecidae	Macaca 1, Presbytis 2(9), Simias* 1
Hylobatidae	Hylobates 1(1)
Hystricidae	Hystrix 1
Leporidae	Nesolagus* 1
Muridae – Murinae	Chiropodomys 1, Leopoldamys 1, Maxomys 3, Mus 1, Rattus 5
Pongidae	Pongo* (1)
Sciuridae	Callosciurus (13), Hylopetes 2, Iomys 1, Lariscus 1, Petaurista (1), Petinomys 1(1), Ratufa (1), Sundasciurus 1
Soricidae	Crocidura 3
Tupaiidae	Tupaia 1(3)
Viverridae	Paguma* (1), Paradoxurus 1

Endemic forms derived from early migrants from Java are for example *Simias concolor* (Cercopithecidae); *Chiropodomys karlkoopmani* (Muridae), *Paradoxurus lignicolor* (Viverridae), *Rattus adustus*, *R. lugens* and *R. enganus* (Muridae – Murinae). On the other hand, endemic taxa detected as recent immigrants from Borneo are among other *Pongo pygmaeus abelii* (Pongidae); *Petaurista elegans sumatrana*, *Petinomys hageni hageni*, possibly *Ratufa bicolor palliata* (Sciuridae); *Tupaia gracilis infalata*, *T. minor humeralis* and *T. m. sincipis* (Tupaiidae). Additionally, at least two endemic subspecies are detected as recent migrants from Southeast Asia. They are the monotypic genus *Paguma larvata leucomystax* (Viverridae) and *Hylobates lar vestitus* (Hylobatidae).

The range of *Chiropodomys gliroides* (Muridae – Murinae), which is detected as an early migrant from Borneo through Java, shows how a population on the mainland contracted and left the population on the Nias Island off western coast of Sumatra isolated (see Figure 4.4). Meanwhile, the occurrence of endemic *C. karlkoopmani* on Mentawai Islands suggests its earlier separation from the population on the mainland. The isolation of the monotypic genus *Simias concolor* (Cercopithecidae) on the Mentawai Islands undoubtedly also happened in this way and was separated even much earlier from its ancestor regarding its separation at higher taxonomical level. The monotypic genus *Nasalis larvatus* (Cercopithecidae) on Borneo is suspected as its ancestor. This species once includes *S. concolor*, based on the close resemblance of some morphological feature, but later *S. concolor* was regarded as a distinct genus.

Sumatran reptiles are represented by 222 taxa, of which, 49 taxa are endemic forms (see Table 4.12) (Uetz 2005, Schulz 1996, Das 1998, McDiarmid *et al.* 1999, Iskandar 2000). This corresponds to 22.1% of the total, which is still lower than Borneo but much higher than Java. It is however much lower than the endemicity among Sumatran amphibians and mammals because reptiles are much better to disperse.

Table 4.12 Endemic reptiles of Sumatra and its nearby islands

Family	Genera with number of endemic species (and endemic subspecies)
Agamidae	Bronchocela 1, Dendragama* 1, Draco (2), Gonocephalus 3, Harpesaurus 3, Lophocalotes* 1, Phoxophrys 1
Anguidae	Ophisaurus 1
Colubridae	Amphiesma 1, Anoplohydrus* 1, Boiga 1(1), Calamaria 10, Elaphe (1), Etheridgeum* 1, Iguanognathus* 1, Internatus 1, Oligodon 6(2), Opisthotropis 1, Pseudorabdion 1, Pseudoxenodon (1)
Gekkonidae	Luperosaurus 1
Scincidae	Larutia 1, Riopa 1, Sphenomorphus 1
Typhlopidae	Typhlops 1
Viperidae	Trimeresurus 1(1)

The most widely differentiated forms are genus *Calamaria* and *Oligodon* (Colubridae) with 10 and 8 endemic taxa respectively. In regard to this high differentiation of both genera, it is undoubted that both are early immigrants from Java that were long isolated and evolved there into new forms separated from their ancestors. This assumption is supported by the occurrence of *Oligodon praefrontalis* that is endemic to Weh Island. The readiness of reptiles to disperse has also been indicated by the occurrence of more taxa, which are confined to the Simeuleu and Enggano Islands. At least 17 taxa have been recorded from Simeuleu Island of which one of them is an endemic form, i.e. *Trimeresurus brongersmai* (Viperidae). On the other hand, 5 taxa occur on Enggano Island with two endemic forms, i.e. *Draco lineatus modiglianii* (Agamidae) and *Elaphe subradiata enganensis* (Colubridae). The occurrence of a relative of *D. l. modiglianii* on Java and Northern Sulawesi, i.e. *D. l. spilonotus*, shows clearly the penetration of this taxon from the Java mainland. Such a penetration might also have been done by *E. s. enganensis* although its only relative, *E. s. subradiata*, was firstly found on Lombok, Sumbawa, Sumba, Komodo, Flores, Alor, Roti, Semau, Timor, and Wetar. Its absence on the intervening islands might be as a result of its extinction there.

Also the endemism among Sumatran birds is considerably higher than that of Java, but lower than that of Borneo. The existence of 244 endemic forms out of 609 indigenous birds restricted to the mainland and nearby islands brings the endemicity to 40% (see Table 4.13) (Andrew 1992, MacKinnon & Phillipps 1993, Jones *et al*. 1995, Laman *et al*. 1996, Stattersfield *et al*. 1998, Clements 2000).

The existence of numerous endemic insular forms on offshore islands of Sumatra, especially on islands off the western coast, has contributed much to the high endemicity among Sumatran birds. Table 4.14 shows the comparison of endemic insular forms on islands off the western coast. The comparison shows that the remote Simeuleu and Enggano islands have higher endemicity compared to the rest of the islands, which are directly or indirectly connected to the mainland. This evidence in turn supports the tendency of the flightlessness in birds on isolated islands due to the lack of predators and competitors there.

Meanwhile, islands off the eastern coast of Sumatra, which are well-known to have been connected to the mainland by the lowering sea level in the last Glacial Maxima, have much less endemic insular forms. There are some taxa restricted to one island group or several island groups. However, only a few of them are restricted to a single island on the eastern coast. They are all found on Belitung Island, i.e. *Chloropsis cochinchinensis bilitonis* (Chloropseidae), *Strix leptogrammica chaseni* (Strigidae) and *Phodilus badius parvus* (Tytonidae).

Table 4.13 Endemic birds of Sumatra and its satellite islands

Family	Genera with number of endemic species (and endemic subspecies)
Accipitridae	Accipiter (3), Spilornis (4), Spizaetus (2)
Alcedinidae	Alcedo (3), Ceyx (2), Pelargopsis (5), Todirhamphus (2)
Apodidae	Aerodramus (4)
Ardeidae	Ardea (1)
Campephagidae	Coracina (6), Pericrocotus (3)
Capitonidae	Megalaima (7)
Caprimulgidae	Caprimulgus (1), Eurostopodus (1)
Chloropseidae	Chloropsis 1(4)
Cisticolidae	Prinia (2)
Columbidae	Ducula (5), Macropygia (6), Treron (2)
Coraciidae	Eurystomus (1)
Corvidae	Dendrocitta 1
Cuculidae	Carpococcyx 1, Eudynamis (1), Phaenicophaeus (3)
Dicaeidae	Prionochilus (1)
Dicruridae	Dicrurus 1(5)
Estrildidae	Lonchura (2)
Eurylaimidae	Calyptomena (1), Cymbirhynchus* (1), Eurylaimus (1), Serilophus* (1)
Fringillidae	Serinus (1)
Hemiprocnidae	Hemiprocne (1)
Monarchidae	Hypothymis (4), Terpsiphone (3)
Muscicapidae	Cinclidium (1), Cochoa 1, Copsychus (8), Cyornis 1(1), Enicurus (2), Eumyias (1), Ficedula (2)
Nectariniidae	Arachnothera (2), Chalcoparia* (2), Cinnyris (1), Leptocoma (2)
Oriolidae	Oriolus (5)
Paramythiidae	Dicaeum (8)
Phasianidae	Arborophila 1(3), Caloperdix* (1), Lophura (3), Polyplectron (2)
Picidae	Dendrocopos (1), Dryocopus (1), Meiglyptes (2), Picus (6), Sasia (1)
Pittidae	Pitta 2(1)
Podargidae	Batrachostomus (1)
Psittacidae	Psittacula (5)
Pycnonotidae	Alophoixus (1), Hypsipetes (1), Pycnonotus 2(4), Tricholestes* (1)
Rallidae	Porphyrio (1)
Strigidae	Glaucidium (1), Ketupa (1), Otus 3(3), Strix (4)
Sturnidae	Aplonis (4), Gracula 2(1)
Sylviidae	Abroscopus (1), Cettia (2), Orthotomus (2), Seicercus (3)
Timaliidae	Garrulax (3), Heterophasia (1), Leiothrix (2), Macronous (3), Malacocincla (2), Malacopteron (2), Napothera 1(4), Pellorneum (2), Pnoepyga (1), Pteruthius (1), Rimator* (1), Stachyris (9), Yuhina (1)
Trogonidae	Harpactes (3)
Turdidae	Brachypterix (1), Myophonus 1(1), Turdus (2), Zoothera (1)
Tytonidae	Phodilus (1)
Zosteropidae	Zosterops 1(3)

Table 4.14 Endemic birds confined to islands off Western Sumatra

Islands off western coast	Number of endemic taxa	Endemicity (%)
Simeuleu I.	23	34.3
Banyak Is.	11	25.6
Nias I.	24	23.1
Batu Is.	11	15.3
Mentawai Is.	16	19.3
Enggano I.	12	33.3

Differentiation on the Mainland

Differentiation on the mainland can be well observed from the distribution of four species and twenty-one subspecies of leaf monkey genus *Presbytis* (Cercopithecidae). Their distribution ranges used in this study are mainly based on data from Wilson & Wilson (1976).

There are at least sixteen sub-endemic centres recognised on the mainland (Fig. 4.31). In general, these sub-endemic centres can be divided into two main groups, i.e. highland group lying along the western coast and lowland group lying along the eastern coast.

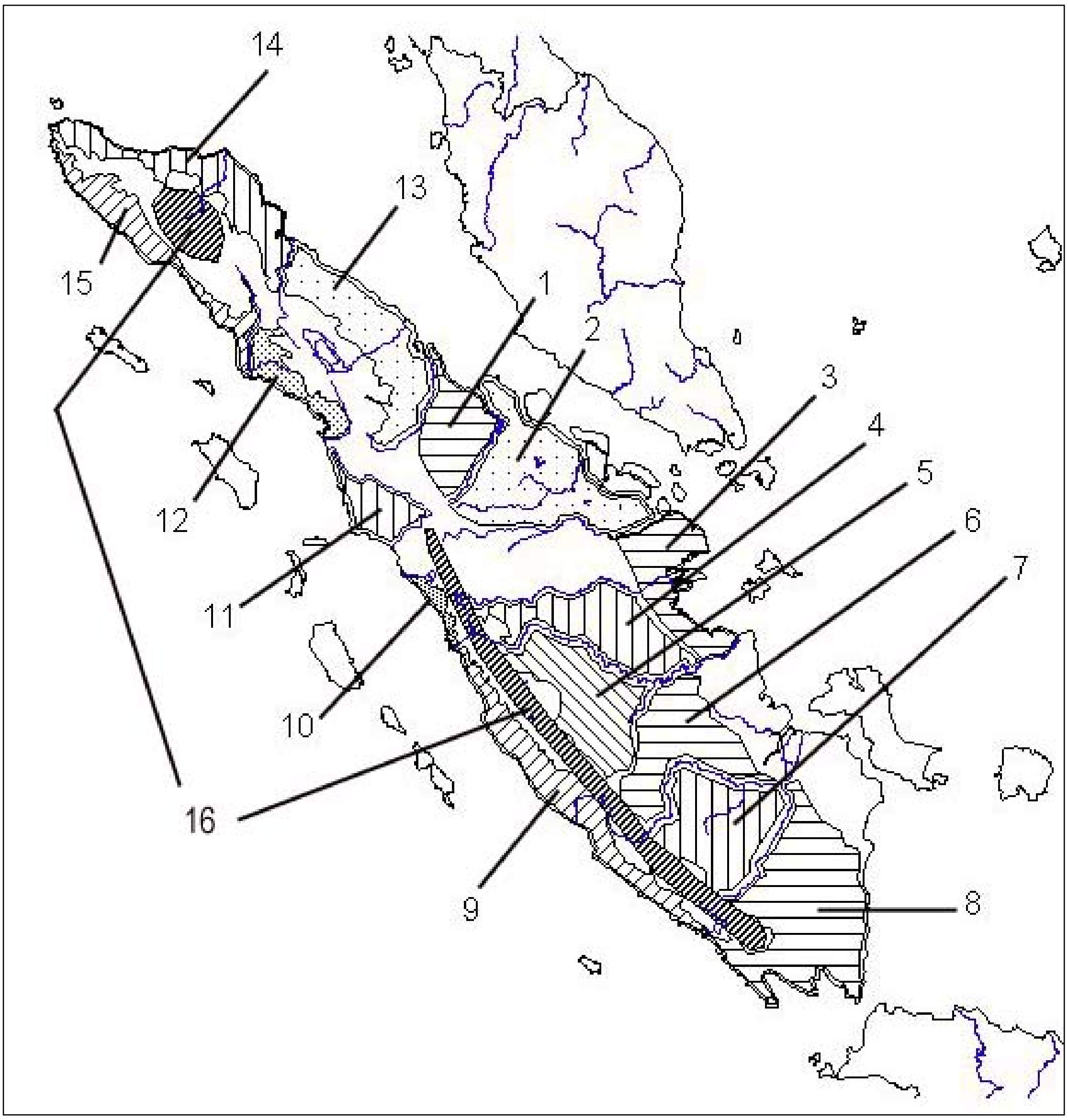


Fig. 4.31 The sixteen sub-endemic centres recognised on the Sumatran mainland: 1) Barumun-Rokan 2) Rokan-Kampar 3) Kampar-Batanghari 4) Upper Kampar – Upper Batanghari 5) Upper Batanghari – Tembesi 6) Tembesi – Musi 7) Musi – Komering 8) Lampung 9) West Coast 10) Lake Maninjau 11) Pasaman 12) West Toba 13) East Toba 14) Northeast Sumatra 15) Northwest Sumatra 16) Leuser – Barisan.

1. Barumun – Rokan

This sub-endemic centre (Fig. 4.31, no.1; Fig. 4.32) is determined by the occurrence of the endemic *Presbytis femoralis paenulata*. This taxon inhabits swamp forests in eastern coastal Sumatra between the Barumun and Rokan rivers. It extends inland, facilitated by swamp forests as far as the lowlands on the eastern slopes of the Barisan Ranges.

2. Rokan – Kampar

Southward of the Rokan River, *P. f. paenulata* is replaced by its close relative, *P. f. percura*, and therefore indicates a new sub-endemic centre (Fig. 4.31, no. 2; Fig. 4.32), limited to the south by the Kampar River. Similar to its relative found on the Barumun – Rokan area, this taxon can be found in swampy areas that extend also far inland to the hill forests of the eastern slopes of the Barisan Ranges.

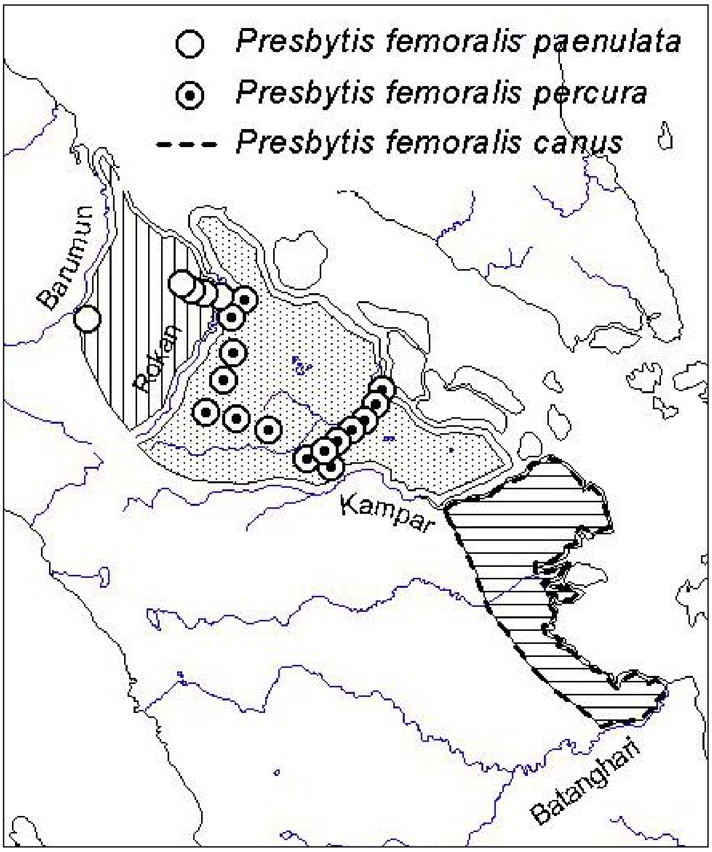


Figure 4.32 The distribution ranges of three subspecies of *Presbytis femoralis* in mangrove forests on eastern coast of West-Central Sumatra. Each subspecies defines an independent sub-endemic centre. Their separation is the result of the rise of sea levels during the warm period in the Post Glacial Period.

3. Kampar – Batanghari

The swamp forests between Kampar and Batanghari rivers (Fig. 4.31, no. 3; Fig. 4.32) is the southernmost range of *Presbytis femoralis*, where it is home to the endemic subspecies *P. f. canus*. In contrast to the first two taxa above, *P.f. canus* is restricted the lower parts of these rivers, where swamp forests are found. The broad lowland forests on the upper rivers have limited its dispersal inland.

4. **Upper Indragiri – Upper Batanghari**

   On lowland forests in the upper rivers, a new species *P. melalophos* has replaced *P. femoralis*. The upper river region between Indragiri and Batanghari (Fig. 4.31, no. 4; Fig. 4.33) is inhabited by a subspecies hitherto still undetermined. While swamp forests limit it to the east, its range to the west is bordered by higher elevation of the east slopes of the Barisan Ranges.

5. **Upper Batanghari –Tembesi**

   This sub-endemic centre (Fig. 4.31, no. 5; Fig. 4.33) has been determined by the range of *Presbytis melalophos nobilis* (Cercopithecidae). Its lowland forests are bordered to the east by a junction of both rivers and of course by their drainage areas to the north and south. To the west, it is limited by the higher elevations of the eastern slopes of the Barisan Ranges.

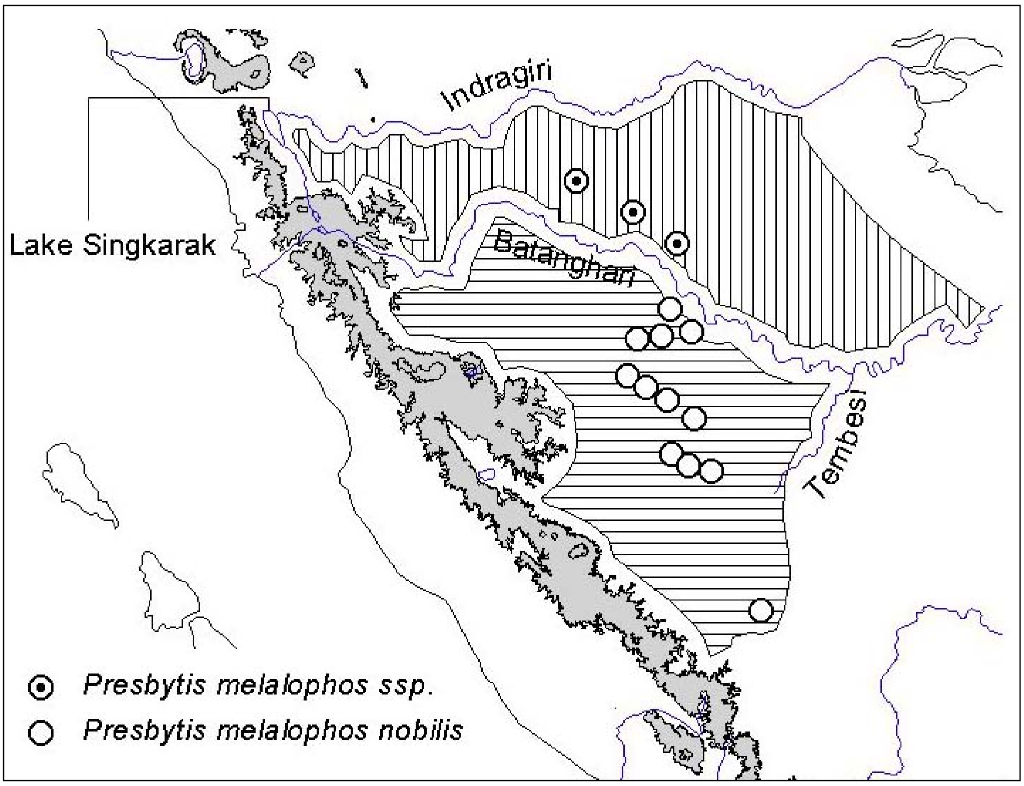


Fig. 4.33 Distribution of two subspecies *Presbytis melalophos* in Central Sumatra, indicating the position of two endemic areas, i.e Upper Indragiri – Upper Batanghari (vertical hatching) and Upper Batanghari–Tembesi River (horizontal hatching). The grey areas are the highlands of Barisan Range.

6. Tembesi – Musi

The upper river region between Tembesi and Musi (Fig. 4.31, no. 6; Fig. 4.34) is occupied by subspecies *Presbytis melalophos fluviatilis*. This region is also mainly made up of lowland forests and it borders to the east on swamp forests of the Southeast Sumatra region. As typical lowland dwellers, the range of *P. m. fluviatilis* is limited to the west by higher elevations of the eastern slopes of the Barisan Ranges.

7. Musi – Komering

Going farther south to the upper river region between Musi and Komering, the other sub-endemic centre (Fig. 4.31, no. 7; Fig. 4.34) exists as indicated by the range of another *Presbytis melalophos* whose sub-specific name has not yet been determined. Its boundaries to the east and west are similar to those of *P. m. fluviatilis*.

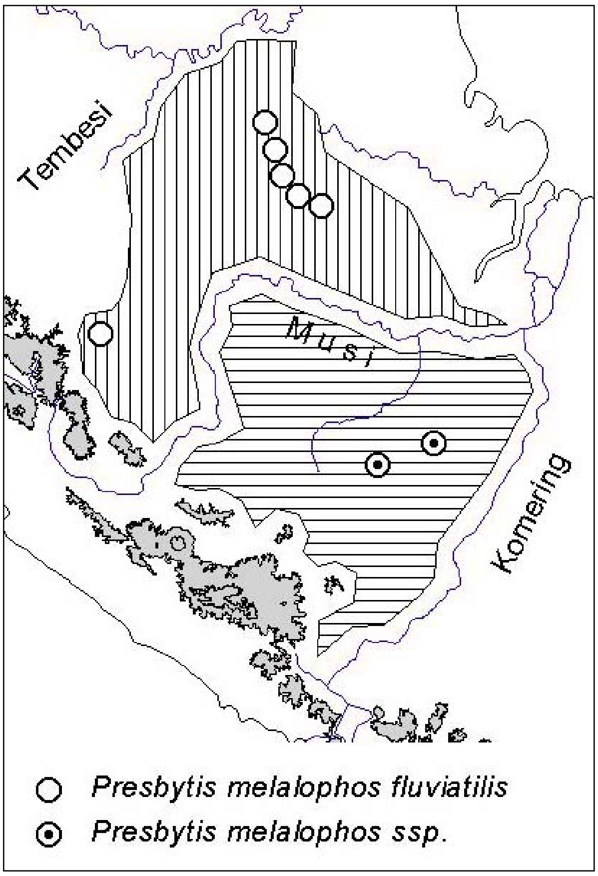


Fig. 4.34 Two sub-endemic centres in Southeast Sumatra are indicated by the ranges of two subspecies of *Presbytis melalophos*, i.e Tembesi – Musi (vertical hatching) and Musi – Komering (horizontal hatching)

8. Lampung

This sub-endemic centre (Fig. 4.31 no. 8; Fig. 4.35) encompasses lowland forests of South-central Sumatra and hill forests in the southwest as indicated by the range of *Presbytis melalophos fuscomurina*. It is bordered to the north by Mt. Pugung (1,964m) lying west of Lake Ranau, L. Ranau itself and the Komering River, which are draining from that lake. To the east, it borders on swamp forests of the southeastern Sumatra division. The break of the Barisan Range in South Sumatra resulted in lowland and highland populations remaining in the same taxonomical level.

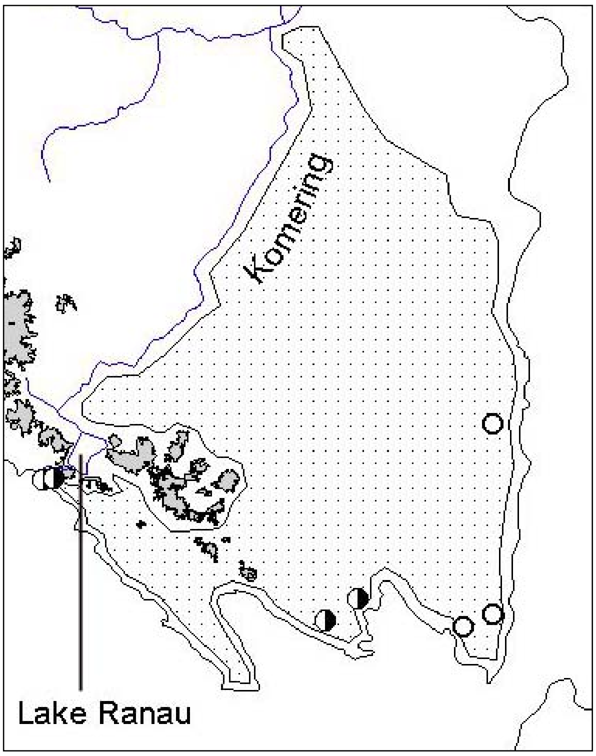


Figure 4.35 Distribution of *Presbytis melalophos fuscomurina* in Southern Sumatra (half-dark = highland form) and white circle = lowland form. The break of Barisan Range resulted these two forms not yet separated.

9. West Coast Sumatra

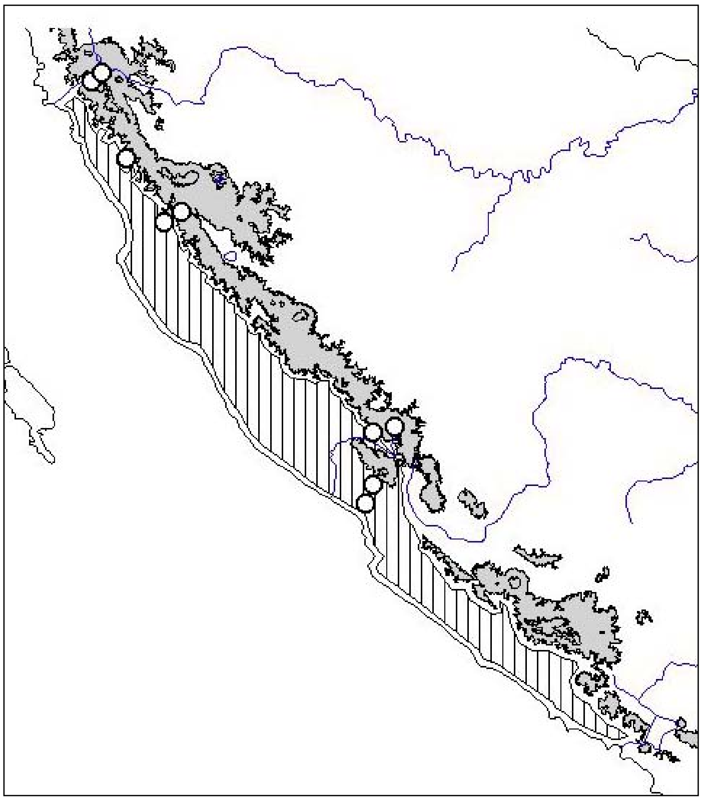


Figure 4.36 The distribution of *Presbytis melalophos melalophos* determines the position of the West-Coast sub-endemic centre (vertical hatching).

The lowlands up to lower montane forests along the western coasts from Mt. Pugung (1,964m) in the south to Mt. Sulasih (2,597m) in the near Alahan Panjang in the north (Fig. 4.31, no. 9; Fig. 36) are inhabited by *Presbytis melalophos melalophos*. To the east, it borders on the higher elevations of the Barisan ranges.

10. Lake Maninjau

This sub-endemic centre (Fig. 4.31, no. 10; Fig. 4.37) is confined on the range of *Presbytis melalophos ferruginea*. It is limited in the south by a river draining from Lake Diatas and in the north by a river draining from Lake Maninjau. Due to the break of the Barisan Range on the east border, the sub-endemic centre may extend beyond this border as proposed by some scientists (Wilson & Wilson 1976; Whitten *et al.* 1997).

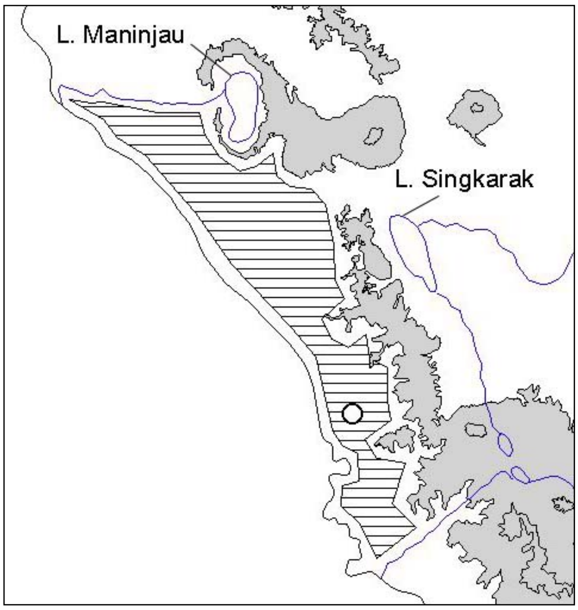


Fig. 4.37 The occurrence of the endemic *Presbytis melalophos ferruginea* westward from Lake Maninjau confines the existence of the Lake Maninjau sub-endemic centre.

11. Pasaman

The occurrence of *Presbytis melalophos aurata* indicates the distinction of this sub-endemic centre (Fig. 4.31, no. 11; Fig. 4.38) north of the Padang Highlands. It occurs between the Gadis River and an unnamed river lying left of Mt. Talaman (2,912m). The upper Gadis River at the same time limits it to the north. The area is low lying with hill forests west of the curved mountain chain of Sorikmarapi, Kulabu and Ophir in the Pasaman district.

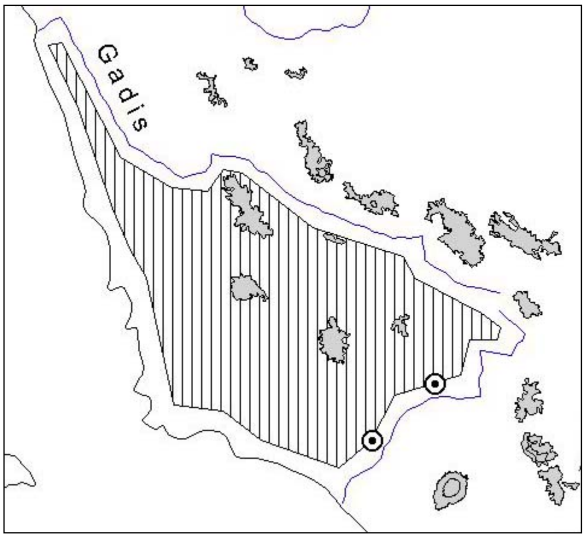


Fig. 4.38 The sub-endemic centre of Pasaman, being confined on the range of *Presbytis melalophos aurata*. The occurrence of a mountain on upper rivers may have isolated this species during the lowering of the tree line in the last Pleistocene Glacial Maxima.

12. West Toba Sub-endemic Centre

This sub-endemic centre (Fig. 4.31, no. 12; Fig. 4.39) is the northernmost range of *Presbytis melalophos*, where the subspecies *P. m sumatrana* occurs. On the north it borders with the Simpangkanan River and to the south with a river, which is drained to the west coast in the nearby Teluk Sibolga. High elevations of the Batak Highlands limit it to the east.

13. East Toba Sub-endemic Centre

Presbytis melalophos margae occurs on the northeastern most ranges of the species; limited in the north by the Wampu River and in the south by the Baruman River, while it is limited to the west by the higher elevations of the Batak Highlands (see Fig. 4.31, no. 13; Fig. 4.39).

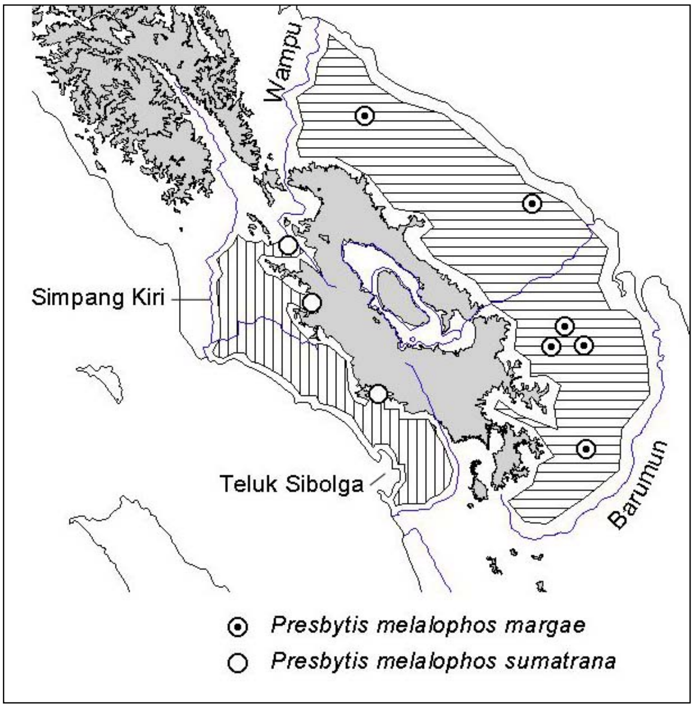


Fig. 4.39 Type distribution of two subspecies *Presbytis melalophos* in the Toba region: *P. m. sumatrana* determines the sub-endemic centre in the West Toba (vertical hatching) and *P. m. margae* in the East Toba (horizontal hatching)

14. Northeast Sumatra

The distinction of this sub-endemic centre (see Fig. 4.31, no. 14; Fig. 4.40) has been indicated by the endemic *Presbytis thomasi thomasi*, whose range is limited to the south by the Wampu River and to the east by the high elevations of the Gayo and Leuser Highlands.

15. Northwest Sumatra

On the other side of Gayo and Leuser Highlands (see Fig. 4.31, no. 15; Fig. 4.40), this region is home to *Presbytis thomasi nubilis*, whose range to the south is limited by the Simpangkiri River.

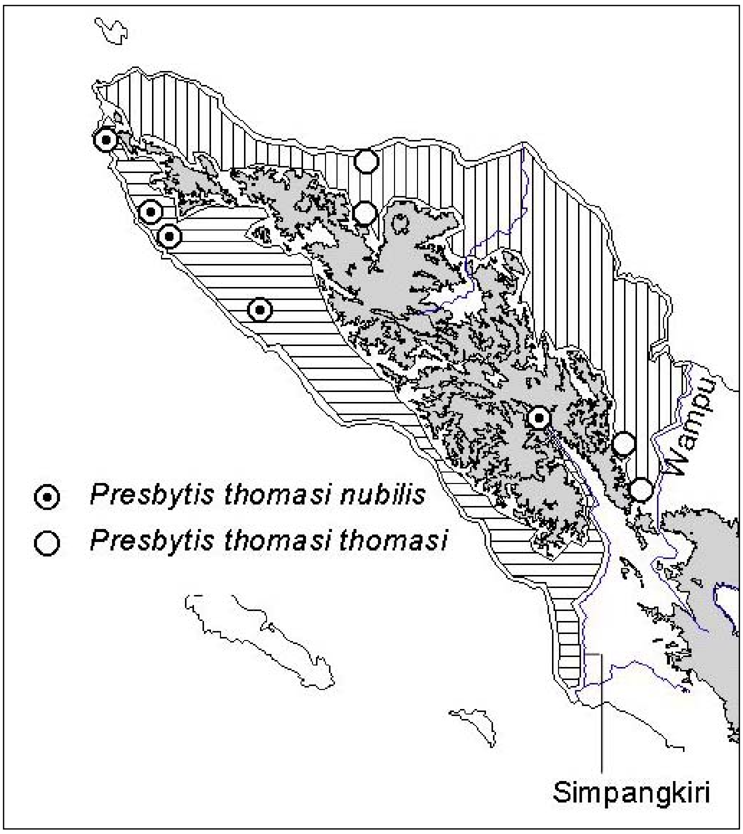


Fig. 4.40 The distinction of northern Sumatra has been indicated by the replacement of *Presbytis melalophos* by *P. thomasi*. Two extant subspecies determines two different sub-endemic centres, i.e lowlands in Northeast Sumatra (vertical hatching) and highlands in Northwest Sumatra (horizontal hatching)

16. The Sumatran montane forest

The position of this sub-endemic centre is defined by the ranges of *Lophura inornata* (Phasianidae) and *Turdus poliocephalus* (Turdidae). The ranges of their subspecies show that two divisions can be distinguished, i.e. the Gayo-Leuseur division and the Barisan Range division (Fig. 4.31, no. 16; Fig. 4.41). The first division lies in the montane forests of Northwest Sumatra and corresponds to the ranges of *L. i. hoogerwerfi* and *T. p. loeseri*. The latter includes the montane forests, which stretch from Ophir District in West-central Sumatra to the Bengkulu Province in southwestern Sumatra and corresponds to the ranges of *L. i. inornata* and *T. p. Indrapurae* as well as *Maxomys inflatus* (Muridae). Close relationship between the two divisions is indicated by taxa, which occur in both subdivisions, for example *Leopoldamys edwardsi* (Muridae), *Nesolagus netscheri* (Leporidae), and *Niviventer rapit* (Muridae).

In spite of this close relationship, the Barisan Range division obviously harbours much more faunal elements which are mostly restricted to the west-central region. Thus, the following mammals occur in this region: *Mus crociduroides* (Muridae), *Tupaia javanica* (Tupaiidae), *Crocidura paradoxura* (Crociduridae), *C. Baluensis*, *Rattus korinchi* (Muridae – Murinae), *Maxomys hylomyoides*, *Chimarrogale phaeura*. On the other hand, the few taxa restricted to the Gayo-Leuser division are for example *Rattus hoogerwerfi* (Muridae – Murinae).

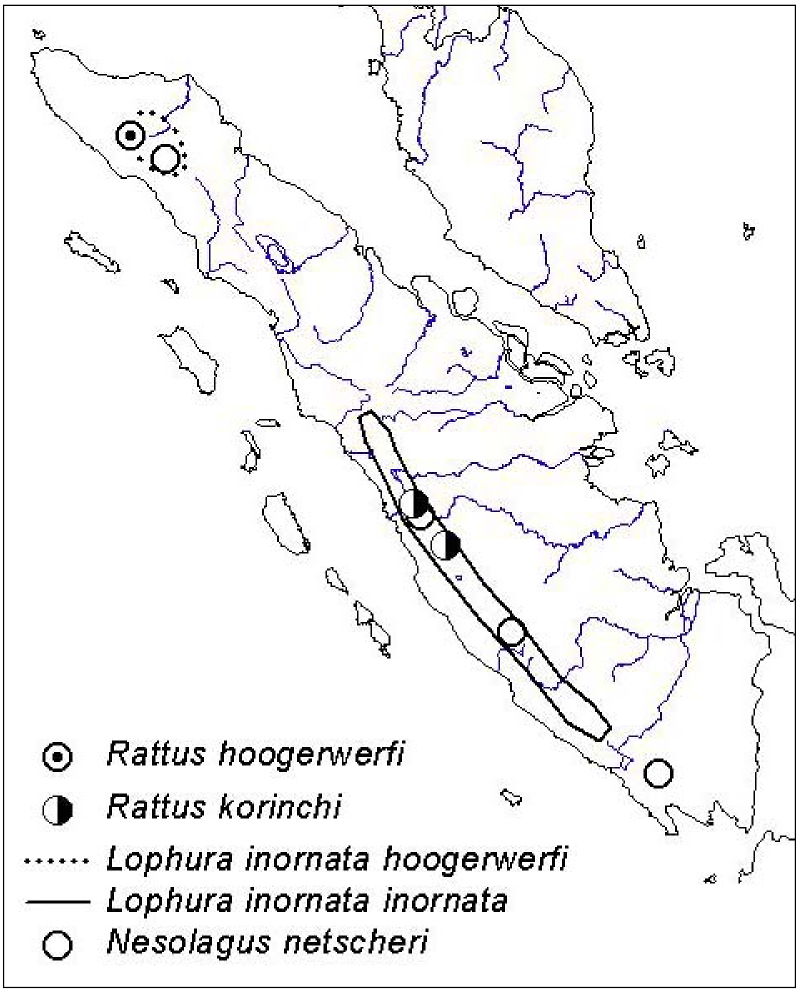


Figure 4.41 Faunal elements of the Gayo-Leuser division (*Rattus hoogerwerfi* and *Lophura inornata hoogerwerfi*) and of the Barisan division (*Rattus korinchi* and *Lophura inornata inornata*). *Nesolagus netscheri* is a polycentric faunal element whose range indicates the close relationship between the Leuser and Barisan divisions.

Other than to the Gayo-Leuser division, some faunal elements of the Barisan Range division are also closely related to taxa found on the montane forests of the Malay Peninsula, Borneo, or Java. These taxa, whose ranges are shared with the Malay Peninsula and Borneo, are for example *C. phaeura* and *N. rapit*. Those shared with only Borneo are *C. baluensis* and *H. semitorquatus*. Finally, those found also on the highlands of Java are *C. paradoxura* and *T. javanica*.

4.1.4 Sulawesian Endemic Centre

This endemic centre (Fig. 4.42) includes the Sulawesian mainland and its satellite islands, i.e. Talaud and Sangihe Islands to the northeast; Togian Islands in the Gulf of Tomini; Banggai Islands and Sula Islands to the east; Kabaena, Muna, Butung and Tukangbesi islands to the southeast; as well as Salayar and islands in the Flores Sea to the south.

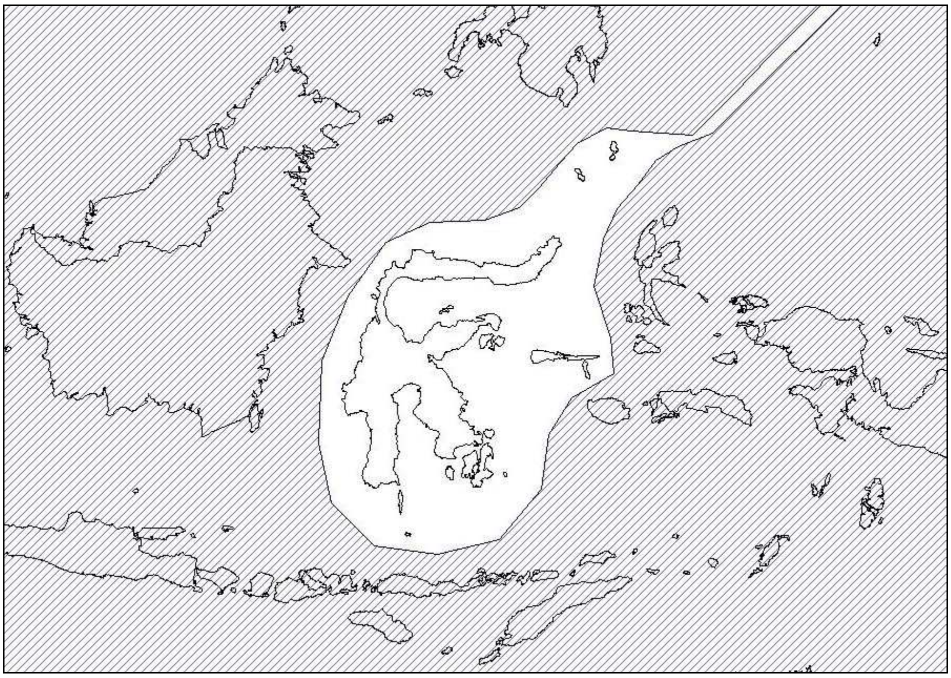


Fig. 4.42 The Sulawesian endemic centre, including Sangihe Is. and Talaud Is. to the northeast and Banggai Is. and Sula Is. to the east.

The composition of Sulawesian amphibians show that similar to Borneo the Sulawesi region also received some amphibian lineages, which drifted from Asia, but much less than those, which drifted to Borneo. Nevertheless, endemism is considerably high with 15 endemic forms out of 29 taxa (51.7%), including the probable occurrence of *Limnonectes finchi* (Ranidae) on North Sulawesi (see Table 4.15) (Tyler 1968, Duellman 1999, Iskandar & Colijn 2000, Frost 2002).

Table 4.15 Endemic amphibians of the Sulawesi mainland and its satellite islands

Family	Endemic species
Bufonidae	*Bufo celebensis*
Microhylidae – Asterophryinae	*Callulops kopsteini*
Microhylidae – Genyophyninae	*Oreophryne celebensis, O. variabilis, O. zimmeri, Limnonectes arathooni, L. heinrichi, L. microtympanum*
Rhacophoridae	*Rhacophorus edentulus, R. georgii, R. monticola*
Ranidae	*Occidozyga celebensis, O. semipalmatus, Rana celebensis, R. macrops*

In contrast to Borneo, an Australian lineage *Litoria infrafrenata infrafrenata* (Hylidae – Pelodryadinae) has been recorded within its faunal elements. This taxon is confined from the Sulawesi region to Talaud Island. In regard to the two well-known different faunal assemblages found in the Indonesian Archipelago; this indicates a turnover of oriental to Australian fauna. Additionally, it suggests the westward back drift of tectonic movements. Otherwise, *L. i. infrafrenata* could not have reached the Talaud Islands, which are separated by broad marine barriers westwards from New Guinea.

A massive reduction in oriental lineages can be well observed in this region. The megophryids that are abundant on Borneo are absent from this island. Bufonids are only represented by Genus *Bufo* with three species. Two of them, i.e. *Bufo melanostictus* and *B. biporcatus*, are recognised as early migrants from Java, while the last, the endemic *B. celebensis*, is possibly a descendant of *B. melanostictus*. The rhacophorids are composed of two genera, i.e. the single *Polypedates leucomystax* recognised as an early migrant from Java and *Rhacophorus* that is likely to have drifted from the Philippines. This *Rhacophorus* is highly differentiated into three endemic species, i.e. *R. edentulus, R. georgii* and *R. monticola*. Also the highly diverse microhyline microhylids on the Great Sundas are only represented here by two subspecies, i.e. *Kaloula pulchra pulchra*, which presumably drifted from the Philippines, and *Kaloula baleata baleata* that is in contrast recognised as an early immigrant from Java. The genyophrynines are only represented by Genus *Oreophryne*, but with highly differentiated species, i.e. *O. celebensis, O. variabilis* and *O. zimmeri*. The ranges of the two last taxa are restricted to Mt. Lompobatang in southwest Sulawesi at altitudes from 1,500m to 2,000m and to Mt. Mengkoka in Southeast Sulawesi at altitudes of 2,000m. While those taxa are high altitude inhabitants, the more widespread *O. celebensis* is confined to lower altitudes. It has been recorded for instance from Bulawa Mts. at ca. 1,200m, Totoiya Valley at 800m, and the summit of Mt. Saudara in North Sulawesi. On the other hand, the occurrence of a new sub family which is missing on the Great Sundas has been recorded, i.e. asterophryne microhylid (*Callulops kopsteini*). This species is known only from Sanana Island in the Sula Islands off East Sulawesi.

In contrast, ranids are more widely represented by five genera and fifteen species. Genus *Fejervarya* is represented by *F. cancrivora*, which is likely to have drifted from the Philippines, and genus *Occidozyga* is represented by two endemic species, i.e. *O. celebensis* and *O. semipalmatus*. The latter is likely to have been derived from *O. sumatrana*, which is found among others on Java to the west. *O semipalmatus* itself presumably further derived *O. celebensis*. Two other genera, i.e. *Limnonectes* and *Rana*, are each well represented by a large number of species. The six species *Limnonectes* reached Sulawesi in two apparent migration routes. The only taxon derived from a Javan lineage is *L. arathooni*, which is restricted to South Sulawesi. It is closely related to L. microdiscus of Java and L. dammermani, which is found on Flores and Lombok. The other *Limnonectes* seem to have reached this island by drifting from the north. They are *L. finchi*, *L. grunniens*, *L. heinrichi*, *L. microtympanum* and *L. modestus*. Molecular study conducted by Emerson et al. (2000) shows that the endemic *L. microtympanum* separated early from *L. modestus*, which is currently found from Sulawesi eastwards to the Moluccas. *L. modestus* itself is closely related to *L. magnus* of Mindanao Island in Southeast Philippines and the next relatives of both taxa are *L. macrocephala* of South Luzon, Polillo and Mindoro islands, *L. leytensis* of the islands south of Luzon and Mindoro, except Palawan, and *L. acanthi* of Balabac, Palawan, Culion and the Busuanga islands. This group then is seen to be closely related to the endemic *L. leporina* of Borneo.

Of the five *Rana*, two of them can be well detected as early immigrants from Java, i.e. *Rana chalconota* and *R. erythraea*, while one of them, *R.sanguinea*, drifted from Palawan Island. The endemic *R. macrops* is closely related to *R. chalconota* and hence presumably derived from that species. The other endemic species, *R. celebensis*, might be derived from the other Javan lineage *R. erythraea* according to its early arrival on Sulawesi. More comprehensive research is necessary to clarify this assumption. The last ranid confined to Sulawesi is a member of genus *Platymantis* that is missing on the Great Sundas. This single subspecies, *P. papuensis occidentalis*, has been recorded from Sanana Island in the Sula Islands off Eastern Sulawesi.

In contrast to amphibians, mammals of both oriental and Australian lineages are more widely represented in this region. Endemism is considerably high with 85 endemic forms out of 92 taxa recorded (92.4%) (see Table 4.16) (This statement is based on data from Musser 1987, Corbet & Hill 1992, Wilson & Reeder 1993, Flannery 1995a, Froehlich & Supriatna 1996, Suyanto *et al.* 1998, Nowak 1999). In comparison to other endemism in mammals from other islands, this is only surpassed by New Guinea. Such high endemism suggest undoubtedly a long period of isolation. The occurrence of numerous endemic monotypic genera supports such a long isolation. On the other hand, the higher number of mammals in comparison to that of amphibians supports the fact that mammals are better capable of dispersing.

Although Australian lineages are only represented by phalangerids, they are however composed of some genera whose members are all strongly differentiated endemic forms, except the widely distributed *Phalanger orientalis orientalis*. A monotypic genus *Ailurops ursinus* occurs with three subspecies, i.e. *A. u. melanotis* on Salebabu of Talaud Islands; *A. u. ursinus* on Sulawesi mainland, Peleng Island and possibly Muna Island; and *A. u. togianus* on Togian Islands. Two extant *Strigocuscus* are both confined to Sulawesi, i.e. *S. celebensis* and *S. pelengensis*, in which the first taxon is widely represented by four subspecies, while the latter has only two subspecies. Of *S. celebensis*, one sub species (*S. c. callenfelsi*) is known from a Pleistocene fossil from South Sulawesi and three others were found recently. Those three nominate races are *S. c. sangirensis* on Sangihe and Siau of Sangihe Island; *S. c. feileri* on North Sulawesi; and *S. c. celebensis* on Central and South Sulawesi. Eastward from Sulawesi mainland, *S. celebensis* is replaced by *S. pelengensis* with two sub species, i.e. *S. p. pelengensis* on Peleng Island of Banggai Island and *S. p. mendeni* on Taliabu and Mangole of Sula Island. The only non-endemic phalangerid is *P. o. orientalis*, which occurred on Sanana Island off Sula Islands. This taxon shares its ranges among others with New Guinea.

Table 4.16 Endemic mammals of the Sulawesi mainland and its satellite islands. An asterisk marks the monotypic genera

Family	Genera with number of endemic species (and endemic sub species)
Bovidae	Bubalus 2
Cercopithecidae	Macaca 7
Muridae – Murinae	Bunomys 7, Crunomys 1, Echiothrix * 1, Eropeplus * 1, Haeromys 1, Lenomys * 1, Margaretamys 3, Maxomys 4, Melasmothrix * 1, Paruromys * 1, Rattus 9, Taeromys 6, Tateomys 2
Muridae – Uromyini	Melomys 2
Phalangeridae	Ailurops * (3), Strigocuscus (6)
Sciuridae	Callosciurus 1(1), Hyosciurus 2, Prosciurillus 3(6), Rubrisciurus * 1
Soricidae	Crocidura 5
Suidae	Babyrousa * (3), Sus 1
Tarsiidae	Tarsius 3
Viverridae	Macrogalidia * 1

In contrast, artiodactylids, carnivors, insectivors, primates and rodents represent oriental lineages diversely. The artiodactylids are composed of only three families, i.e. bovidae, cervidae and suidae. Similar to phalangerids, suids are represented by endemic forms that are strongly differentiated. The monotypic genus *Babyrousa babyrussa* has been recorded on this island with three subspecies, i.e. *B. b. celebensis* on the Sulawesi mainland; *B. b. tongeanensis* on Togian Island; and *B. b. frosti* on Mangole, Sanana and probably Lifamatola of Sula Island. Another sub-species (*B. b. babyrussa*) is found on Buru Island and is considered as the result of introduction. The only other suid found is Sus celebensis, which was recorded on the mainland and on the nearby islands of Togian, Peleng, Butung, Muna, Lembeh and Salayar. Of bovids, the two *Bubalus* found are often ordered by some authors into subgenus Anoa restricted to Sulawesi and the nearby islands. *B. depressicornis* inhabits the lowlands of Sulawesi. At higher elevations, it is replaced by *B. quarlesi* with a disjunct population on Buton Island to the southeast. The occurrence of the only cervid on this mainland, Cervus timorensis, is mostly considered as a result of ancient human introduction. Its natural ranges are presumed to be on Java and Bali.

Carnivors and insectivors are each represented by one family, i.e. Viverridae and Soricidae, respectively. The viverrids are represented by an endemic monotypic genus, *Macrogalidia musschenbroeki* and a widespread *Paradoxurus hermaphroditus*. The first taxon is found in both lowland and montane forests up to about 2,600m and seems to be dependent on primary forests. Once it was reported that it was restricted to the northern peninsula, but recently it is known to occur in most parts of the island. The latter is often found among human habitations, probably because of the presence of rats and mice. Perhaps due to this habitat, its broad ranges on the East Indies, such as on Sulawesi and on Sula Islands, are mostly considered as the result of human introduction (Corbet & Hill 1992; Nowak 1999).

Primates in the Sulawesi region are represented by only two genera and two families, i.e. *Macaca* (Cercopithecidae) and *Tarsius* (Tarsiidae), but both are highly differentiated at species level. The Sulawesian macaques are closely related to *M. nemestrina*, which is found among others on West Borneo. They are all clustered to the *silenus* species group. Seven macaques have been recorded from the Sulawesi region, i.e. *M. brunnescens, M. hecki, M. maura, M. nigra, M. nigrescens, M. ochreata* and *M. tonkeana*. Their monophyly is indicated by allopatrically separated ranges.

Tarsius is the single recent genus of Tarsiidae. Of the five extant species, three of them are found on Sulawesi and the nearby islands. The other two members occur on the Great Sunda Islands (*T. bancanus*) and the East Philippines (*T. syrichta*). Two of the three Sulawesian tarsiers have very restricted ranges. *T. dianae* is known only from the type locality in Lore Lindu National Park in the west-central area at an elevation of 700m. *T. pumilus* has been recorded from Mt. Latimojong in the south-central region at 2,200m elevation and Rano-Rano in the west-central at 1,800m elevation. The last form, *T. spectrum*, occurs throughout the mainland and on the nearby islands of Sangihe, Peleng and Salayar. The forms *T. pelengensis* of Peleng Island and *T. sangirensis* of Sangihe Island are sometimes regarded as species distinct from *T. spectrum*, but they were not regarded as such by Corbet and Hill (1992), Flannery (1995), or Groves (in Wilson and Reeder 1993).

Finally, rodents are represented richly by 58 taxa of three families, i.e. Hystricidae, Muridae, and Sciuridae. The only hystricid confined to is *Hystrix javanica* whose presence on Southwest Sulawesi is presumed to be as a result of human introduction. Disjunct populations occur on Java, Madura, Bali, Lombok, Sumbawa, Rinca, Flores, and Tanah Jampea. In contrast to this, sciurids are relatively well represented by four genera and four species. The monotypic genus *Rubrisciurus rubriventer* is restricted to the mainland. Also two extant *Hyosciurus* are only known from the mainland. *H. ileile* is restricted to lowlands of Sulawesi and *H. heinrichi* to mountains of Central Sulawesi (Mt. Latimojong). Contrastly, *Callosciurus elbertae* and *C. notatus microtis* are confined to islands off Southwest Sulawesi. Relatives of *C. n. microtis* occur from the Malay Peninsula to Lombok in the Lesser Sundas.

The last Sulawesian sciurid is *Prosciurillus*, whose range is endemic to Sulawesi and the nearby islands. This genus is highly differentiated into five species. Monotypic species *P. abstrusus* and *P. weberi* are restricted to the Mt. Mengkoka region in the southeast and to the Luwuk area in the south-central region respectively. On the other hand, *P. murinus* occurs throughout most of Sulawesi, including on the small island of Lembeh off Northeast Sulawesi. Two subspecies have been described: *P. m. necopinus* from Mt. Lehio (Southwest of Lake Lindu) in the west-central region and *P. m. griseus* from Bumbulan, Menado District in North Sulawesi. The two other *Prosciurillus* are highly differentiated. The primary forest inhabitant *P. leucomus* is separated into four sub species, i.e. *P. l. leucomus* of the North Peninsula; *P. l. occidentalis* of Northwest peninsula; *P. l. hirsutus* of West Peninsula; and *P. l. sarasinorum* of Southeast Peninsula, including the nearby Buton and E Kabaena. On Sangihe Island off Northeast Sulawesi, *P. rosenbergi*, that was once considered as a sub species of *P. leucomus*, can be found, with two recognised subspecies, i.e *P. r. rosenbergi* on Sangihe and Siau and *P. r. tingahi* on Tahulandang and Ruang.

The most diversified rodents confined here are murids with two subfamilies, i.e. murines and uromyines. The uromyines are only represented by *Melomys caurinus* and *M. talaudium*, which are both endemic to Karakelong Island in Talaud Islands. Their relatives occur on the Northern Moluccas, New Guinea, and on the eastern Outer Banda Arc. On the other hand, murines are widely represented by 13 genera and 40 taxa. At least five genera are monotypic, i.e. *Echiothrix leucura*, *Eropeplus canus*, *Lenomys meyeri*, *Melasmothrix naso*, and *Paruromys dominator*. Four other genera are highly differentiated; their ranges are restricted to Sulawesi and the nearby islands. They are *Bunomys*, *Margaretamys*, *Taeromys* and *Tateomys*. The other four genera share their ranges with other islands, but members confined to the Sulawesi region are mostly restricted to this area only. They are *Crunomys*, *Haeromys*, *Maxomys*, and *Rattus*.

Of monotypic genera, *E. leucura* is restricted to tropical lowland evergreen rainforest in Northern and Central Sulawesi. *L. meyeri* has been recorded in lowland and montane forests from the north, central and southwest peninsula as well as from Sangihe Island to the northeast. Also its sub fossil remains have been recorded on the southwest peninsula. This taxon is considered to be closely related to *E. canus*, which in contrast, is known only by five specimens from the Mt. Lehio area (Southwest of Lake Lindu) in the west-central region. There it inhabits montane forests between 1,800 and 2,200m, apparently replacing *L. meyeri* at these altitudes. On the other hand, *M. naso* is thought to be closely related to *Tateomys* (see account thereof). *M. naso* has been recorded from Rano-Rano at an elevation of 1,800m and on a nearby mountain, at about 1,900-2,300m in Central Sulawesi. There it is considered common in the cool and wet moss forest (Nowak 1999). The last, *P. dominator*, apparently has the widest ecological range among monotypic genera forms. It is found in forests from coastal lowlands to the highest mountains of Sulawesi. Two subspecies have been described, i. e *P. d. camurus* (Pinedapa, C Sulawesi) and *P. d. ursinus* (Wawa Karaeng, Lompobattang, Southwest Sulawesi). Some authors consider a possible close affinity to Taeromys.

Of genera that are endemic to Sulawesi and the nearby islands, genus *Bunomys* has the highest number of taxa with 7 species. All the seven species of *Bunomys* are terrestrial and live in tropical forests and scrub. Two species, *B. andrewsi* and *B. chrysocomus*, have the widest ranges among *Bunomys*. The first taxon has been recorded from lowland forest throughout the mainland, except for on the northeastern peninsula, including the island of Buton to the southeast. The latter is restricted to the mainland and occurs at middle to high elevations. Two other species, *B. heinrichi* and *B. coelestis*, are endemic to extreme Southwest Sulawesi. Record of *B. heinrichi* has been recorded from Mt. Lompobatang. The other three taxa are *B. fratorum* of Northeast Sulawesi found in both lowlands and mountains; *B. penitus* of Central and Southeast Sulawesi found in mountains; and *B. prolatus* of East-central Sulawesi (Mt. Tambusisi region). This is followed by *Taeromys* with six species. All of the six species of *Taeromys* live in forests. Two species, *T. celebensis* and *T. callitrichus*, have a broad range, probably throughout the mainland. The first taxon is found mainly at lower elevations, while the latter both in lowlands and montane forests. The four other occur in more restricted areas i.e. *T. taerae* on Northeast Sulawesi; *T. hamatus* on C Sulawesi; *T. punicans* on central and Southwest Sulawesi; and *T. arcuatus* on Southeast Sulawesi.

Margaretamys with three extant species are arboreal forest dwellers. *M. beccarii* occurs from sea level to the upper limits of lowland tropical rainforest in northeastern and central Sulawesi. The next two species, *M. elegans* and *M. parvus*, have a more restricted distribution, being found in the montane forests of Mt. Nokilalaki in central Sulawesi at elevations of 1,600-2,270 m. and 1,800-2,270 m. respectively. *Tateomys* also has restricted distribution. *Tateomys* is thought to be closely related to *Melasmothrix* so that it is mostly considered as a synonym of that current monotypic genus. Like *Melasmothrix*, the two extant *Tateomys* dwell in cool mountain forests where the humidity is very high and nearly all surfaces are covered by moss. *T. macrocercus* is known by eight specimens from the southwestern slope of Mt. Nokilalaki, northeast of Lake Lindu in Central Sulawesi at altitudes of 2,000-2,250m and *T. rhinogradoides* by nine specimens from the Latimojong Mts. in south-central Sulawesi at altitudes of 2,200-2,300m.

Close affinities to Northern Borneo and the nearby Palawan Island of the Philippines are indicated by the occurrence of relatives of *Haeromys minahassae* on both regions, i.e. *H. margarettae* and *H. pusillus*. *H. minahassae* itself is endemic to the lowlands and mountains of Northeast and Central Sulawesi. Also *Crunomys celebensis* shows an affinity to the East Philippines where the other three extant species occur. On Sulawesi, *C. celebensis* is only known by three specimens collected from the Valley of Lake Lindu in the west-central area at an elevation of around 1,000m. Contrastly, the four Sulawesian *Maxomys* (*M. dollmani, M. hellwaldii, M. musschenbroekii,* and *M. wattsi*) show close affinitys to the Great Sunda Island where most of their relatives occur.

Sulawesian *Rattus* are members of the *rattus* group, *xanthurus* group and the native New Guinean Group. Those belonging to the rattus group are *R. nitidus*, *R. argentiventer*, *R. hoffmani*, *R. mollicomulus*, and *R. koopmani*. The *xanthurus* group is endemic to Sulawesi with *R. xanthurus* of North, Central, and possibly Southeast Sulawesi; *R. marmosurus* of North and Central Sulawesi; *R. foramineus* and *R. bontanus* of Southwest Sulawesi; and *R. pelurus* of Peleng Island. The only native New Guinea group found is *R. elaphinus* of Taliabu Island on Sula Island east of Sulawesi. Of the *Rattus* group, *R. hoffmani*, *R. mollicomulus* and *R. koopmani* are restricted to Sulawesi, but *R. nitidus* and *R. argentiventer* are widely distributed with most of their ranges being considered as the result of introduction.

Of the 106 reptiles confined to Sulawesi, about 37 of them are endemic forms (34.9%) (see Table 4.17), which is lower than that of Borneo (36.2%) and New Guinea (53.6%). The statement is based on data from Uetz (2005), Schulz (1996), Das (1998), McDiarmid *et al.* (1999) and Iskandar (2000). Close affinities are indicated to the Great Sundas. The number of shared taxa account for 37 taxa to Java and 35 taxa each to Borneo and Sumatra. In contrast to mammals, there are no monotypic genera within their endemic forms.

Table 4.17 Endemic reptiles of the Sulawesi mainland and its nearby islands.

Family	Genera and number of endemic species (and endemic sub species)
Agamidae	Bronchocela 1, Draco 1
Boidae (Pythoninae)	Python (2)
Colubridae	Amphiesma 2, Boiga 1(1), Calamaria 7, Calamorhabdium 1, Chrysopelea (1), Enhydris 1, Gonyosoma 1, Lycodon 1, Pseudorabdion 1, Rabdion* 1
Cylindrophiidae	Cylindrophis 1
Dibamidae	Dibamus 1
Gekkonidae	Cyrtodactylus 1, Luperosaurus 1
Geoemydidae/Bataguridae	Leucocephalon* 1
Scincidae	Eugongylus 1, Scincella 1, Sphenomorphus 4, Tropidophorus 1
Typhlopidae	Cyclotyphlop* 1, Typhlops 1
Viperidae	Trimeresurus 1

The endemism among Sulawesian birds is only surpassed by New Guinean birds. With 308 endemic forms out of 410 birds confined here, its endemsm accounting for 75.1% (see Table 4.18) (Baltzer 1990, Andrew 1992, del Hoyo et al. 1992, 1994, 1996, 1997, 1999, 2001, Jones *et al.* 1995, Coates & Bishop 1997, Stattersfield *et al.* 1998, Clements 2000). This endemism is lower than that of mammals. It seems that the occurrence of some mammals on remote satellite islands resulted in this lower endemism.

The most differentiated *Lophozosterops squamiceps* (Zosteropidae) has divided the mainland into 6 biogeographic divisions, which concurs with the mainland's separation by allopatric ranges of Sulawesian macaques at lower altitudes.

Table 4.18 Endemic birds of the Sulawesian mainland and its satellite islands

Family	Genera with number of endemic species (and endemic subspecies)
Acanthizidae	Gerygone (1)
Accipitridae	Accipiter 3(4), Aviceda (1), Pernis (1), Spilornis (2), Spizaetus 1
Alcedinidae	Actenoides (5), Ceyx (3), Cittura* (2), Halcyon (3), Pelargopsis (3), Todirhamphus 1
Apodidae	Aerodramus (5)
Artamidae	Artamus 1
Bucerotidae	Aceros 1, Penelopides (2)
Cacatuidae	Cacatua (1), Coracina 5(11)
Campephagidae	Lalage 1
Caprimulgidae	Caprimulgus (3), Eurostopodus 1(1)
Cisticolidae	Cisticola (1)
Columbidae	Chalcophaps (1), Crytophaps* 1, Ducula 3(1), Gallicolumba (3), Macropygia (4), Ptilinopus (8), Treron (2), Turacoena 1
Coraciidae	Coracias 1
Corvidae	Corvus 1(2), Cacomantis (1), Centropus (2), Cuculus 1, Eudynamis (2), Phaenicophaeus (3)
Dicruridae	Dicrurus 1(1)
Estrildidae	Erythrura (2), Lonchura (3)
Fringillidae	Serinus (1)
Hemiprocnidae	Hemiprocne (19
Megapodiidae	Macrocaphalon* 1, Megapodius 1(3)
Meliphagidae	Myza (5), Myzomela (4)
Meropidae	Meropogon* 1
Monarchidae	Eutrichomyias* 1, Hypothymis (2), Monarcha 1(3), Terpsiphone (1)
Muscicapidae	Culicicapa (1), Cyornis 2(4), Eumyias (4), Ficedula 2(2), Rhinomyias (3), Saxicola (1)
Nectariniidae	Aethopyga (2), Anthreptes (3), Cinnyris (4), Leptocoma (4)
Oriolidae	Oriolus (7)
Pachycephalidae	Colluricincla 1, Coracornis* 1, Hylocitrea* (2), Pachycephala 1(5)
Paramythiidae	Dicaeum 1(8)
Picidae	Dendrocopos 1, Mulleripicus (2)
Pittidae	Pitta 1(7)
Podicipedidae	Tachybaptus (1)
Psittacidae	Alisterus (2), Eos (3), Loriculus 4, Prioniturus 1(3), Tanygnathus (3), Trichoglossus 1(4)
Pycnonotidae	Alophoixus (3)
Rallidae	Amaurornis 2, Aramidopsis* 1, Gallirallus (3), Gymnocrex 1
Rhipiduridae	Rhipidura (5)
Scolopacidae	Scolopax 1
Strigidae	Ninox 3, Otus 1(5)
Sturnidae	Acridotheres 1, Aplonis (2), Basilornis 2, Enodes* 1, Scissirostrum* 1, Streptocitta 1(2)
Sylviidae	Acrocephalus (1), Bradypterus (1), Megalurus timoriensis (1), Orthotomus (4), Phylloscopus (2)
Timaliidae	Malia* (3), Trichastoma (4)
Turdidae	Cataponera* (4), Geomalia* 1, Heinrichia* (3), Turdus (2), Zoothera (3)
Turnicidae	Turnix (3)
Tytonidae	Tyto 2(2)
Zosteropidae	Lophozosterops (6), Zosterops 1(7)

Differentiation within the mainland

Differentiation of lowlands on the mainland is well illustrated by the ranges of Sulawesian macaques and *Bufo celebensis* (Bufonidae) while of highlands by the ranges of *Lophozosterops squamiceps* (Zosteropidae). Data for Sulawesian macaques and *Bufo celebensis* are based on mitochondrial DNA analyses conducted by Evans *et al.* (2002) and the taxonomic account of *L. squamiceps* following Clements (2000). Both the lowlands and highlands can be divided into seven sub-endemic areas (Fig. 4.43 and Fig. 4.44). Thus, there are in total fourteen sub-endemic centres recognised on Sulawesi.

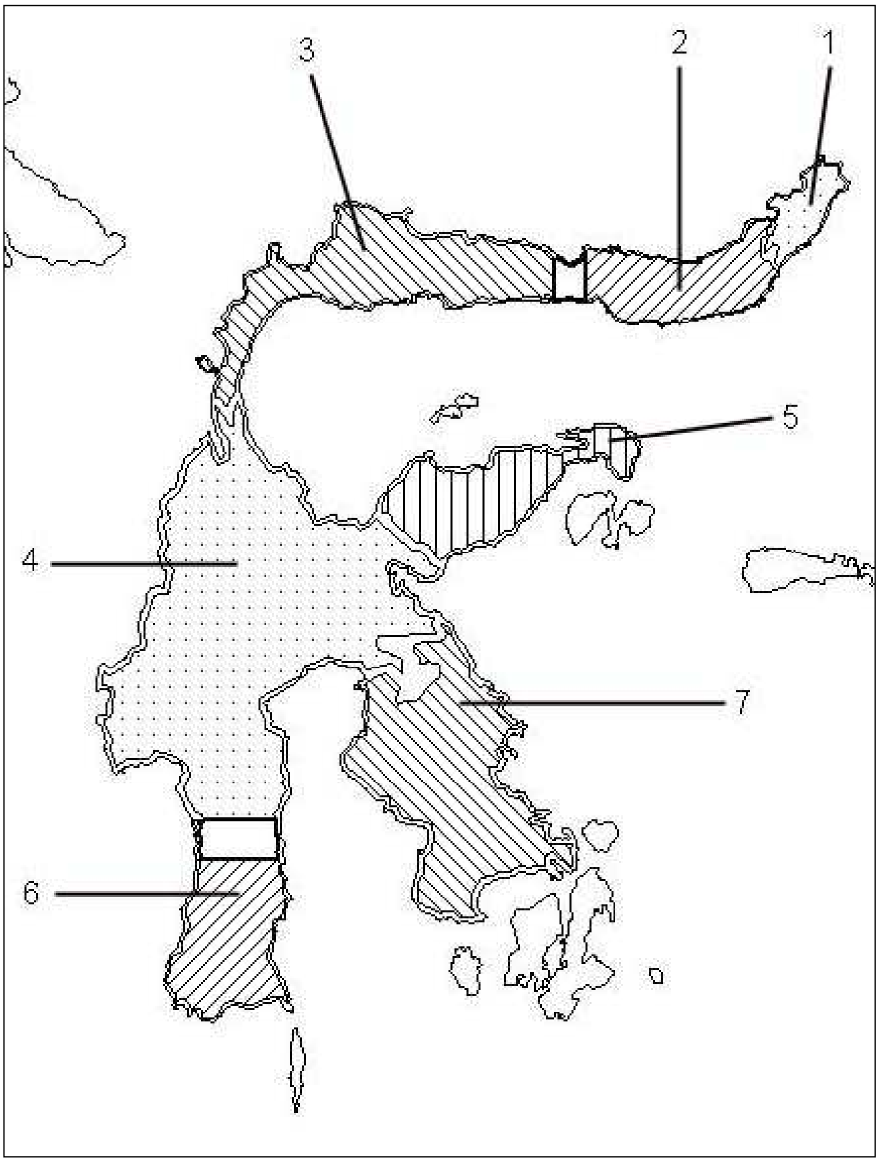


Figure 4.43 The seven sub-endemic centres on lowlands in Sulawesi: 1) NE Sulawesi 2) NC Sulawesi 3) NW Sulawesi 4) WC Sulawesi 5) EC Sulawesi 6) SW Sulawesi 7) SE Sulawesi.

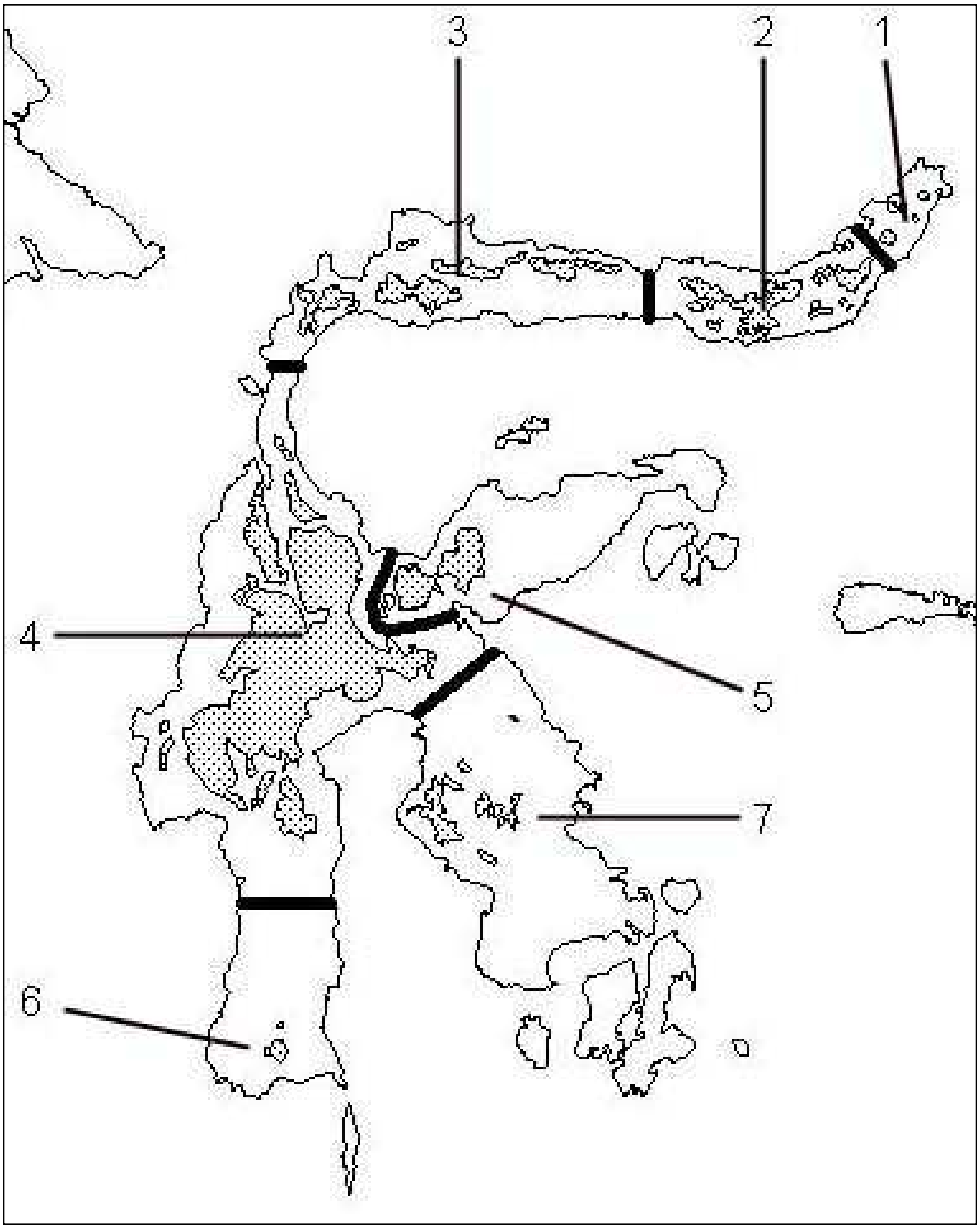


Figure 4.44 The seven sub-endemic centres on highlands (stipples) in Sulawesi: 1) NE Sulawesi 2) NC Sulawesi 3) NW Sulawesi 4) WC Sulawesi 5) EC Sulawesi 6) SW Sulawesi 7) SE Sulawesi. Possible border (thick line) of the highlands of EC Sulawesi lies more westward than that of the lowlands of EC Sulawesi sub-endemic centre. Additionally, endemic forms in the highlands of EC Sulawesi are concentrated on mountains in the western part although recently other mountains above 1,000m and even some over 2,000m are found to the east (not built).

1. Lowlands of Northeast Sulawesi

The existence of this sub-endemic centre (Fig. 4.43, no. 1; Figure 4.45) has been indicated by the occurrences of the endemic *Macaca nigra* (Trachypithecidae), *Taeromys taerae* (Muridae), and *Eurostopodus diabolicus* (Caprimulgidae). The first species once included *M. nigrescens* based on an evident interbreeding between the two populations (Groves 1980 in Nowak 1999). The last species is only known from a single 1931-specimen from Mt. Kelabat at altitudes ca. 250m (Clements 2000, Stattersfield *et al.* 1998).

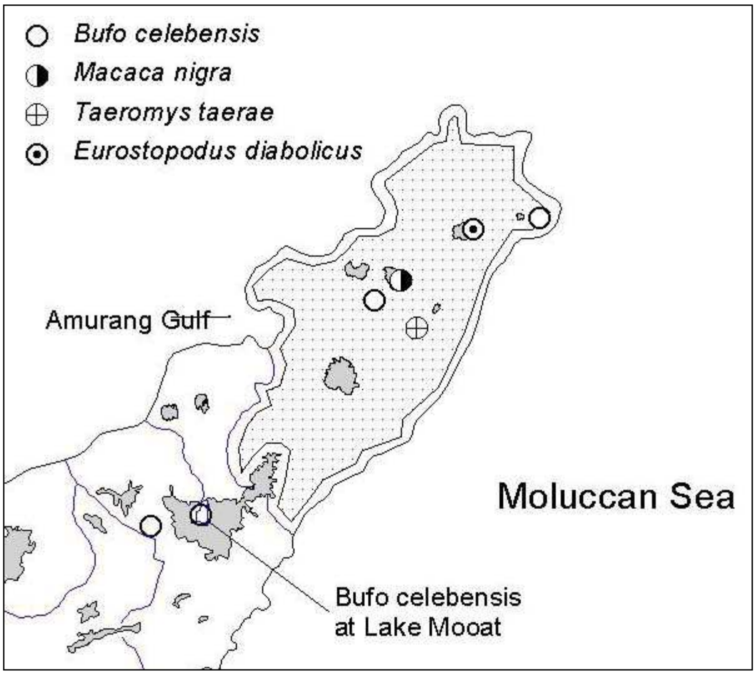


Figure 4.45 Type distribution of faunal elements found in the lowlands of Northeast Sulawesi (stipples). The grey areas are highlands above 1,000 m. Population of *Bufo celebensis* collected from Lake Mooat is closely related to that occur in the lowlands of North-central Sulawesi.

This sub-endemic centre includes the northeastern end of the peninsula; being bounded on the west by a river draining northwards to Amurang Gulf, and another river, whose headwaters arise exactly on the opposite side and thus draining southwards to the Moluccas Sea. These borders lie a bit eastward from the borders proposed by Evans *et al.* (2003). The borders proposed in this work thus also explains why their *Bufo celebensis*' population, which is collected at Lake Mooat, is genetically closely related to populations occuring in the North-Central Sulawesi rather than to those in the Northeast peninsula.

2. Lowlands of North-central Sulawesi

The borders to the east are the west borders of the lowlands of Northeast Sulawesi (see account thereof) and the borders to the west are flat lowlands around Lake Limboto (Fig. 4.43, no. 2; Figure 4.46). This area is home to the endemic *Macaca nigrescens* (Trachypithecidae) that was once considered as a subspecies of *M. nigra* to the east (see account thereof). Any previous contact with M. *tonkeana*, which in this account included *M. hecki*, to the west probably no longer exists: a gap of ca. 30 km was reported by Sugardjito et al. (1989 in Corbet & Hill 1992). The existence of natural barriers of the flat lowlands to the west is supported by the ranges of *Bufo celebensis*. The population collected on Tolabulu area is genetically distantly related to that collected on Paguyaman.

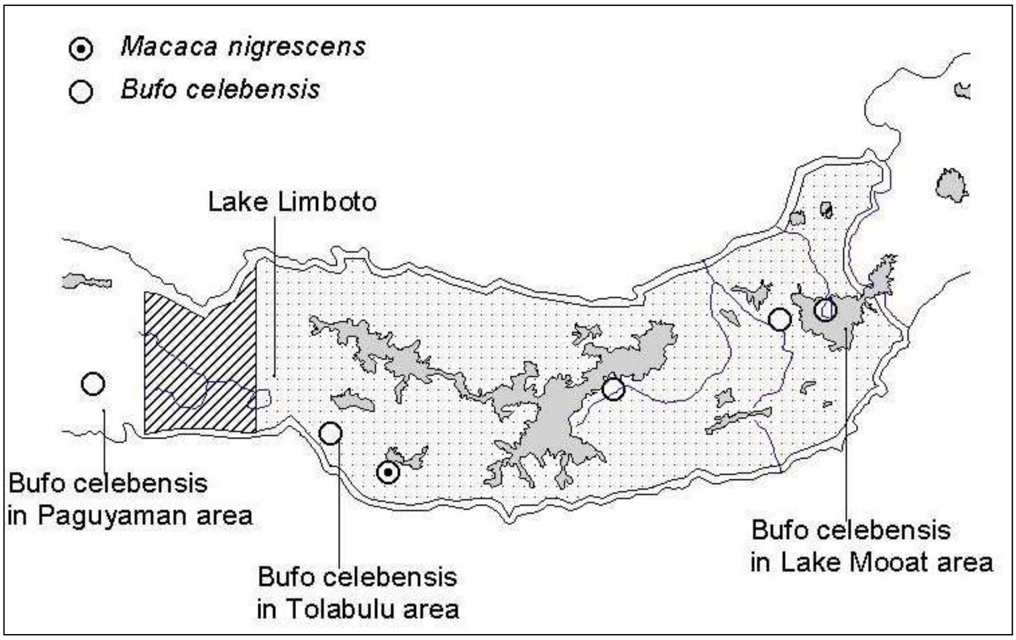


Figure 4.46 Distribution of faunal elements in lowlands of North-central Sulawesi (stipples). The grey areas are highlands above 1,000m. The border to the west is a gap of ca. 30km (diagonal hatching).

3. Lowlands of Northwest Sulawesi

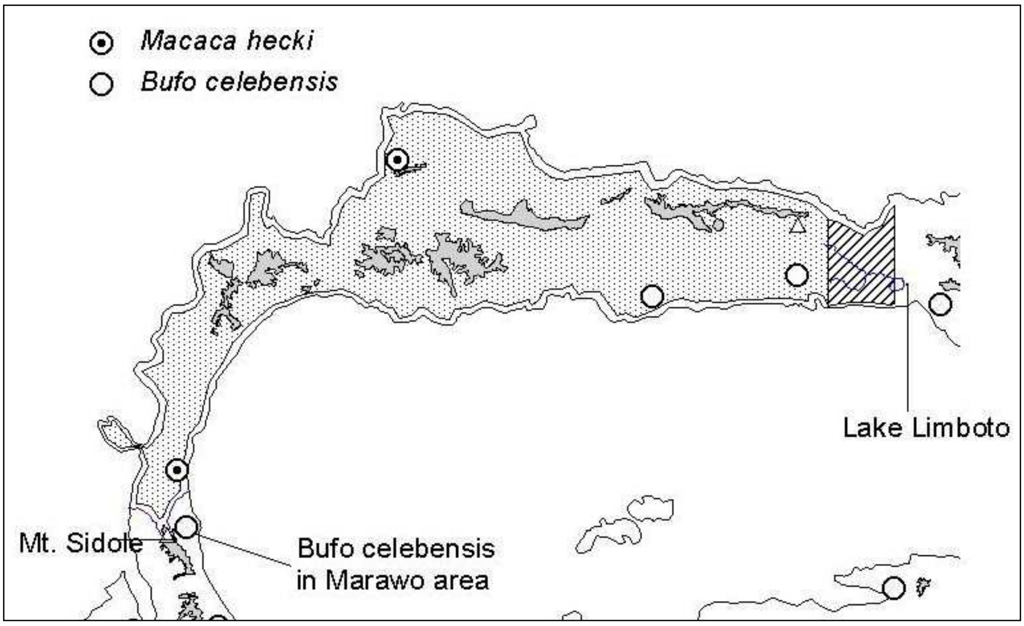


Figure 4.47 The lowlands of Northwest Sulawesi sub-endemic centre (stipples) with its faunal elements. The grey areas are highlands above 1,000m. The border to the east is a gap of ca. 30km (diagonal hatching).

The position of this sub-endemic centre (Fig. 4.43, no. 3; Fig. 4.47) is mainly defined on the range of the endemic *Macaca hecki*. This species was once considered as a subspecies of *M. tonkeana*, which is recently found to the south. This sub-endemic centre stretches from the flat lowlands east of Lake Limboto southwestwards to the area just north of Mt. Sidole (2,100m) and two rivers arise from this mountain. These southern boundaries lie a bit northward from those of Evans *et al*. (2002) and thus explain why his *Bufo celebensis'* populations, which is collected from the Marawo area to the south of the borders on this study, are genetically more closely related to those occuring on West-central Sulawesi.

4. Lowlands of West-central Sulawesi

This sub-endemic centre (Fig. 4.43, no. 4; Fig. 4.48) is the widest among the other sub-endemic centres on this island. It is bordered to the north by Mt. Sidole (2,100m) and two rivers arise from this mountain; to the east by a river draining to the Poso Gulf nearby Toja area and other river draining to Towori Gulf nearby Liworo area and the highlands where two rivers arise; to the southeast by a mountain (1,360m) lying northeast of Lake Matana, Lake Matana itself, Lake Mahalona and Lake Towuti, as well as a tributary draining from Lake Towuti; and to the southwest by the Tempe Depression. Extensive natural hybridisation between its faunal elements, Macaca *tonkeana*, with *M. maura*, which is found to the south, have been recorded in the northern area of the Tempe Depression (Froelich & Supriatna 1996; Evans *et al.*, 2003)

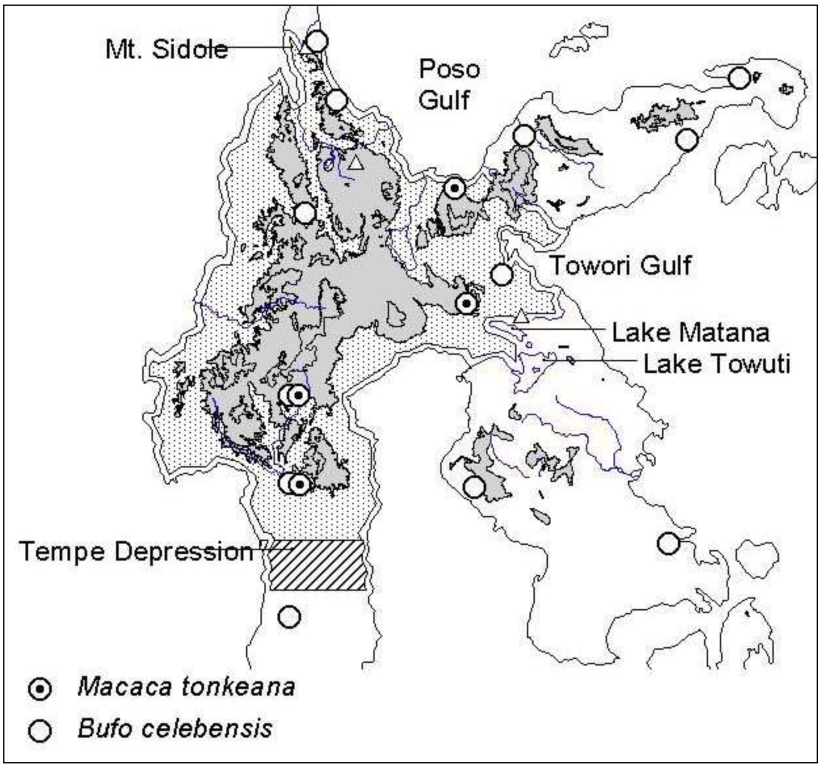


Figure 4.48 The lowlands of West-Central Sulawesi sub-endemic centre (stipples) with its faunal elements. The grey areas are highlands above 1,000m. Hybrids with *Macaca maura* to the south are found on Tempe Depression (diagonal hatching).

5. Lowlands of East-central Sulawesi

The distinction of this sub-endemic centre (Fig. 4.43, no. 5; Fig. 4.49) can only be recognised through molecular genetic analyses (Evans *et al.* 2003). Based on DNA analysis, they were able to show that populations of *Macaca tonkeana* and *Bufo celebensis*, which are confined to this area, are distantly related to those found on West-central Sulawesi. From the taxonomical account itself, it is still difficult to prove the existence of this sub-endemic centre. This in turn indicates generally the youngest separation of its faunal elements from an evolution point of view compared to other sub-endemic centres. This assumption is supported by the lack of endemic taxa in this area. The border to the west is the east border of the lowlands of West-central Sulawesi (see account thereof).

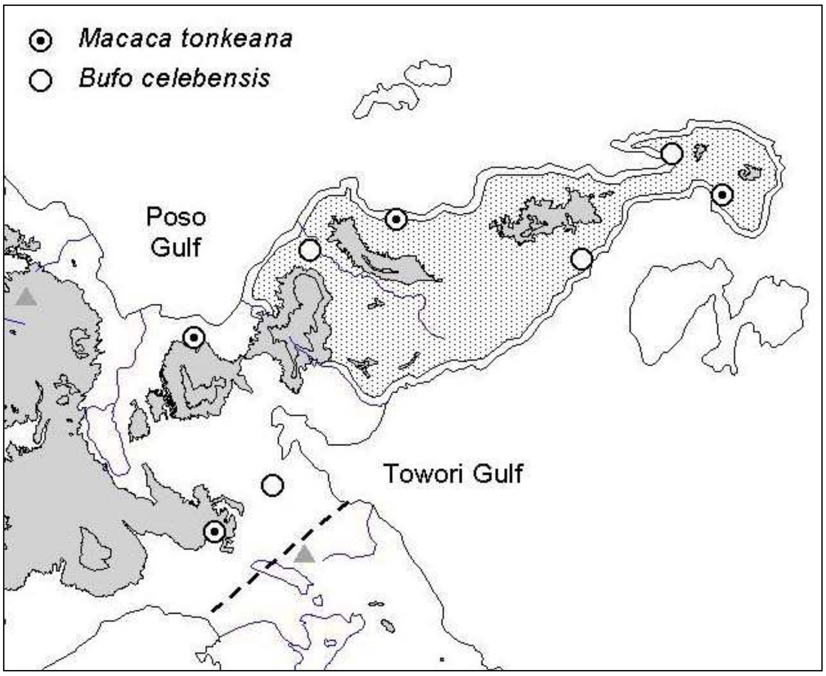


Figure 4.49 The sub-endemic centre of the Lowlands of East-central Sulawesi (stipples). It is lacking in endemic taxa; indicating its only recent separation.

6. Lowlands of Southwest Sulawesi

This sub-endemic centre (Fig. 4.43, no. 6; Fig. 4.50) is bounded to the north by the Tempe Depression. Populations of *Bufo melanostictus* in the north and south of this depression belong to different clades (Evans et al. 2003). The distinction of this area has been determined by the occurrence of the endemic *Macaca maura* restricted to this sub-endemic centre. Hybrids from *M. maura* and *M. tonkeana* are found on the Tempe Depression in the intervening areas between Central and Southwest Sulawesi (Froehlich & Supriatna 1996; Evans *et al.* 2003)

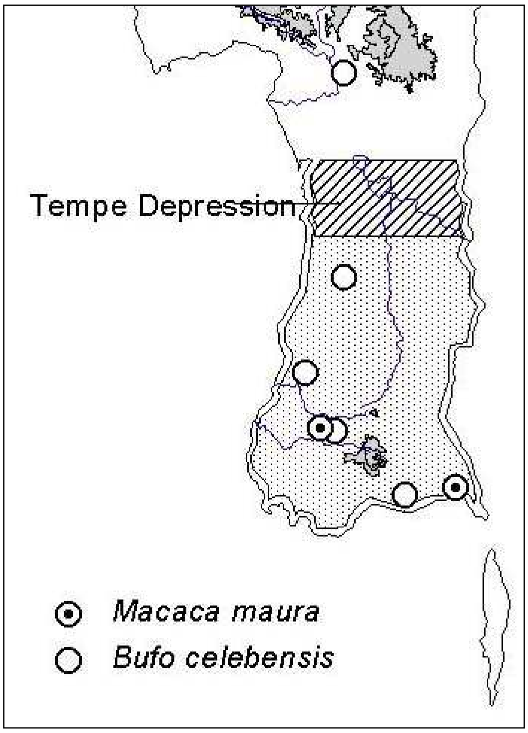


Figure 4.50 The sub-endemic centre of the Lowlands of Southwest Sulawesi (stipples) with its faunal elements. Extensive natural hybridisations with *Macaca tonkeana* to the north are found on Tempe Depression.

7. Lowlands of Southeast Sulawesi

The range of *Macaca ochreata* determines the existence of this sub-endemic centre (Fig. 4.43, no.7; Fig. 4.51). It borders on the north with a mountain (1,360m) lying northeast of Lake Matana, Lake Matana itself, Lake Mahalona and Lake Towuti, as well as a tributary draining from Lake Towuti. Populations of *Bufo celebensis* occurred on this area are closely related to those in the Southwest Sulawesi (Evans *et al*. 2003).

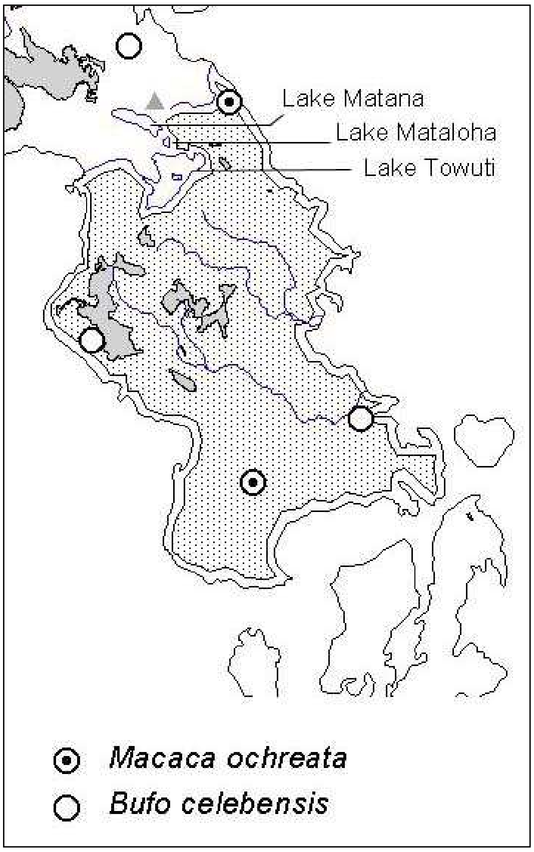


Figure 4.51
The type distribution of faunal elements in sub-endemic centre of Lowlands of Southeast Sulawesi (stipples).

8. Highlands of Northeast Sulawesi

The exact border of this sub-endemic centre (Fig. 4.44, no.1; Fig. 4.52) is difficult to determine due to insufficient information of the ranges of its faunal elements. One of them is *Lophozosterops squamiceps stresemanni* (Zosteropidae), whose range is only noted to be confined to the montane forests of Northeast Sulawesi with altitudinal ranges from 1,000 to 2,500 metres (Clements 2000, Stattersfield *et al.* 1998).

9. Highlands of North-central Sulawesi

The range of *Lophozosterops squamiceps striaticeps* (Zosteropidae) as a faunal element of this sub-endemic centre (Fig. 4.44, no.2; Fig. 4.52) also is only noted to occur on the montane forests of North-central Sulawesi with altitudinal ranges from 1,000 to 2,500 metres (Clements 2000, Stattersfield *et al.* 1998). Thus its borders to the east can only be estimated due to such insufficient information. In contrast to this, it seems that its borders to the west can be determined more precisely as the next montane forests to the west are relatively widely separated from this sub-endemic centre and thus apparently belongs to other sub-endemic centre.

10. Highlands of Northwest Sulawesi

The sub-endemic centre (Fig. 4.44, no. 3; Fig. 4.52) apparently involves the whole montane forest in Northwest Sulawesi, although *Lophozosterops squamiceps heinrichi* is the only faunal elements, whose range can be known precisely, i.e, on Mt. Tentolo-Matinan (2,217m).

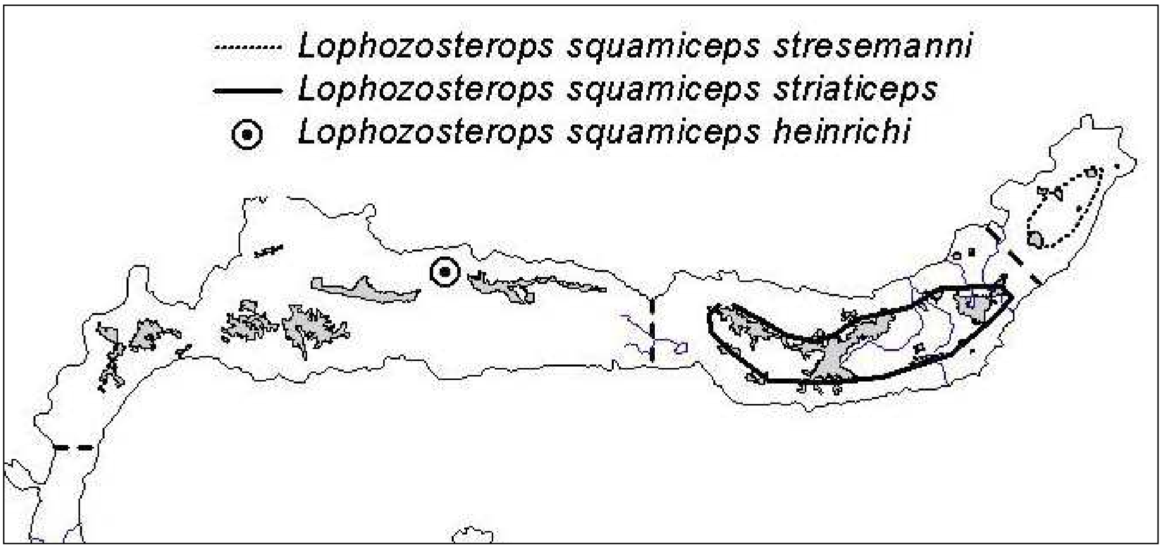


Figure 4.52 The distribution of three subspecies of *Lophozosterops squamiceps* on mountains in North Sulawesi. The ranges of *L. s stresemanni* and *L. s. striaticeps* have been estimated due to insufficient information. Thus, the borders of each sub-endemic centres also can only been estimated (broken-line).

11. Highlands of West-central Sulawesi

This sub-endemic centre (Fig. 4.44, no. 4; Fig. 4.53) harbours the most endemic forms. Most of them are restricted to a very small areas, for example, *Melasmothrix macrocercus* (Muridae-Murinae) is known only from the southwest slope of Mt. Nokilalaki, Northeast of Lake Lindu at altitudes of 2,000-2,250m; *Eropeplus canus* in montane forest of Mt. Lehio (SW of Lake Lindu) between 1,800 and 2,200m; and *Crunomys celebensis* is known only at and near the type locality, near Village of Tomado in the valley of Lake Lindu at altitudes of 800-1,050m. The last species is the only member of the genus occurring outside Philippines.

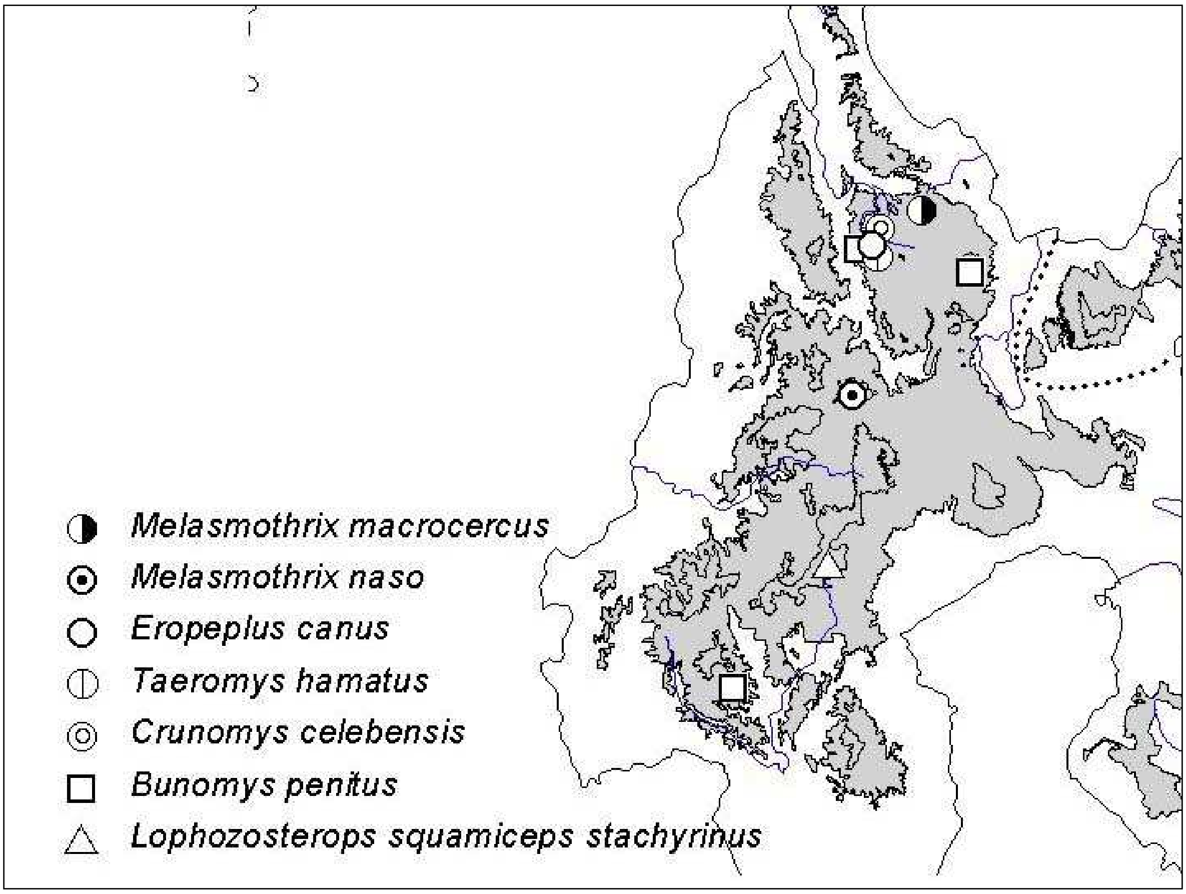


Figure 4.53 The distribution of seven faunal elements of the highlands of West-central Sulawesi sub-endemic area.

12. Highlands of East-central Sulawesi

In contrast to the lowlands, the existence of the highland sub-endemic centre (Fig. 4.44, no.5; Fig. 4.54) in East-central Sulawesi has been well defined on the ranges of, for instance, *Bunomys prolatus* and *Maxomys wattsi*. Both species are known only from their type localities in Mt. Tambusisi. Although there are recently some other mountains attaining over 2,000m eastward from Mt. Tambusisi, they are lacking in endemic forms.

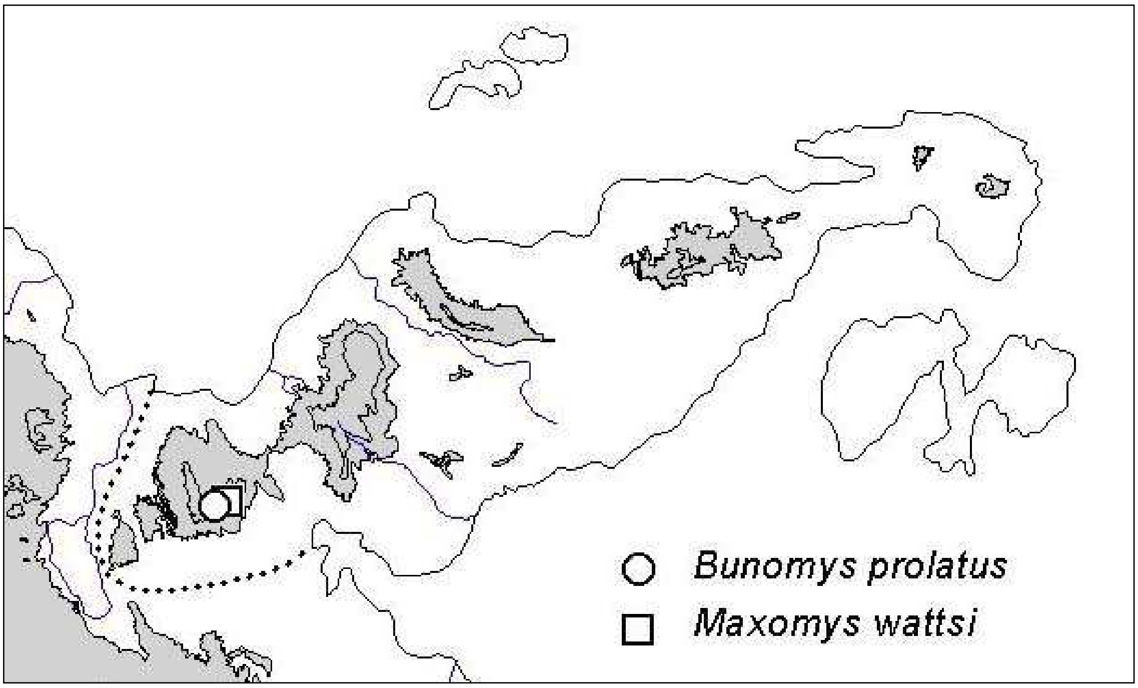


Figure 4.54 Distribution of faunal elements in the highlands of East-central Sulawesi (bounded to the west by a broken-line). Although currently highlands can be found throughout the peninsula, endemic faunal elements, such as *Bunomys prolatus* and *Maxomys wattsi*, are only restricted to Mt. Tambusisi region.

13. Highlands of Southwest Sulawesi

This sub-endemic centre (Fig. 4.44, no. 6; Fig. 4.55) is restricted to Mt. Lompobatang region. Its faunal elements are for instance *Bunomys coelestis*, *Rattus mollicomulus* (Muridae) and *Lophozosterops squamiceps squamiceps* (Zosteropidae). The first species is also found in the montane forest of Southeast Sulawesi and thus, indicating the relationship between the two sub-endemic centres. The two latter species contrastly are endemic to the montane forest of Mt. Lompobatang.

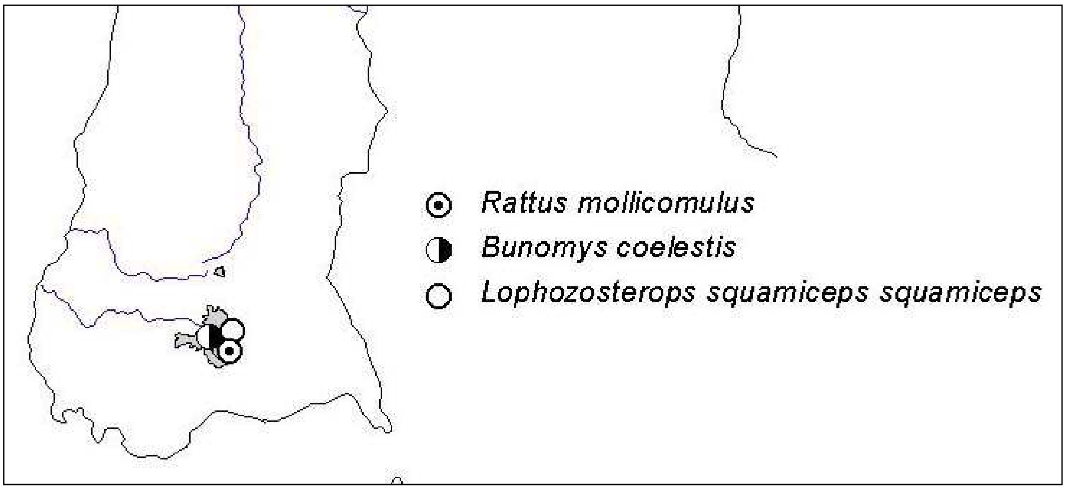


Figure 4.55 The sub-endemic centre in highlands of Southwest Sulawesi is restricted to Mt. Lompobatang region.

13. Highlands of Southeast Sulawesi

The position of this sub-endemic centre (Fig. 4.44, no. 6; Fig. 4.56) can be defined on the ranges of *Bunomys coelestis*, *Maxomys dollmani*, *Taeromys arcuatus*, and *Lophozosterops squamiceps analogus*. While the last species is restricted to Mt. Mengkoka, the others are also known from the other sub-endemic centres. *M. dollmani* and *T. arcuatus* also occur in the montane forest of West-Central Sulawesi and *B. coelestis* in the montane forest of Southwest Sulawesi.

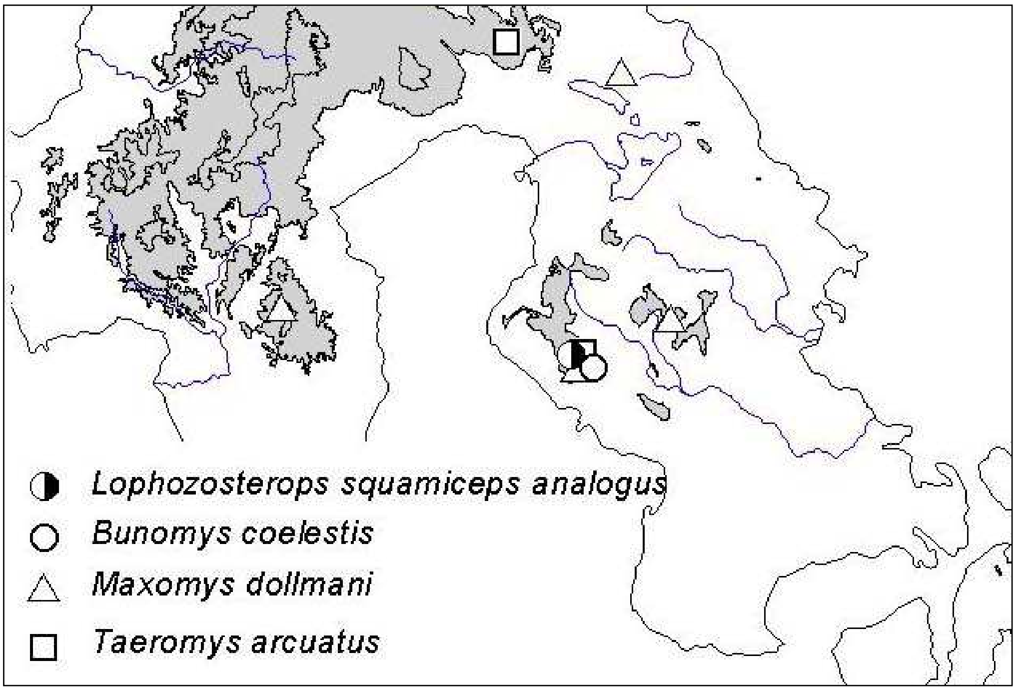


Fig. 4.56 Faunal elements of the highlands in Southeast Sulawesi are remarkably concentrated on Mt. Mengkoka region. A close relationship is indicated to highlands in West-Central Sulawesi (*Maxomys dollmani, Taeromys arcuatus*), but also to highlands in Southwest Sulawesi (*B. coelestis*)

4.1.5 Northern Moluccas Endemic Centre

The Northern Moluccas endemic centre (Fig. 4.57) includes the main Halmahera Island and the nearby Morotai, Ternate & Tidore, Bacan Island, Obi & Bisa, Damar & Joronga, Widi Island, as well as the islands of Gebe, Gag, and Kofiau to the east. All the nearby islands are separated from the main Halmahera Island by deep marine barriers.

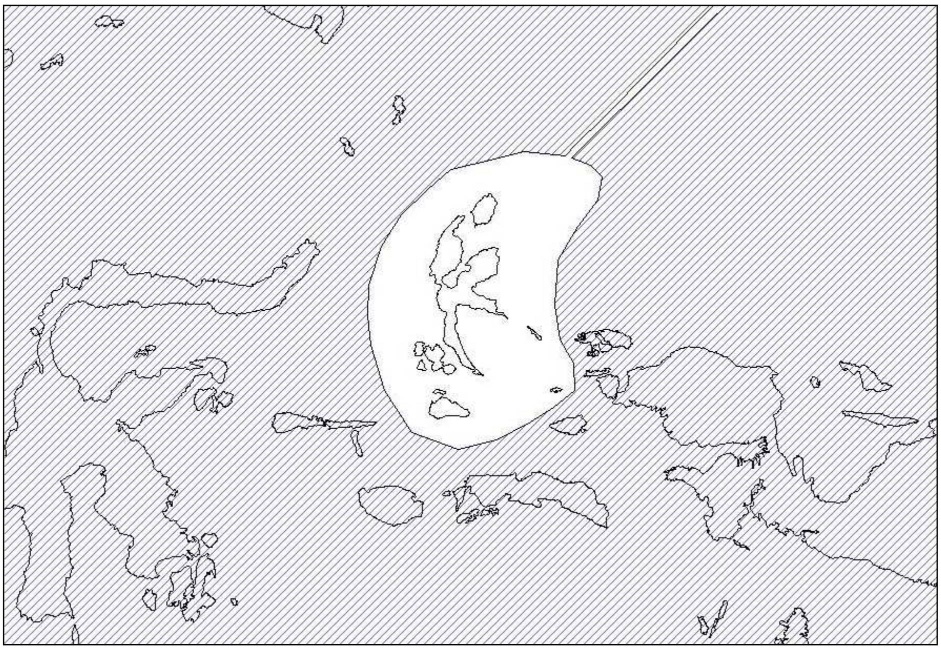


Figure 4.57 The Northern Moluccan Endemic Centre (unshaded)

Amphibians found on the northern Moluccas are very few in number, but the endemism is relatively high. The seven endemic species out of thirteen species recorded brings the endemism to 53.8%, lower than that of Borneo and New Guinea (see Table 4.19). This statement is based on the data from Tyler 1968, Duellman 1999, Iskandar & Colijn 2000 and Frost 2002.

Table 4.19 Endemic amphibians of Northern Moluccas

Family	Taxa
Hylidae – Pelodryadinae	*Nyctimystes rueppelli*
Microhylidae – Asterophryinae	*Callulops boettgeri, C. dubius*
Microhylidae – Genyophryninae	*Cophixalus montanus, Oreophryne frontifasciata, O. mollucensis*
Ranidae	*Rana moluccana*

Australian lineages poorly found on Sulawesi are better represented in this region by three pelodryadine hylids. One of them, *L. infrafrenata infrafrenata* is known as a faunal element of the Talaud Islands off Northeast Sulawesi. Other species are *L. nigropunctata* and a member of a missing genus on Sulawesi, *Nyctimystes rueppelli*. The former occurs on Gebe

Island as well as on Northern New Guinea and in the nearby Yapen Island. The latter is confined to Halmahera and the Morotai islands.

Oriental lineages are represented in this region by genyophrynine and asterophryine microhylids. They are also better represented here than in the Sulawesi region. The genyophrynines recorded are *Oreophryne moluccensis*, which is found on the Halmahera, Ternate and Bacan islands; *O. frontifasciata* of Morotai Island off Northeast Halmahera; and a member of genus missing on Sulawesi, i.e. *Cophixalus montanus* of Halmahera Island. Two *Callulops* known only from the type locality on Halmahera Island, i.e. *Callulops boettgeri* and *C. dubius*, represent the asterophryines. Contrastly, ranids diversified highly in the Great Sundas and are also still well represented in Sulawesi, however they are only poorly represented in this region. The ranids that are found are *Limnonectes grunniens*, *L. modestus*, *Platymantis papuensis papuensis*, *Rana sanguinea* and *R. moluccana*. Except for *R. moluccana*, all are non-endemic forms with broad distribution ranges.

The endemism among mammals resembles that of amphibians with seven endemic forms out of 12 taxa (58.3%) (see Table 4.20) (Corbet & Hill 1992, Wilson & Reeder 1993, Flannery 1995a, Suyanto *et al.* 1998, Nowak 1999). The most endemic forms found here are of Australian origin, i.e. phalangerids of genus *Phalanger*. They are *P. ornatus* of Halmahera, Morotai, Ternate, Tidore, and Bacan; *P. rothschildi* of Obi and Bisa; and *P. alexandrae* of Gebe Island. The strong differentiation at species level of that genus indicates their early migration to this region as tectonic movements drifted them from the New Guinea mainland, which is currently broadly separated by marine barriers, where most *Phalanger* occur. Such early migration is supported by the occurrence of their relative, *P. orientalis breviceps* on Bismarck Arch. and Solomon Island far to the east. Another Australian origin recorded is *Petaurus breviceps papuanus* (Petauridae) on Bacan, Ternate, Halmahera, and Gebe islands. It occurs also on New Guinea and nearby islands, New Britain and Kei Island in the Outer Banda Arc.

Table 4.20 Endemic mammals of Northern Moluccas

Family	Taxa
Phalangeridae	*Phalanger alexandrae, P. ornatus, P. rothschildi*
Muridae – Murinae	*Rattus morotaiensis, R. sp.*
Muridae – Uromyini	*Melomys howi, M. obiensis*

As regards oriental lineages, the occurrence of two endemic murines of genus *Rattus* in this region also indicates their early migration. They are *R. morotaiensis* restricted to the Halmahera, Morotai and Bacan islands and an undetermined *Rattus* on Bisa Island. Eastward of this, they are replaced by *R. praetor coenorum* of New Guinea, whose ranges perhaps include Salawati and Gebe Island as well. Another early migrant is *Melomys obiensis* (Muridae - Uromyini) that is endemic to Obi and Bisa islands. On the other hand, *Hydromys chrysogaster* (Muridae – Hydromyini) has a broad range, including Obi, New Guinea, Japen, Biak-Supiori, possibly Numfoor and Salawati, D'Entrecasteaux Island, Kiriwina, Aru Island, Kei Besar, Australia including satellite islands, and Tasmania. Other oriental lineages, which are found, are mostly considered as human introduction, i.e. *Viverra tangalunga* (Viverridae), *Suncus murinus* (Soricidae), and *Cervus timorensis* (Cervidae).

The Northern Moluccan reptiles are closely related to those of Sulawesi with 19 shared taxa and also to those of New Guinea with 15 shared taxa. Of 41 reptiles confined here, 9 of them (30%) are endemic forms (see Table 4.21) (Uetz 2005, Schulz 1996, Das 1998, McDiarmid *et al.* 1999, Iskandar 2000). Some genera are highly differentiated in this region, for example *Tropidonophis* (Colubridae), *Emoia* (Scincidae), and *Varanus* (Varanidae). The plasticity of those genera indicates their early migration. Additionally, one of non-endemic forms, i.e. *Brachyorrhos albus* (Colubridae), is a monotypic genus.

Table 4.21 Endemic reptiles of Northern Moluccas

Family	Taxa
Agamidae	*Hydrosaurus weberi*
Boidae	*Candoia carinata tasmai, Morelia tracyae*
Colubridae	*Calamorhabdium kuekenthali, Dendrelaphis caudolineatus modestus, Tropidonophis punctiventris, T. halmahericus.*
Gekkonidae	*Cyrtodactylus deveti*
Scincidae	*Sphenomorphus consobrinus*
Varanidae	*Varanus caerulivirens, V. yuwonoi*

In contrast to reptiles, affinities indicated by birds are closely ordered to New Guinea with 51 shared taxa (27.6%) and to Seram and nearby islands in the central Moluccas with 48 shared taxa (25.6%). Of 185 birds recorded from this region, 107 of them (57.8%) are endemic forms (see Table 4.22). (Andrew 1992, del Hoyo et al. 1992, 1994, 1996, 1997, 1999, 2001, Jones *et al.* 1995, Coates & Bishop 1997, Stattersfield *et al.* 1998, Clements 2000). Most of them are separated at subspecies level and only 2 taxa at specific level. Among these endemic forms, it is worth noting that *Tanysiptera galatea* (Alcedinidae), an inhabitant of lowland or swamp forests, has the most numerous races. At least seven subspecies occur in this region. They are *T. g. browningi* on Halmahera, *doris* on Morotai, *T. g. emiliae* on Rau off western Morotai Island, *T. g. sabrina* on Kayoa Island in the north of Bacan Island, *T. g. margarethae* on Bacan Island, *T. g. obiensis* on Obi and Bisa islands and *T. g. brunhildae* on Doi Island off Southern Halmahera.

Rau Island is an extremely small island, lying a close distance from and connected to Morotai Island by a 200m isobath. Similar to this are Kayoa Island to Bacan Island and Doi Island to Halmahera Island. In regard to this, the occurrence of distinct populations on these small islands separated from the nearby much bigger islands is very important because they show the existence of various habitats in smaller spatial scales only rarely evidenced from other groups.

Table 4.22 Endemic birds of Northern Moluccas

Family	Genera with number of endemic species (and endemic subspecies)
Accipitridae	Accipiter 1(4), Aviceda (1)
Aegothelidae	Aegotheles 1
Alcedinidae	Alcedo (2), Ceyx (1), Tanysiptera (7), Todirhamphus 2
Apodidae	Aerodramus (2)
Ardeidae	Butorides (1)
Cacatuidae	Cacatua 1
Campephagidae	Coracina 1(5), Lalage 1
Columbidae	Ducula (2), Gymnophaps (1), Macropygia (1), Ptilinopus 3(2)
Coraciidae	Eurystomus 1
Corvidae	Corvus 1
Cuculidae	Cacomantis 1, Centropus 1, Eudynamis (1)
Dicruridae	Dicrurus (2)
Estrildidae	Erythrura (1)
Megapodiidae	Megapodius (1)
Meliphagidae	Melitograis* 1, Myzomela (4), Philemon 1
Monarchidae	Monarcha (4), Myiagra (2)
Muscicapidae	Eumyias (1), Ficedula (1)
Nectariniidae	Leptocoma (1)
Oriolidae	Oriolus 1
Pachycephalidae	Pachycephala (5)
Paradisaeidae	Lycocorax*(3), Semioptera* (2)
Paramythiidae	Dicaeum (2)
Pittidae	Pitta (5)
Psittacidae	Alisterus (1), Eclectus* (1), Eos (2), Geoffroyus (2), Loriculus 1, Lorius (3)
Pycnonotidae	Alophoixus (2)
Rallidae	Habroptila* 1
Rhipiduridae	Rhipidura (2)
Scolopacidae	Scolopax 1
Strigidae	Ninox (2), Otus (3)
Sylviidae	Phylloscopus (2)
Zosteropidae	Zosterops (3)

4.1.6 New Guinean Endemic Centre

This endemic centre (Fig. 4.58) includes the New Guinean mainland and its offshore islands, i.e. Aru Islands to the southwest; D'Entrecasteaux Islands, Louisiade Archipelago and Trobriand Islands to the southeast; islands of Bagabag, Karkar, Manam, and Schouten to the north; islands on the Geelvink Bay to the northwest; and islands of Waigeo, Batanta, Salawati and Misool to the west. Except Waigeo and Batanta islands, all islands are connected to the mainland by the 200m isobath.

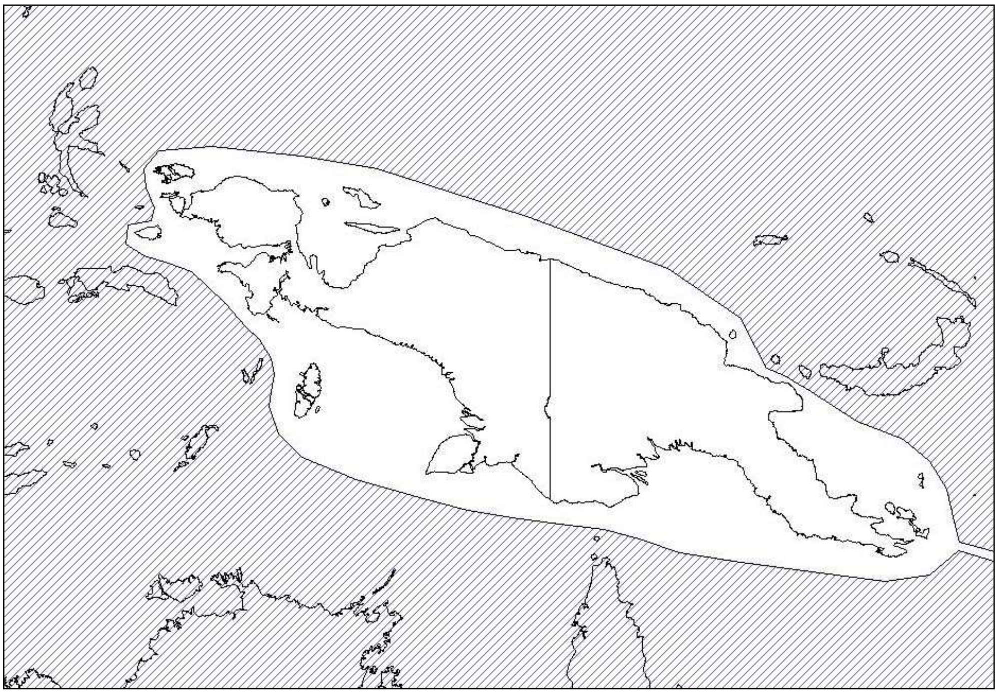


Figure 4.58 New Guinean Endemic Centre (hollow), including Aru Islands to the southwest; Trobriand Islands, D'Entrecasteau Islands, and Louisiade Islands to the southeast; as well as Waigeo, Batanta, Salawati and Misool to the northwest.

In the Indonesian Archipelago, New Guinea and the nearby islands have the highest endemicity of all fauna. Endemism among birds is the highest in the world with 330 endemic species (Clements, 2000). Also amphibians, that are only poorly represented on other islands, except Borneo (see account thereof), are richly represented on this island with 247 taxa recorded, of which 225 of them are endemic forms (91.1%) (see Table 4.23). (This statement is based on data from Zweifel 1956, 1958, 1962, 1969, 1971, 1972, 1979, 1980, 1983, 2000, Tyler 1968, Tyler & Davies 1978, Menzies 1985, 1999, Burton 1986, 1990, Blum & Menzies 1988, Zweifel & Parker 1989, Richards *et al.* 1994, Burton & Zweifel 1995, Sumida *et al.* 1998, Duellman 1999, Günther 2001, Kraus & Allison 2001, 2002). It is the highest level of endemism among New Guinean fauna groups. In regard to this, it somehow resembles that of Bornean endemism. As the high endemism in Bornean amphibians has also mainly been contributed to by oriental lineages, which drifted from Asia, the high endemism in New Guinean amphibian has also been mainly contributed by Australian lineages, which drifted to this region. This has been accentuated by oriental lineages, which also drifted to this region.

Table 4.23 Endemic amphibians of New Guinea and its satellite islands. The asterisk marks the monotypic genera

Family	**Genera with number of endemic species**
Hylidae – Pelodryadinae	Litoria 47, Nyctimystes 21
Microhylidae – Asterophryinae	Asterophrys 2, Barygenys 7, Callulops 11, Hylophorbus 7, Mantophryne 3, Pherohapsis* 1, Xenobatrachus 18, Xenorhina 7
Microhylidae – Genyophryninae	Albericus 12, Aphantophryne 3, Austrochaperina 17, Choerophryne 3, Cophixalus 17, Copiula 5, Genyophryne* 1, Liophryne 6, Oreophryne 16, Oxydactyla 5, Sphenophryne* 1
Myobatrachidae	Lechriodus 3, Mixophyes 1
Ranidae	Platymantis 5, Rana 6

The occurrence of the strong differentiated *Nyctimystes* (Hylidae – Pelodryadinae) on New Guinea is only possible through an early arrival of its ancestor on New Guinea. Of the 24 extant species, 21 of them are restricted to the mountainous region of New Guinea and the nearby islands. One species, *N. daymani*, shares its range with northern Australia. Two other species are found in the Northern Moluccas (*N. rueppelli*) and in the rainforests of Northeast Queensland (*N. dayi*). Also the range of widespread *Litoria infrafrenata infrafrenata* of *L. caerulea* group (Hylidae – Pelodryadinae) shows clearly that this taxon reached New Guinea by tectonic movement. While its occurrence on most islands in the Moluccas is suspected to be the result of tectonic movements, the population on Cape York in Northeast Australia is obviously existed through recent migration in the Last Glacial Maxima as a land bridge once connected southern New Guinea to North Australia. Some scientists, for example Aplin *et al.* (1993 in Flannery 1995), have proposed that such a land bridge existed several times before the Pleistocene Period, but there is no evidence from the zoogeographic records to support this assumption

Litoria is well represented on this region. There are 61 taxa confined here out of 122 extant species of which 46 of them are endemic forms. Of the fifteen non-endemic forms, two of them, i.e. *L. i. infrafrenata* and *L. nigropunctata*, are also found on the Northern Moluccas and even *L. i. infrafrenata* extends further west to Talaud Island off the northeastern coast of Sulawesi, and three of these non-endemic forms, i.e. *L. aruensis*, *L. amboinensis* and *L. vagabunda* are also found on the Central Moluccas (see accounts thereof). One species, *L. thesaurensis*, extends to the Bismarck Archipelago and the Solomon Islands and nine other species share their ranges with Australia. They are *L. bicolor*, *L. caerulea*, *L. eucnemis*, *L. genimaculata*, *L. gracilenta*, *L. nasuta*, *L. nigrofrenata*, *L. rothii*, and *L. rubella*.

While most of New Guinean *Litoria* is suspected to have arrived here through ancestors who migrated early on to New Guinea and their descendants, the other Australian lineages confined to this region, i.e. lymnodynastine myobatrachids, seem to represent a recent migrant. They are relatively poorly represented, by only three genera and five species. Two genera are each represented by a single species, i.e. the endemic *Mixophyes hihihorlo* and the more widespread *Limnodynastes convexiusculus*, whose range is shared with Australia. The last genus *Lechriodus* is strongly differentiated into three species, which are all restricted to New Guinea and the nearby Aru Island, i.e. *L. aganoposis*, *L. melanopyga* and *L. platyceps*.

Oriental lineages drifting to this region are genyophrynine and asterophryine microhylids as well as ranids. The genyophrynine and asterophryne microhylids have the highest level of diversity on this island. Of eleven extant genera genyophrynines, most of them are restricted to New Guinea and the nearby islands located within the 200m isobath. Such genera are *Aphantophryne*, *Copiula*, *Choerophryne*, *Albericus*, *Liophryne*, *Oxydactyla*, monotypic genus *Genyophryne* and monotypic genus *Sphenophryne*. The other three genera have more widespread ranges, i.e. *Oreophryne*, *Cophixalus* and *Austrochaperina*. The Oreophryne ranges from the Philippines through Sulawesi, southwards to the Lesser Sundas and eastwards through the Northern Moluccas and New Guinea, to New Britain in the Bismarck Archipelago. Of the 28 extant species, 16 of them are restricted to New Guinea and the nearby islands. The second genus, *Cophixalus*, occurs on the Moluccas, New Guinea and on Northern Australia; being represented on New Guinea and the nearby islands by 17 out of 31 extant species. The last genus, *Austrochaperina*, inhabits New Guinea, Northern Australian and New Britain in which 18 out of 23 species are found in New Guinea and the nearby islands. A single species shares its range with Northern Australia, i.e. *A. gracilipes*, which is indicated as a recent emigrant to the Cape York Peninsula in the Pleistocene Period.

Also asterophrynes are mostly restricted to New Guinea and the nearby islands within the 200m line. Those with such ranges are *Hylophorbus (ada di batanta, outside 200m)*, *Mantophryne*, monotypic genus *Pherophapsis*, *Xenorhin*a, *Xenobatrachus*, *Asterophrys* and *Barygenys*. The only genus distributed more broadly is *Callulops*, which is found from the Moluccas to New Guinea, including the nearby Louisiade Archipelago to the southeast. Of the 15 extant species, 11 of them inhabit New Guinea and the other species, *C. fuscus*, is found on the nearby Batanta Island off the northwest of New Guinea as well as on the Ceram and Ambon Islands in the Central Moluccas. In spite of its close distance to the mainland, Batanta Island is separated by a deep trench and the occurrence of this species there, indicates faunal exchanges by tectonic movements.

Thus in comparison to Sulawesi and the Northern Moluccas, there is obviously an increase of the number of genyophrynines and asterophrynes confined to this region. Similar to the increasing number of taxa of the two subfamilies on New Guinea described above, several genera of other oriental lineages of ranids show the same phenomenon. Genus *Platymantis* represented on Sulawesi and the Northern Moluccas region, each by only a single subspecies, are found on this region diversely with six taxa, of which three of them are endemic forms. The three non-endemic forms are *P. batantae*, *P. punctata*, and *P. p. papuensis*. The first two taxa share their ranges with Batanta Island in which *P. punctata* is also found on Waigeo Island in the north of Batanta Island. The third taxon shares its range among others with Batanta Island and Biak-Supiori, the Northern Moluccas and it extends even further east to the Bismarck Archipelago. Genus *Rana* is also better represented by 8 species of which six of them are restricted to New Guinea and the nearby 200m isobath islands. The two non-endemic forms are *R. daemeli* and *R. grisea*. The first taxon is also found on Northeast Queensland and the third is also found on Ceram Island to the west.

The rest of the ranids are poorly represented. The single *Limnonectes*, whose range is also found on Java Sulawesi and the Moluccas, is *L. grunniens*. Another ranid, *Fejervarya cancrivora*, is regarded as a result of introduction, but the occurrence of its relative, *F. verruculosa* on Wetar and perhaps Timor and Babar, indicates a possible natural occurrence of *F. cancrivora* on this island. Unfortunately, the record of *F. verruculosa* itself is questionable. This *F. verruculosa* is currently limited to the Wetar Island in the Outer Banda Arc, but Iskandar (2000) reported a possible occurrence on the Babar and Timor islands and the Menzies (1987) from Papua New Guinea.

Of mammals, the endemism accounts for 89.5%, which resulted from 205 endemic forms out of 228 taxa recorded (see Table 4.24). (The data is based on the works of Wilson & Reeder 1993, Flannery 1995b, Suyanto *et al.* 1998, Nowak 1999). This high endemism is only possible by a long duration of isolation, certainly much longer than since the Last Glacial Maxima. This in turn suggests that, as in amphibians, most New Guinean mammals reached this island through island drifts. On the other hand, its lower endemism than that of amphibians is obviously as the result of more faunal exchanges undergone in mammals as the sea level lowered in the Last Glacial Maxima connecting this island to Australia.

Australian lineages are represented by numerous families, i.e. *Acrobatidae*, *Burramyidae*, *Dasyuridae*, *Macropodidae*, *Peramelidae*, *Peroryctidae*, *Petauridae*, *Phalangeridae*, *Pseudocheiridae*, *Tachyglossidae* and the conilurine Murid. Except the last one, new Guinean forms of these families are mostly endemic to New Guinea and the nearby islands within the 200m line, except possibly *Zaglossus bruijnii bruijnii* (Tachyglossidae); *Myoictis melas melas* (Dasyuridae); possibly *Dendrolagus inustus inustus*, *D. matschiei*, possibly *Macropus agilis papuanus*, *Thylogale browni browni*, *T. brunii* (Macropodidae); *Dactylopsila trivirgata trivirgata*, *Petaurus breviceps papuanus* (Petauridae); *Phalanger orientalis orientalis*, *Spilocuscus maculatus chrysorrhous*, *S. m. maculatus*, *S. papuensis* (Phalangeridae); *Echymipera kalubu kalubu*, *E. k. philippi*, and *E. rufescens rufescens* (Peroryctidae). The possible records from outside the 200m line are those of *Z. b. bruijnii* and *D. i. inustus* from Waigeo Island and *M. a. papuanus* from Southern New Ireland in the Bismarck Archipelago. Only a few taxa share their ranges with Australia, i.e. *Tachyglossus aculeatus lawesi* (Tachyglossidae); *Isoodon macrourus* (Peramelidae); and *Phalanger intercastellanus* (Phalangeridae).

Table 4.24 Endemic mammals of New Guinea and its satellite islands. An asterisk marks the monotypic genera

Family	**Genera with number of endemic species (and endemic subspecies)**
Acrobatidae	Distoechurus 1
Burramyidae	Cercartetus (1)
Dasyuridae	Antechinus 4(4), Dasyurus 2, Murexia 1(2), Myoictis (2), Neophascogale 1, Phascolosorex 1(3), Planigale 1, Sminthopsis 1(1)
Macropodidae	Dendrolagus 4(9), Dorcopsis 2(6), Dorcopsulus 2, Thylogale 1(2)
Muridae – Conilurini	Conilurus (1)
Muridae – Hydromyini	Crossomys* 1, Hydromys 3, Leptomys 3, Mayermys* 1, Microhydromys 2, Neohydromys* 1, Parahydromys* 1, Paraleptomys 2, Pseudohydromys 2
Muridae – Murinae	Rattus 3(11), Stenomys 3(5)
Muridae – Uromyini	Abeomelomys (2), Anisomys* 1, Chiruromys 1(4), Coccymys 2, Hyomys 1(2), Lorentzymys* 1, Macruromys 2, Mallomys 2(5), Melomys 10(7), Pogomelomys 1(2), Pogonomys 3(2), Uromys 2(4), Xenuromys* 1
Peroryctidae	Echymipera 3(3), Microperoryctes 2(3), Peroryctes 1(2)
Petauridae	Dactylopsila 3(3), Petaurus 1(1)
Phalangeridae	Phalanger 3(7), Spilocuscus 2(2)
Pseudocheiridae	Pseudochirops 2(6), Pseudochirulus 2(10)
Tachyglossidae	Zaglossus (4)

The Conilurini are an essentially Australian Group consisting of over 50 species of which, only two subspecies are found in New Guinea, i.e. *Conilurus penicillatus randi* and *Pseudomys delicatulus delicatulus*. Both are restricted to the eucalypt savannah in the lower Fly River region in Southern New Guinea. They are regarded as recent immigrants from Australia during the last ice age some 25-15.000 years ago (Flannery 1995).

Meanwhile, oriental lineages drifting to this island are represented by murids and by both the single viverrid (*Paradoxurus hermaphroditus*) and soricid (*Suncus murinus*). The occurrence of the last two taxa are mostly regarded as human introduction. In contrast, murids are represented by numerous taxa from three subfamilies of which two of them, i.e. hydromyini and uromyini, are not found on the Western Indonesian Archipelago. The last subfamily to be found is the widespread murines, which is represented by two genera, i.e. *Rattus* and the endemic *Stenomys*.

Hydromyini and Uromyini reach the highest diversity on New Guinea. Of nine genera of hydromines found, eight of them are endemic, i.e. *Crossomys*, *Parahydromys*, *Pseudohydromys*, *Neohydromys*, *Microhydromys*, *Mayermys*, *Leptomys*, and *Paraleptomys*. One species of the last genus, *Hydromys chrysogaster*, has a wide range from Obi Island in the Northern Moluccas to the D'Entrecasteaux Islands off Southeast New Guinea and even further south to Australia and Tasmania. Uromyines are also still quite highly represented by endemic genera, of 13 genera confined there, four of them are monotypic genera (*Abeomelomys*, *Anisomys*, *Lorentzimys*, *Xenuromys*), six genera are endemic (*Chiruromys*, *Coccymys*, *Hyomys*, *Macruromys*, *Mallomys*, *Pogonomelomys*), and the rest of the genera (*Pogonomys*, *Uromys*, *Melomys*) include members, whose ranges are also found outside the 200m line, such as Waigeo, Batanta, Biak-Supiori, and Owi to the northwest; Bismarck Archipelago to the northeast; and even further east to Solomon Island.

New Guinean *Rattus* belongs to the *Rattus* Group, New Guinea Group, and the Australian Group. The occurrences of two members of the *Rattus* Group, i.e. *Rattus argentiventer* and *R. nitidus*, are regarded as the result of introduction. The seven species of the New Guinea Group are restricted to New Guinea and the nearby islands, and last, the single Australian Group, *R. sordidus*, is found on two disjunct areas, e.g. on the south central part (*R. s. ariama*) and on the southeastern part as well as on the nearby Yule Island (*R. s. gestri*).

Endemism among New Guinean reptiles are obviously much lower than those of New Guinean amphibians, mammals and birds, but it is still the highest in comparison to that of other islands with 150 endemic forms out of 280 taxa recorded (53.6%) (see Table 4.25). (This statement is based on data from Uetz 2005, Schulz 1996, McDiarmid *et al.* 1999, Iskandar 2000). This includes *Bronchocela cristatella* (Agamidae), which is recorded as *Calotes cristatellus* there, but exludes the probable occurrences of *Draco lineatus amboinensis*, *Physignathus lesueurii* (Agamidae); *Cosymbotus platyurus* (Gekkonidae); *Carlia longipes*, *C. storri* (Scincidae); *Typhlops diardii* (Typhlopidae) as well as the questionable species *Acanthophis barnetti* and *A. crotalusei* (Hydrophiidae). Several genera are highly differentiated on New Guinea, for example *Hypsilurus* (Agamidae); *Tropidonophis* (Colubridae); *Emoia* (Scincidae); *Varanus* (Varanidae), and *Elseya*. Of monotypic genera, only *Apodora papuana* (Boidae) and *Heurnia ventromaculata* (Colubridae) represents endemic form. The other monotypic genera have broader ranges, i.e *Bothrochilus boa*, *Leiopython albertisii* (Boidae), *Brachyorrhos albus* (Colubridae),

Table 4.25 Endemic reptiles of New Guinea and its offshore islands. An asterisk marks the monotypic genera

Family	Genera with number of endemic species (and endemic subspecies)
Agamidae	Hypsilurus 8
Boidae	Apodora* 1, Morelia 1
Chelidae	Chelodina 4, Elseya 5
Colubridae	Dendrelaphis 3, Heurnia* 1, Stegonotus 2, Tropidonophis 9(1)
Gekkonidae	Cyrtodactylus 8, Gehyra 5, Lepidodactylus 5, Nactus 1
Hydrophiidae	Aspidomorphus 2, Micropechis* (2), Pseudechis 1, Toxicocalamus 9
Pygopodidae	Liasis 1
Scincidae	Cryptoblepharus 1, Emoia 28, Eugongylus 1, Fojia* 1, Lipinia 7, Lobulia 2, Papuascincus 4, Prasinohaema 3, Sphenomorphus 17, Tribolonotus 1
Trionychidae	Pelochelys 2
Typhlopidae	Ramphotyphlops 3, Typhlops 4
Varanidae	Varanus 7(1)

As already mentioned above, the endemism among New Guinean birds, with 330 endemic species out of 736 species recorded, is the highest in the world, surpassing that of Australia (238 species), Philippines (185 species), Brazil (181 species), Peru (114 species) and Madagascar (98 species) (Clements 2000).

The number of endemic subspecies is considerably higher than that of monotypic endemic species. Along with the number of monotypic endemic species, it amounts to 1,277 out of 1,404 taxa recorded corresponding to 91% (see Table 4.26). (The data is based on the works of Beehler *et al.* 1986, Andrew 1992, del Hoyo et al. 1992, 1994, 1996, 1997, 1999, 2001, Jones *et al.* 1995, Stattersfield *et al.* 1998, Clements 2000).

Table 4.26 Endemic birds of New Guinea and its offshore islands. An asterisk marks the monotypic genera

Family	Genera with number of endemic species (and endemic subspecies)
Acanthizidae	Acanthiza 1, Crateroscelis (13), Gerygone 2(24), Sericornis 3(27)
Accipitridae	Accipiter 1(10), Aviceda (4), Circus (1), Elanus (1), Erythrotriorchis* 1, Harpyopsis* 1, Henicopernis 1, Hieraetus (1), Macheiramphus* (1), Megatriorhis* 1
Aegothelidae	Aegotheles 3(11)
Alaudidae	Mirafra (2)
Alcedinidae	Alcedo (4), Ceyx (1), Clytoceyx* (2), Dacelo 1(4), Melidora* (3), Syma (9), Tanysiptera 4(7), Todirhamphus (6)
Anatidae	Salvadorina* 1
Apodidae	Aerodramus 2(12), Mearnsia (2)
Ardeidae	Butoridas (2), Egretta 1, Zonerodius 1
Artamidae	Artamus 1
Bucerotidae	Aceros (1)
Cacatuidae	Cacatua (3), Probosciger* (3)
Campephagidae	Camphochaera* (2), Coracina 1(30), Lalage (6)
Caprimulgidae	Eurostopodus 2
Casuariidae	Casuarius 1
Cinclosomatidae	Androphobus* 1, Cinclosoma (4), Ifrita* (2), Ptilorrhoa (18)
Cisticolidae	Cisticola 1
Climacteridae	Cormobates (4)
Columbidae	Chalcophaps (1), Ducula 1(15), Gallicolumba (7), Geopelia (1), Goura (6), Gymnophaps (1), Henicophaps (2), Macropygia 1(8), Otidiphaps* (4), Ptilinopus 1(32), Reinwardtoena (2), Trugon* (3)
Coraciidae	Eurystomus (1)
Corvidae	Corvus 1(2)
Cracticidae	Cracticus (5), Gymnorhin* (1), Peltops 2
Cuculidae	Cacomantis (5), Caliechthrus 1, Centropus 1(8), Chrysococcyx 1(3), Eudynamis (1), Microdynamis* (2), Rhamphomantis* (2)
Dicruridae	Chaetorhynchus* 1, Dicrurus (1)
Estrildidae	Erythrura 1, Lonchura 4(25), Neochmia (1), Oreostruthus* (3)
Falconidae	Falco (1)
Grallinidae	Grallina 1
Hemiprocnidae	Hemiprocne (1)
Hirundinae	Hirundo (1)
Jacanidae	Irediparra* (2)
Laniidae	Lanius (1)
Maluridae	Clytomyias* (2), Malurus (11), Sipodotus* 1
Megapodiidae	Aepypodius 1(2), Megapodius 2(2), Talegalla (9)
Melanocharitidae	Melanocharis 1(20), Toxorhamphus (14)
Meliphagidae	Conopophila (1), Entomyzon* (1), Glycichaera* (3), Lichenostomus (9), Lichmera (3), Melidectes 4(20), Melilestes (4), Meliphaga (28), Melipotes 2(3), Melithreptus (1), Monarcha (9), Myzomela 1(19), Oreornis* 1, Philemon 2(2), Ptiloprora 1(12), Pycnopygius (10), Timeliopsis (6), Xanthotis (18)
Monarchidae	Arses 1(6), Machaerirhynchus (7), Monarcha 4(19), Myiagra 1(5)
Motacillidae	Anthus (4)
Muscicapidae	Saxicola (2)
Nectariniidae	Cinnyris (1), Leptocoma (10)
Neosittidae	Neositta (9)
Oriolidae	Oriolus 1
Orthonychidae	Orthonyx (3)
Pachycephalidae	Aleadryas* (4), Colluricincla (24), Eulacestoma* (2), Pachycare* (4), Pachycephala 4(27), Pitohui 1(37), Rhagologus* (3)
Paradisaeidae	Astrapia 3(4), Cicinnurus 1(5), Cnemophilus (5), Epimachus 1(8), Loboparadisea* (2), Lophorina* (6), Macgregoria* (2), Manucodia 2(11), Melampitta 1(3), Paradigalla 2, Paradisaea 2(11), Parotia 2(8), Ptiloris (2), Seleucidis* (2)
Paramythiidae	Dicaeum (12), Oreocharis* 1, Paramythia* (4)
Petroicidae	Amalochichla (5), Drymodes (3), Eopsaltria (2), Eugerygone* (2), Heteromyias (5), Microeca 1(8), Monachella* (1), Pachycephalopsis (12), Peneothello (12), Petroica 1(2), Poecildryas 1(9), Tregellasia (9)
Phasianidae	Anurophasis* 1, Coturnix (8)

Table 4.26 (cont.)

Family	Genera with number of endemic species (and endemic subspecies)
Pittidae	Pitta (10)
Podargidae	Podargus (3)
Podicipedidae	Tachybaptus (1)
Pomatostomidae	Pomatostomus (3)
Psittacidae	Alisterus (4), Chalcopsitta (8), Charmosyna 2(13), Clycopsitta (12), Eclectus* (2), Eos 1(1), Geoffroyus (10), Loriculus (3), Lorius (9), Micropsitta (8), Neopsittacus (5), Oreopsittacus* (3), Pseudeos* 1, Psittacella (14), Psittaculirostris 2(6), Psitteuteles 1, Psittrichas* 1, Trichoglossus (4)
Ptilonorhynchidae	Ailuroedus (13), Amblyornis 3(6), Archboldia 2, Chlamydera (2), Sericulus 1(2)
Rallidae	Amaurornis (1), Eulabeornis* (1), Fulica (1), Gallinula (1), Gallirallus (3), Gymnocrex (1), Megacrex* (2), Porzana (4), Rallina 1(13)
Rhipiduridae	Rhipidura 1(23)
Scolopacidae	Scolopax (1)
Strigidae	Ninox (7), Otus 1, Uroglaux* 1
Sturnidae	Aplonis 2(3), Mino 2(2)
Sylviidae	Megalurus 1(9), Phylloscopus (8)
Turdidae	Turdus (5)
Turnicidae	Turnix (4)
Tytonidae	Tyto (5)
Zosteropidae	Zosterops 2(15)

Differentiation within mainland

Within the mainland, there are at least fifteen sub-endemic centres as illustrated on figure 4.59. These on the northern New Guinea are restricted to the narrow areas along the northern coasts, while on the southern New Guinea occupy broader extent.

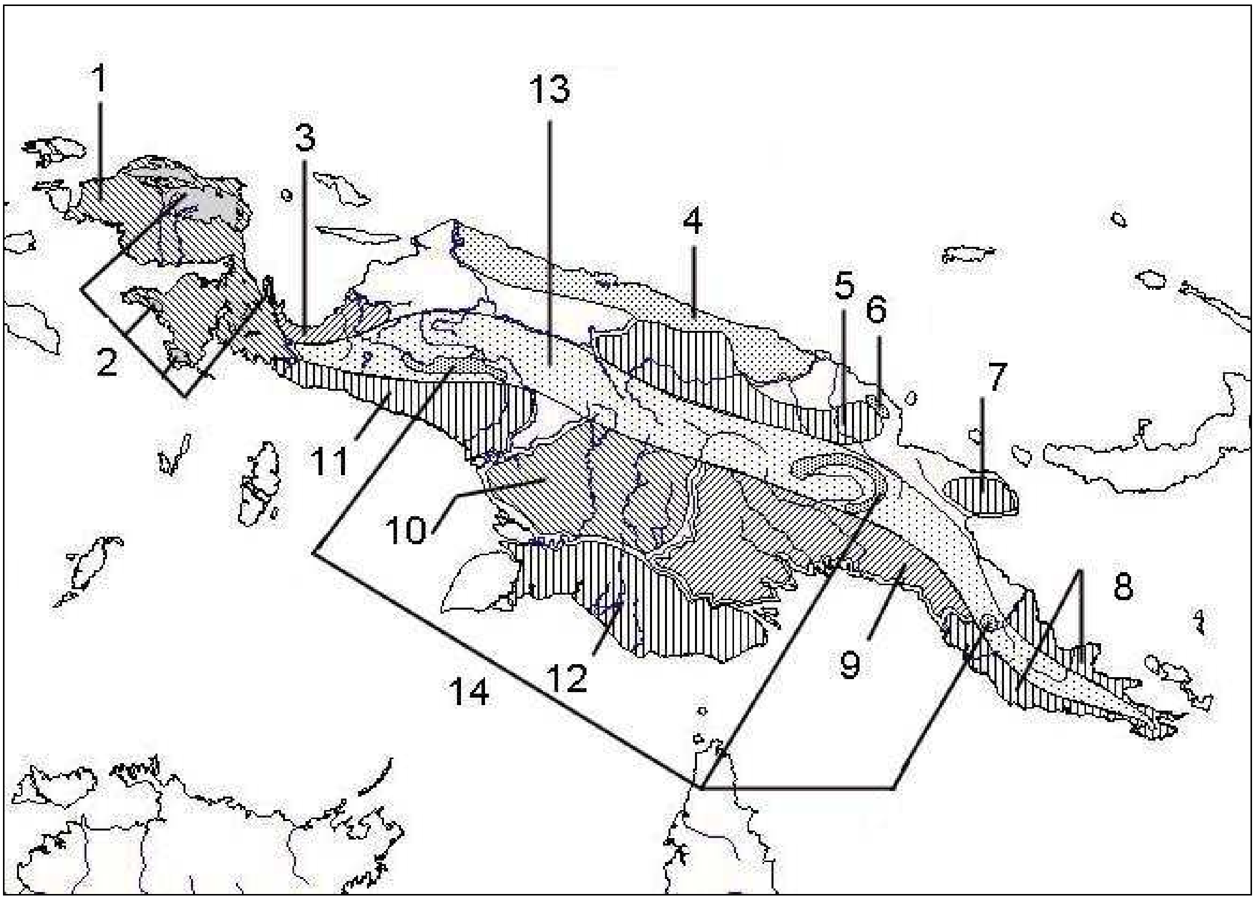


Fig. 4.59 Fourteen sub-endemic centres on New Guinea mainland: 1) Lowlands of Vogelkop, 2) Highlands of Vogelkop, 3) Bird's neck, 4) Northern North Coastal Range, 5) Southern North Coastal Range, 6) Adelbert Range, 7) Huon, 8) Mambare – Anabunga, 9) Gulf of Papua, 10) South-Central New Guinea, 11) South Papua, 12) Trans-Fly, 13) Central Cordillera, 14) Subalpine & alpine zones of Central Cordillera.

1. Lowlands of the Bird's Head

This sub-endemic centre (fig. 4.59, no. 1; fig. 4.60) includes lowlands of the Bird's Head; being bounded on the east by the North-Northwest – South-Southeast Wondiwoi Mts., streching from Wandamen Peninsula to Lake Jamur. Its existence has been defined by the ranges of *Hylophorbus picoides, H. tetraphonus* and *H. wondiwoi* (Microhylidae – Asterophyinae); *Dendrolagus inustus inustus*, *Dorcopsis muelleri muelleri* (Macropodidae); and *Pseudochirulus canescens bernsteini* (Pseudocheiridae). Also found here is the monotypic group *Litoria vagabunda* (Hylidae - Pelodryadinae), whose record on the Bird's Head is known only from Sorong area, but its disjunct population occurs on Seram Island in Central Moluccas. This island is currently separated from New Guinea by deep marine barriers and certainly never connected to New Guinea by a landbridge in the last glacial maxima. Some faunal elements, such as *D. i. inustus, D. m. muelleri,* and *P. c. bernsteini*, extend further east beyond the border. Such of these taxa have mostly close relatives occuring on the lowlands in the northern New Guinea (see account thereof).

For the distribution of *H. picoides*, Günther (2001) noted that specimens currently reported as *H. rufescens* from the Bird's Head and Batanta Island, off the western tip of the main island of New Guinea, are most similar to *H. picoides*. Without further investigation, these populations however can not yet been certainly assessed to *H. picoides*, but they absolutely do not belong to *H. rufescens*.

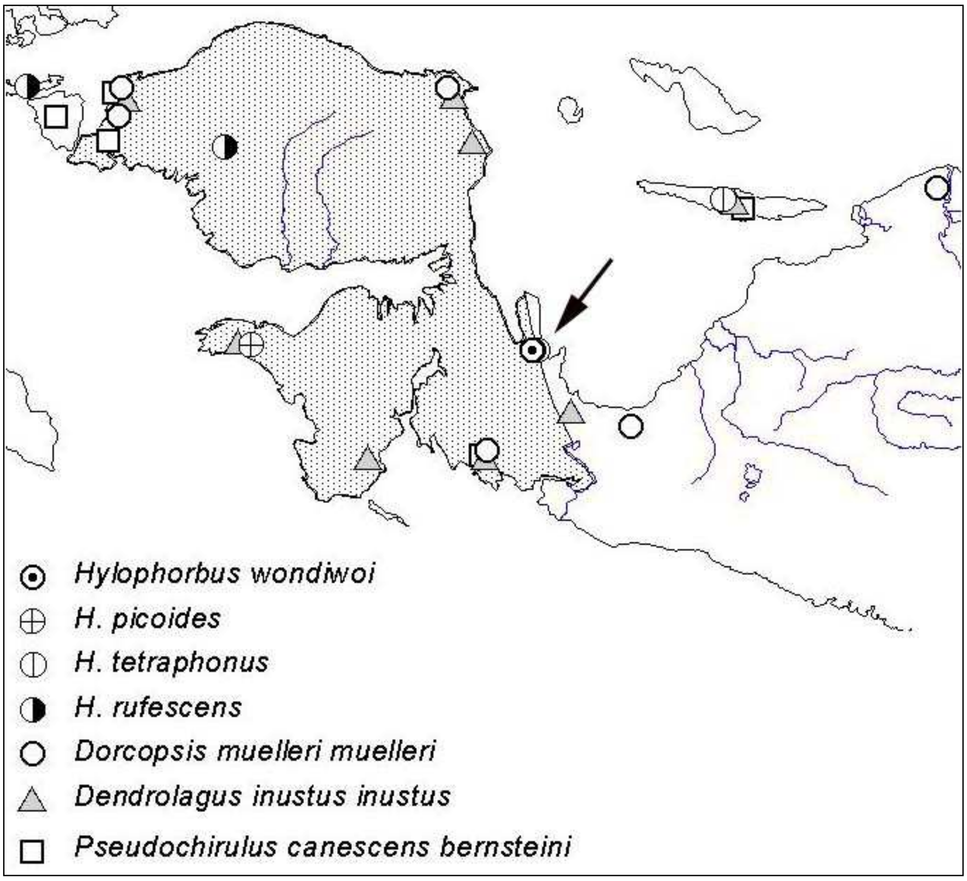


Fig. 4.60 Type distribution of seven faunal elements of the Bird's Head lowlands sub-endemic centre (stipples). An arrow marks type locality of Hylophorbus wondiwoi, H. picoides, and H. tetraphonus. Population of *Hylophorbus rufescens* on this sub-endemic centre and on Batanta Island, off northwestern coasts of the Bird's Head, may have represented *H. picoides* (see text)

2. Highlands of the Bird's Head

This sub-endemic centre (Fig. 4.59, no. 2; Fig 4.61) is restricted to montane forests of the Bird's Head, ie. Tamrau, Arfak, Fakfak, Kumawa, including Wondiwoi Mts. in the Wandammen Peninsula to the east. However, among these mountains, the Arfak harbours the highest number of endemic forms, such as *Litoria chloronota* (Hylidae – Pelodryadinae), *Xenobatrachus arfakianus* (Microhylidae - Asterophryinae), *Antechinus naso mayeri*, *Phascolosorex dorsalis dorsalis* (Dasyuridae), *Pseudochirops albertisii albertisii, P. coronatus* and *Pseudochirulus schlegeli* (Pseudocheiridae). The extent of this sub-endemic centre itself is well defined by the ranges of *Ptiloprora erythropleura erythropleura* (Meliphagidae), *Ducula chalconota chalconota* (Columbidae), *Clytomyias insignis insignis* (Maluridae), *Melanocharis longicauda longicauda* (Melanocharitidae), *Melidectes ochromelas ochromelas* and *Melipotes gymnops* (Meliphagidae), *Pachycare flavogrisea flavogrisea* and *Pachycephala schlegelii schlegelii* (Pachycephalidae), *Drymodes superciliaris beccarii* (Petroicidae), *Amblyornis inornatus* (Ptilonorhynchidae), and *Phylloscopus poliocephalus poliopcephalus* (Sylviidae).

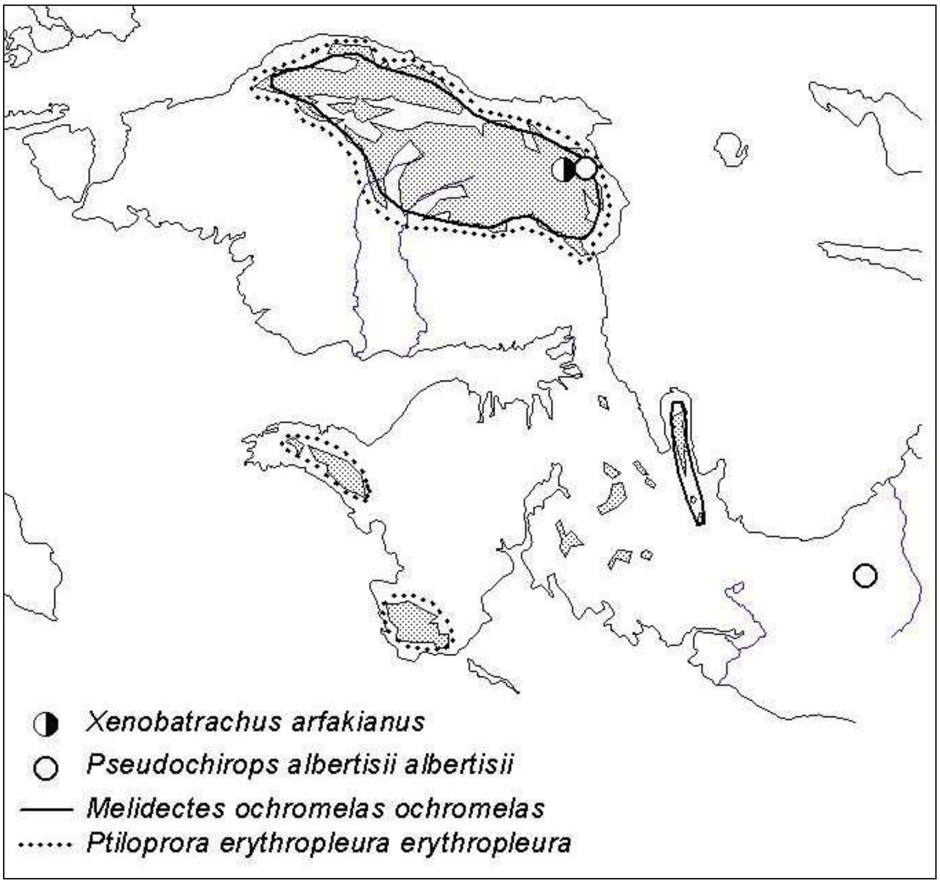


Fig. 4.61 The sub-endemic centre of the mountains of the Bird's Head (stipples). The Arfak Mts. has remarkably high levels of endemism.

Although *Pseudochirops albertisii albertisii* (Pseudocheiridae) is a montane forest dweller, being found only in montane forests above 1,000 metres, its distribution resembles some faunal elements of the lowlands of the Bird's Head sub-endemic centre. While *P. a. albertisii* is confined to the Arfak Mountains and the Weyland Range, its close relatives are restricted to the montane forests of North Coast Ranges (*P. a. schultzei*) and of Japen Island (*P. a. insularis*). This evidence shows a close affinity between this sub-endemic centre with those on the Northern New Guinea and Japen Island. However, the closer connections are mainly indicated to the highlands of the Central Cordillera as suggested by the most faunal elements ascribed to this sub-endemic centre.

3. The Bird's Neck

This sub-endemic centre (Fig. 4.59, no. 3; Fig 4.62) occupies lowlands to lower montane forests in the northern part of the Bird's Neck, from the eastern slopes of Wondiwoi Mts. in the Wandamen Peninsula in the west to the Wapoga River in the east. Its existence can be defined by the ranges of *Hylophorbus sextus* (Microhylidae), *Litoria macki*, *L. wapogaensis* (Hylidae), *Dorcopsis dorianus mayri* (Macropodidae) and *Talegalla fuscirostris meyeri* (Megapodiidae). The first three species are known only from their type localities in the headwaters of the Wapoga River at 1,070 m elevations (Günther, 2001; Frost, 2002). *D. d. mayri* has been recorded from the eastern slope of the Wondiwoi Mts. (Flannery, 1995) and the last, *T. fuscirostris* sometimes can be found as high as 800 m (Jones *et al*. 1995).

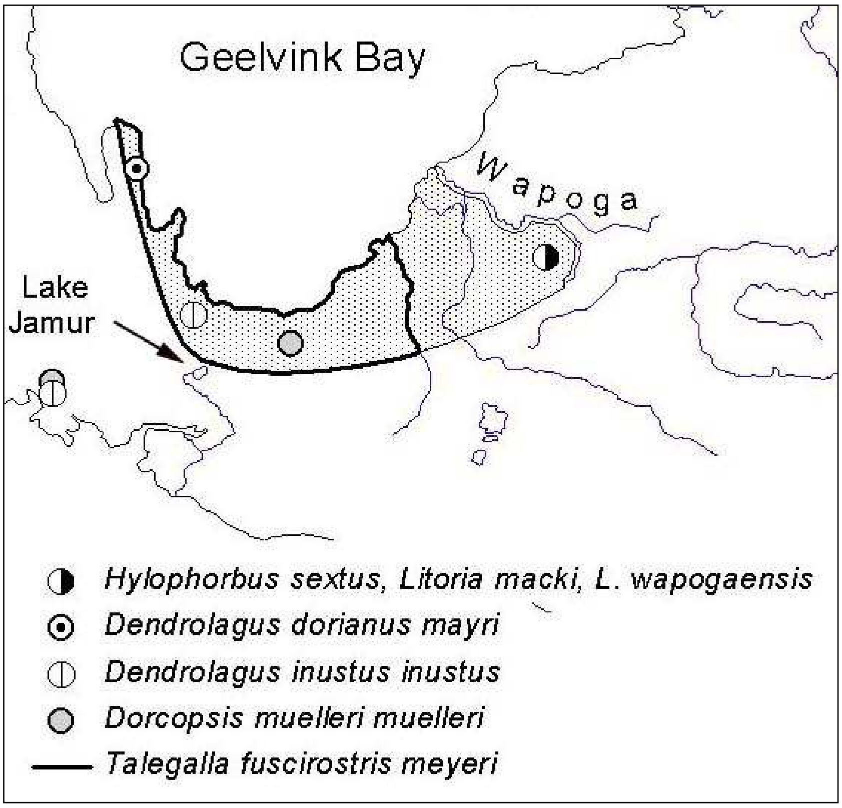


Fig. 4.62 The sub-endemic centre of the Bird's Neck. The headwaters of the Wapoga River has high levels of endemism, especially of amphibians.

Penetration to this sub-endemic centre from the Vogelkop Peninsula is high, i.e. *Dendrolagus inustus inustus*, *Dorcopsis muelleri muelleri* (Macropodidae) and *Pseudochirops albertisii albertisii* (Pseudocheiridae). Also found here are for example *Colluricincla megarhyncha ferruginea* & *Pitohui kirhocephalus tibialis* (Pachycephalidae).

Other than to the Bird's Head, close affinity has also been indicated to lowlands on southern New Guinea. This has been well indicated by the occurrence of the close relatives of *T. f. meyeri* there, i.e *T. f. occidentis* on the South Papua sub-endemic centre, *T. f. ssp*. On the South-Central New Guinea sub-endemic centre, *T. f. fuscirostris* on the Gulf of Papua sub-endemic centre, and *T. f. aruensis* on the Trans-Fly sub-endemic centre and Aru Islands.

4. Northern North Coastal Range

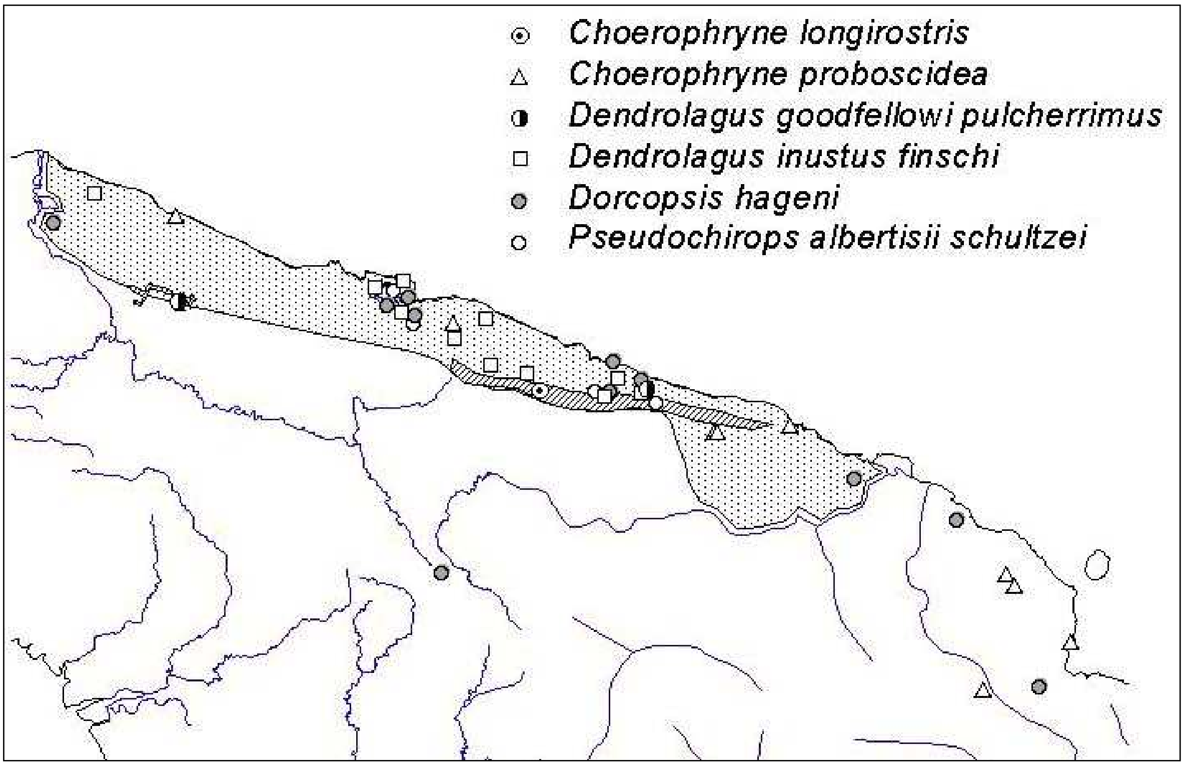


Figure 4.63 The sub-endemic centre of the Northern North Coastal Range (stipples) lies basically on the northern side of the North Coastal Range (diagonal hatching). The wet Northeast Trade winds have facilitated its extension to the southern side in the eastern end. *Pseudochirops albertisii* and *Dendrolagus inustus* are represented by other subspecies in the Vogelkop Peninsula.

The distribution of faunal elements in this sub-endemic centre (Fig. 4.59, no. 4; Fig 4.63) is dependent on isolated rainforests in the northern slopes of the Gauttier Mts., the Foya Mts., and the North Coastal Ranges (Bewani Mts., Torricelli Mts., Prince Alexander

Mts.), including the generally precipitous mountaintops, and the coastal plain to the north. It also includes the eastern part of the southern slopes of the North Coastal Range, which is wetter than the western part because it receives the wet Northeast Trade Winds. On the west, it is bounded by the Mamberamo River and on the east, by the Sepik River. Regarding its wetter climate, it is relatively easy to distinguish it from other independent sub-endemic centre southward from this (Refer to No. 5), which has a more arid climate. The type distribution of three genyophrynines of genus *Choerophryne* show clearly how the Northern North Coastal Range is separated from the southern one (see fig. 4.64).

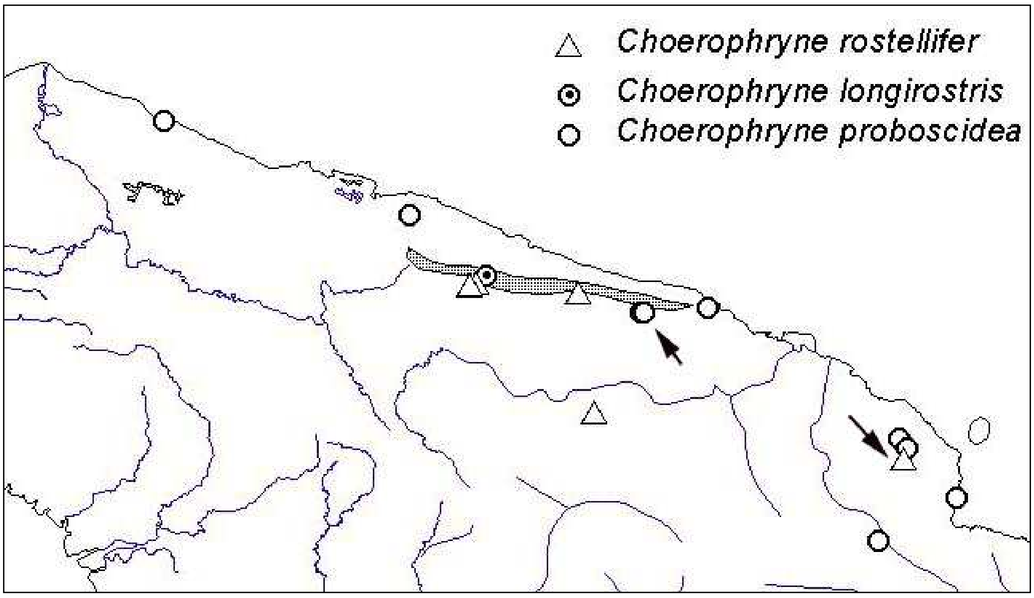


Figure 4.64 The type distribution of three *Choerophryne*, showing clearly the separation of the wetter Northern North Coastal Range from the drier Southern North Coastal Range by the North Coastal Range (stipples). *Choerophryne proboscidea* and *C. longirostris* are restricted to the northern side and mountaintops of the North Coastal Range, whereas *C. rostellifer* occurs on the southern side. A penetration of *C. proboscidea* to the southern side of the North Coastal Range (marked by an arrow) is apparently facilitated by the wetter climate at the eastern end of the southern side due to the wet Northeast Trade Winds. The occurrence of disjunct populations of *C. proboscidea* on the wetter northeastern side of the Northwest-Southeast Adelbert Range suggests a close affinity between the two areas. Meanwhile, *C. rostellifer* (marked by an arrow) is confined to the drier other side of the Adelbert Range.

The mountaintops in this area has high levels of endemism. They are for example *Austrochaperina adamantina*, *A. aquilonia* (Microhylidae – Genyophryinae); *Zaglossus bruijnii ssp.* (Tachyglossidae); *Dendrolagus scottae* (Macropodidae), *Petaurus abidi* (Petauridae), *Pseudochirops albertisii schultzei* and *Pseudochirulus canescens gyrator* (Pseudocheiridae), *Microhydromys musseri*, *Paraleptomys rufilatus* (Muridae – Hydromyini), *Amblyornis flavifrons* (Ptilonorhynchidae), and *Ptiloprora mayri* (Meliphagidae).

Also found here are for example *Litoria mystax* (Hylidae); *Austrochaperina basipalmata* (Microhylidae – Genyophryninae); *Dendrolagus goodfellowi pulcherrimus*, *Dendrolagus inustus finschi* (Macropodidae), *Pseudochirops albertisii schultzei*, and *Pseudochirulus canescens gyrator* (Pseudocheiridae) (see fig. 4.62). The occurrence of the close relatives of the last three taxa on the Vogelkop Peninsula show that this sub-endemic centre is closely related to that peninsula (see accounts thereof). Additionally, close relationship has also been indicated to lowlands of Northeastern New Guinea as being shown by disjunct population of *Choerophyne proboscidea* there.

It is worth noting that despite most faunal elements are confined to lowland rainforests, there is a taxon, i.e. *Dendrolagus goodfellowi pulcherrimus* (Macropodidae), whose habitat is primarily the oak forest (Flannery, 1995) – a zone which experiences less rainfall. Whithin this sub-endemic centre, it is known from the Torricelli Mountains and the Foya Mountains.

5. Southern North Coastal Range

It includes these more arid areas, i.e the southern side of the Gauttier Mts., the Foya Mts. and the North Coastal Range in northern New Guinea, the northern slopes of the Eastern Central Cordillera and the southwestern slopes of the Adelbert Range in northeastern New Guinea (Fig. 4.59, no. 5; Fig 4.65). Its existence can be defined by the ranges of *Austrochaperina hooglandi* and *Choerophryne rostellifer* (Microhylidae – Genyophryninae) (see also fig. 4.63) as well as *Dendrolagus goodfellowi buergersi* (Macropodidae). Within this sub-endemic centre, the Hunstein Range in the northern slope of the Eastern Central Cordillera has acted as an effective natural barrier for some taxa. *A. hooglandi*, for example, has the westernmost record on Mt. Hunstein. In contrast to this, *D. g. buergersi* has the easternmost record on Mt. Hunstein. Also the following taxa have the easternmost records on Mt. Hunstein, i.e *Xenorhina arboricola* and *Xenobatrachus zweifeli* (Microhylidae – Asterophryinae).

6. Adelbert Range

The sub-endemic centre (Fig 4.59, no. 6; Fig. 4.66) is restricted to montane forest of this range. It has high levels of endemism, especially in amphibians, for example *Albericus brunnhildae* and *Albericus gudrunae* (Microhylidae – Genyophryninae), *Barygenys parvula* and *Xenobatrachus tumulus* (Microhylidae – Asterophryinae). Close affinity is indicated to the montane forest of the Huon Peninsula. This has at least shown by the shared range of *Austrochaperina mehelyi* (Microhyidae – Genyophryninae) for both areas.

Additionally, the occurrence of *Choerophryne proboscidea* here suggests also a close affinity to the Northern North Coastal Range sub-endemic centre.

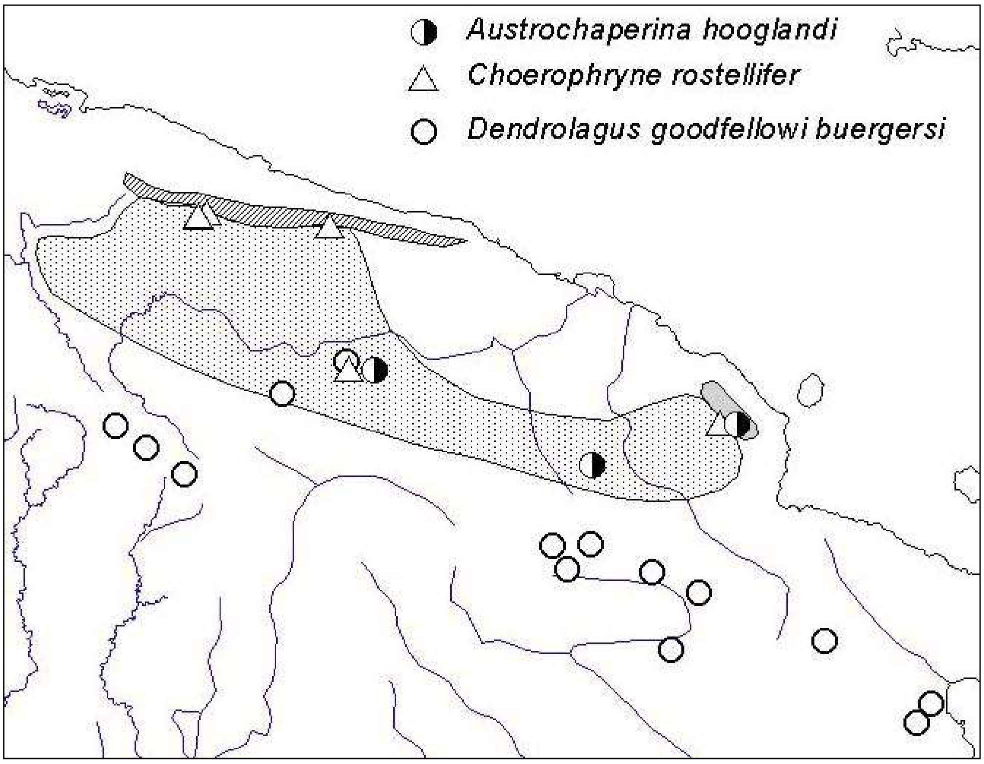


Figure 4.65 The sub-endemic centre of the Southern North Coastal Range (stipples) lies on the leeward side of the North Coastal Range (diagonal hatching) and the Adelbert Range (grey-shaded).

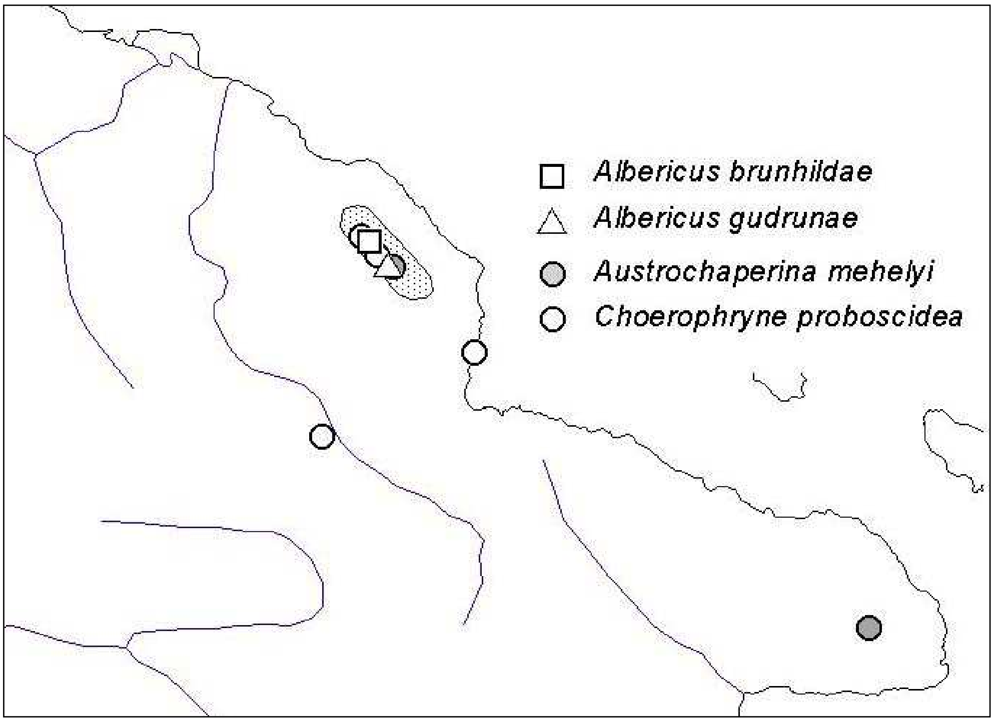


Figure 4.66 Type distribution of faunal elements of the Adelbert Range sub-endemic centre (stipples). Close affinity to the Northern Coastal Range has been indicated by *Choerophryne proboscidea* (see also Fig. 4.63).

7. Huon Peninsula

The sub-endemic centre (Fig 4.59, no. 7; Fig. 4.67) in this peninsula is found on montane forests of Saruwaged Range in the southern part of the peninsula, while the Finnisterre Range to the north part is lacking in endemic forms. The existence of this sub-endemic centre has been indicated by the occurrence of these endemic forms: *Austrochaperina polysticta*, *A. parkeri* (Microhylidae – Genyophryninae), *Xenobatrachus huon* (Microhylidae – Asterophryinae), *Dendrolagus matschiei* (Macropodidae); *Peroryctes raffayana rothschildi* (Peroryctidae), *Thylogale browni lanatus* (Macropodidae), *Phalanger carmelitae coccygis* (Phalangeridae), *Pseudochirops corinnae argenteus* (Pseudocheiridae), *Mallomys aroaensis hercules*, *Uromys anak rothschildi*, *Hyomys goliath strobilus* (Muridae – Uromyini), and *Rattus steini försteri* (Muridae – Murinae). Close affinities to the sub-endemic centre of Adelbert Range has been indicated by *Austrochaperina mehelyi* (see account thereof), while to the Central Cordillera by the rest taxa listed above.

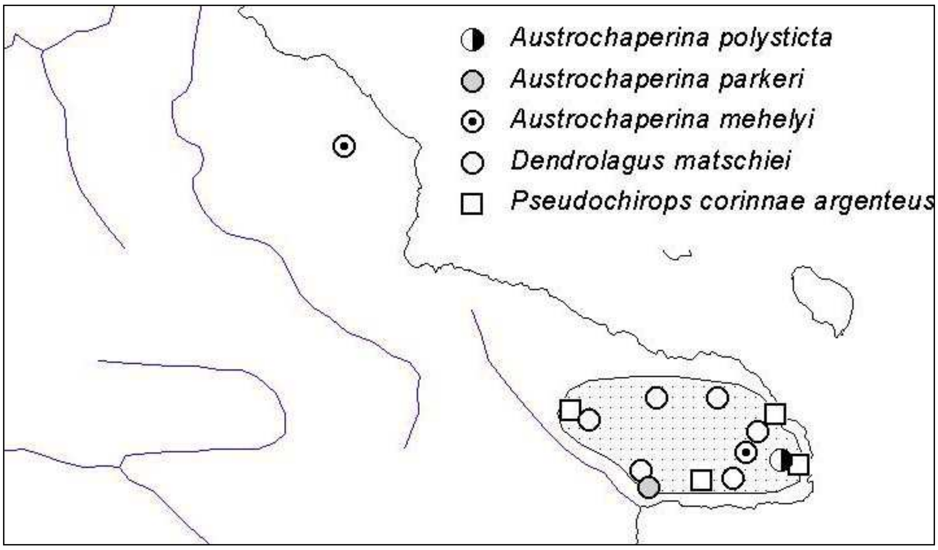


Figure 4.67 The Huon sub-endemic centre is confined to the Saruwaged Range on the southern part (stipples). *Pseudochirops corinnae* is represented by other subspecies on the Central Cordillera.

8. Mambare – Anabunga

This sub-endemic centre (Fig 4.59, no. 8; Fig. 4.68) is lowlands in the southeastern New Guinea, being dominated by monsoon woodlands and grasslands. Thus, its faunal elements are not surprisingly mostly adapted to such drier habitats, for example *Litoria congenita* (Hylidae – Pelodryadinae), *Pherohapsis menziesi* (Microhylidae – Asterophryinae), *Macropus agilis papuanus* (Macropodidae), *Isoodon macrourus* (Peramelidae) and *Rattus sordidus gestri* (Muridae – Murinae). However, it is worth noting that this sub-endemic centre is also home for primary forest dwellers, such as

Dorcopsis luctuosa luctuosa (Macropodidae), *Peroryctes broadbenti* (Peroryctidae) and *Rattus leucopus dobodurae* (Muridae – Murinae). These typical primary rainforest dwellers have their northernmost ranges mostly on Mambare River in the eastern coasts and on Anabunga River in the western coasts. In contrast to this, the northernmost ranges of dry forest dwellers lie rather southward of these two rivers, i.e. on Popondetta area in the eastern coasts and on Brown River in the western coasts. This feature shows clearly an invasion of dry forests once from the south, undoubtedly as the result of the lowered sea levels in the Last Glacial Maxima. Thus, the Brown River and Popondetta area have marked the northernmost replacement of primary rainforests by drier woodlands and grasslands.

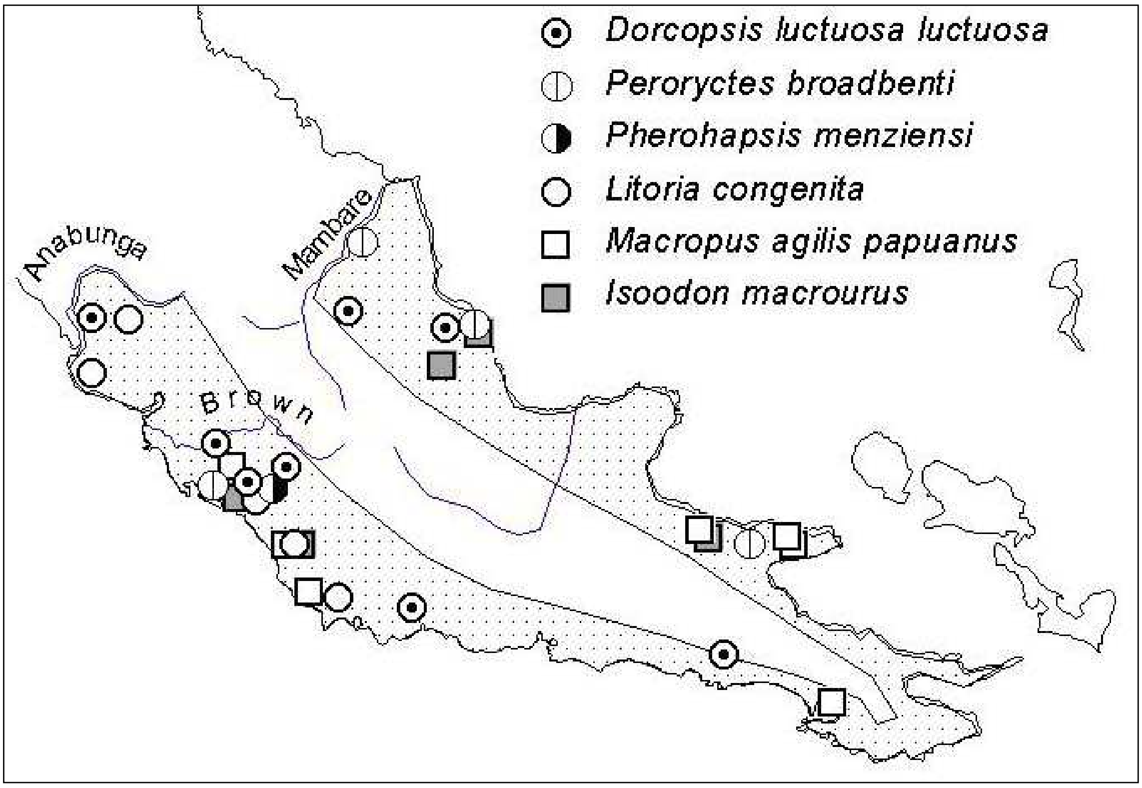


Figure 4.68 The sub-endemic centre of Mambare – Anabunga (stipples) harbours primary rainforest dwellers (*Dorcopsis luctuosa luctuosa*, *Peroryctes broadbenti*) as well as grassland and woodland dwellers (*Pherohapsis menziensi*, *Litoria congenita*, *Macropus agilis papuanus* and *Isoodon macrourus*).

Close affinity to the Trans-Fly sub-endemic centre (see account thereof) has been indicated by the occurrence of close relatives of most taxa there. This suggests the existence of a migration corridor once connecting the two areas in the last glacial maxima as the sea level lowered. Later in the post glacial period, the sea levels retreated to its current levels and broken up the gene flow between these two areas. While the *Dorcopsis* populations on these two areas are represented by two different subspecies, the *Isoodon* and *Macropus* each remain at the same taxonomic level. These indicate that the separation of the last two taxa may have occurred much later compared to *Dorcopsis*.

9. Gulf of Papua

The existence of this sub-endemic centre (Fig 4.59, no. 9; Fig. 4.69) has been indicated by the ranges of *Austrochaperina guttata* (Microhylidae – Genyophryninae), *Chiruromys vates* (Muridae – Uromyini), *Dorcopsis spadix* (Macropodidae), and *Talegalla fuscirostris fuscirostris* (Megapodiidae). It is a large area of elevated limestone lying along the southern flanks of the Central Cordillera; bordered to the west by the Fly and Strickland rivers, to the east by the Anabunga River, and to the north by high elevations of the Central Cordillera. The absence of typical dry habitat dwellers on this area shows that it may have only less affected by monsoonal climate in the glacial period, contrastly to Popondetta – Brown and Trans-Fly sub-endemic centres.

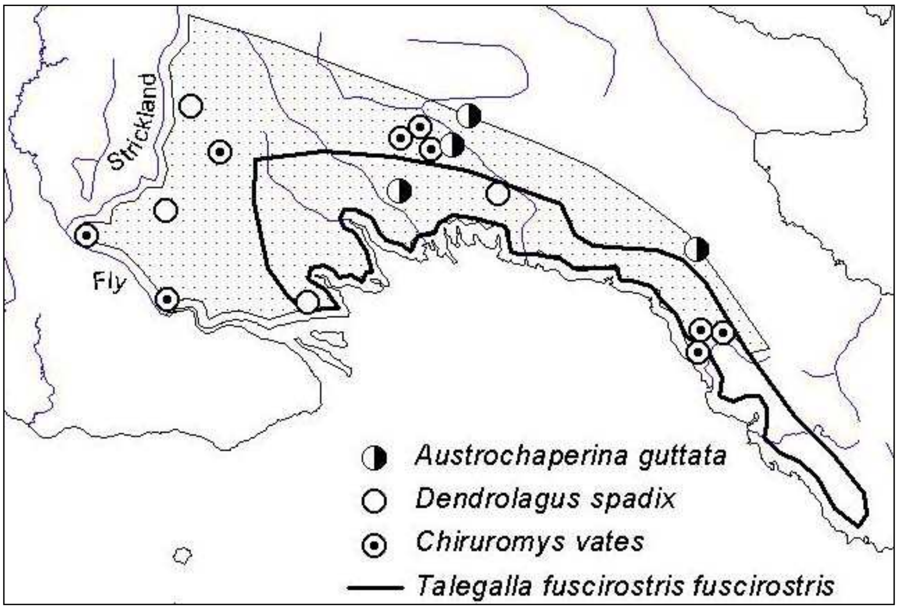


Fig. 4.69 The distribution of four faunal elements of the Gulf of Papua sub-endemic centre (stipples)

10. South-Central New Guinea

This sub-endemic centre (Fig. 4.59, no. 10; Fig. 4.70) is limited by the Pulau River to the west and by the Strickland River to the east. To the south, it is bordered on the sub-endemic centre of Trans-Fly and to the north on that of the Central Cordillera. Its faunal elements are generally restricted to gallery forest or rainforest margins. This has been well shown by these forms: *Litoria havina* and *L. majikthise* in the headwaters of Ok Tedi, *Echymipera echinista* (Peroryctidae), *Rattus leucopus ringens*, *R. sordidus ariama* (Muridae – Murinae) and *Talegalla fuscirostris ssp.* (Megapodiidae). Close affinities are generally arranged to sub-endemic centres on southern New Guinea and northern Australia.

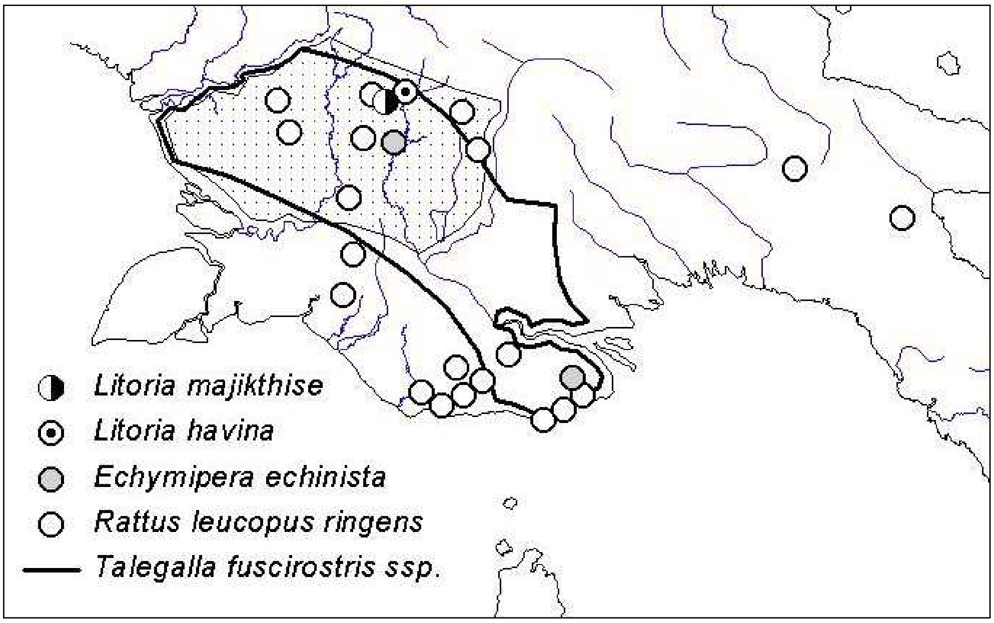


Fig. 4.70 The sub-endemic centre of the South-Central New Guinea (stipples). Its faunal elements are closely related to the Trans-Fly sub-endemic centre (*Echymipera echinista, Rattus leucopus ringens, Talegalla fuscirostris ssp.*)

11. South Papua

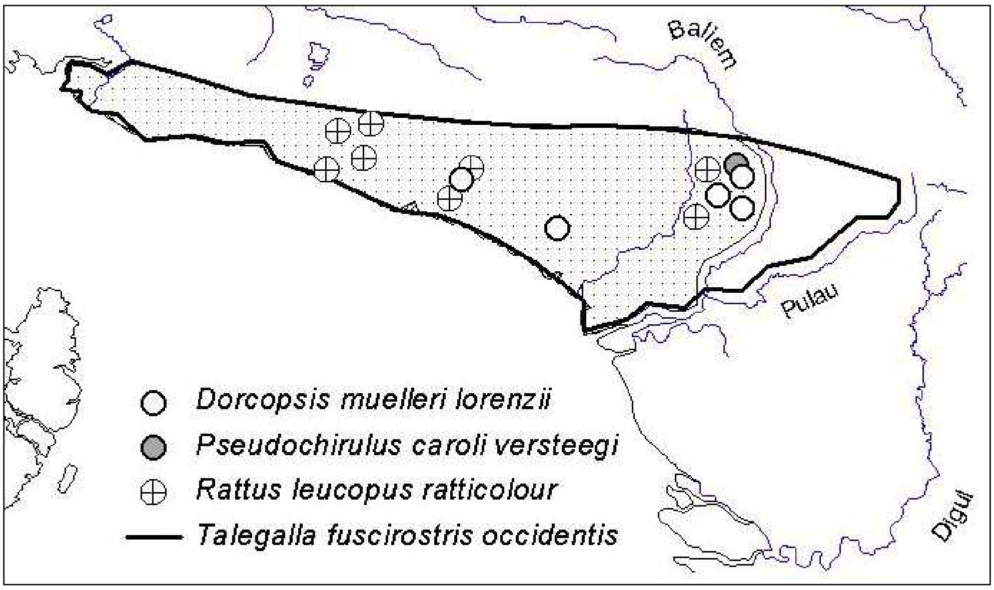


Fig. 4.71 The sub-endemic centre of South Papua (stipples). Close relative of *Dorcopsis muelleri lorenzii* occurs on the Vogelkop Peninsula (*D. m. muelleri*), of *Pseudochirulus caroli versteegi* on the Central Cordillera (*P. c. caroli*), of *Rattus leucopus ratticolour* on South-Central New Guinea sub-endemic centre (*R. l. ringens*) and on Mambare – Anabunga sub-endemic centre (*R. l. dobodurae*), and of *Talegalla fuscirostris occidentalis* on the Bird's Neck sub-endemic centre (*T. f. meyeri*), on South-Central New Guinea (*T. f. ssp.*) and on Trans-Fly (*T. f. aruensis*).

The sub-endemic centre (Fig 4.59, no. 11; Fig. 4.71) includes lowland forests in the southern Papua, from the Etna Bay in the west to the Lorentz River in the east. Higher elevations of the rugged Central Cordillera limit it to the north. In spite of a very close distance with the Vogelkop Peninsula, there are only less penetration from there to this sub-endemic centre, contrastly to northern New Guinea. The few taxa, which penetrated to this area, is for example *Dorcopsis muelleri lorenzii* (Macropodidae). Otherwise, this sub-endemic centre can be defined by the ranges of *Pseudochirulus caroli versteegi* (Pseudocheiridae), *Melomys rufescens callidor*, *Rattus leucopus ratticolour*, and *R. steini steini* (Muridae – Uromyini). *Tallegala fuscirostris occidentis* (Megapodidae) extends a few eastwards, but it can still be considered as its faunal elements.

12. Trans-Fly

This sub-endemic centre (Fig 4.59, no. 12; Fig. 4.72) lies in the southern most part of the New Guinea mainland; being bounded by the Digul River on the west and by the Fly River on the east as well as by the D'Albertis junction on the north. Ecological features on this area resemble those on the Mambare – Anabunga sub-endemic centre. Therefore, their faunal elements are closely similar in composition. They are, for example, *Litoria congenita* (Hylidae – Pelodryadinae), *Macropus agilis papuanus* (Macropodidae), *Isoodon macrourus* (Peroryctidae) and *Rattus sordidus ariama* (Muridae – Murinae). Rainforest dwellers, such as *Dorcopsis luctuosa phyllis* (Macropodidae) and *Rattus leucopus ringens* (Muridae – Murinae) is restricted to rainforest gallery along river drainage.

Through a landbridge once existed by the lowered sea levels, close affinities are also awaited to fauna on the northern Australia and this is fulfilled by, for example, *Thylogale stigmatica oriomo* (Peroryctidae), *Dactylopsila trivirgata kataui* (family), *Conilurus penicillatus randi* (Muridae), and *Melomys rufescens niviventer* (Muridae - Uromyini). Their relatives are represented by other subspecies there. On the other hand, *Litoria rubella* (Hylidae), *Austrochaperina basipalmata* (Microhylidae) and *Pseudomys delicatulus delicatulus* (Muridae) share their ranges for both southern New Guinea and northern Australia. In contrast to this, some other faunal elements do not share with this continent, but they are restricted to this sub-endemic centre. They are for example the monotypic group *Litoria quadrilineata* (Hylidae), *Dasyurus spartacus* (Dasyuridae), *Echymipera kalubu oriomo* (Dasyuridae), *Leptomys signatus* (Muridae – Hydromyini) and *Talegalla fuscirostris aruensis* (Megapodiidae). Some others show even interestingly close affinity to Moluccan islands instead to Australian continent. Taxa with such a range are for example *Thylogale brunii* (Macropodidae) and *Spilocuscus maculatus chrysorrhous* (Phalangeridae). The former occurs also on Aru Is. and Kai Is., while the latter on Aru Islands, Kei Islands, Tioor, Ambon, and Buru (Flannery 1995). Regarding deep marine barriers to those Moluccan islands, perhaps only tectonic movements have been responsible for such enigmatic ranges.

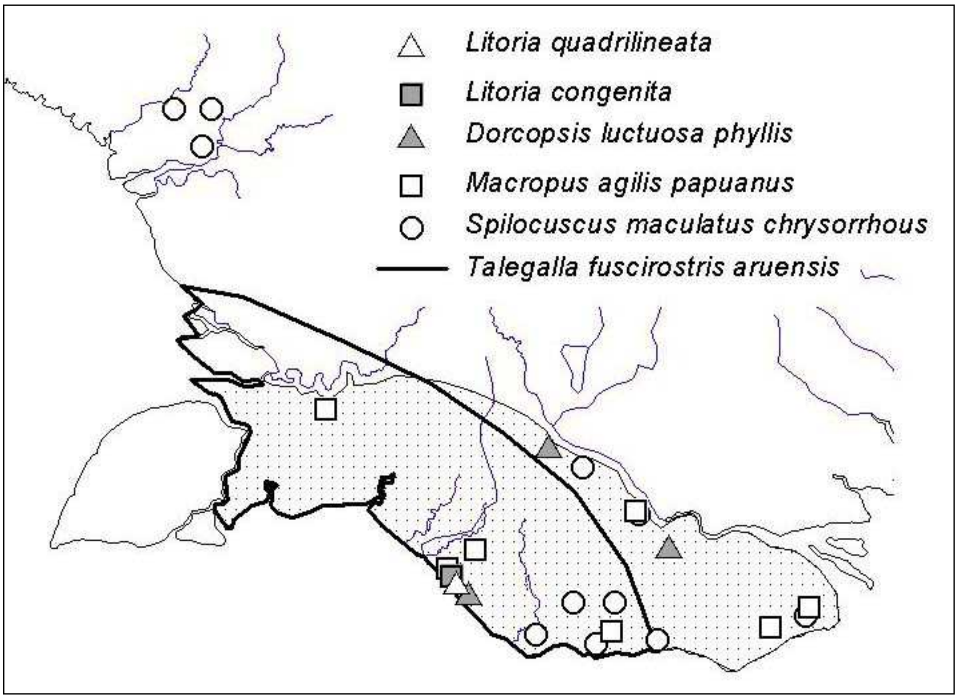


Figure 4.72 Type distribution of faunal elements of Trans-Fly sub-endemic centre (stipples). *Litoria congenita* and *Macropus agilis papuanus* are also faunal elements of the Mambare – Anabunga sub-endemic centre, while *Dorcopsis luctuosa* is represented by other subspecies there. The occurrence of *Spilocuscus maculatus chrysorrhous* on Moluccan islands suggests its dispersal by tectonic movements.

13. Central Cordillera

This sub-endemic centre (Fig 4.59, no. 13; Fig. 4.73) lies on the rugged highlands, running along the spine of the New Guinea mainland, from the Weyland Range in the west to the Owen Stanley Range in Southeast New Guinea. Its existence can be defined by the ranges of *Dorcopsulus vanheurni* (Macropodidae), *Phalanger carmelitae carmelitae* (Phalangeridae), *Pseudochirops cupreus* (Pseudocheiridae), *Cercartetus caudatus caudatus* (Burramyidae), *Mayermys ellermani* (Muridae – Hydromyini), *Aegotheles albertisi salvadorii* (Aegothelidae), *Geoffroyus simplex buergersi*, *Neopsittacus musschenbroekii major*, *Psitteuteles goldiei* (Psittacidae) and *Acanthiza murina* (Acanthizidae).

The range of *C. c. caudatus* is very interesting. While it appears to be restricted to the Central Cordillera at altitudes above 1,500 metres within New Guinea, its close relative, *C. c. macrurus*, inhabits rainforest at higher elevations (above 300 metres) in the Cape York and Atherton Tableland in the Northern Australia (Flannery, 1995). The two populations may have been connected each other once by gallery rainforest in the south-central New Guinea.

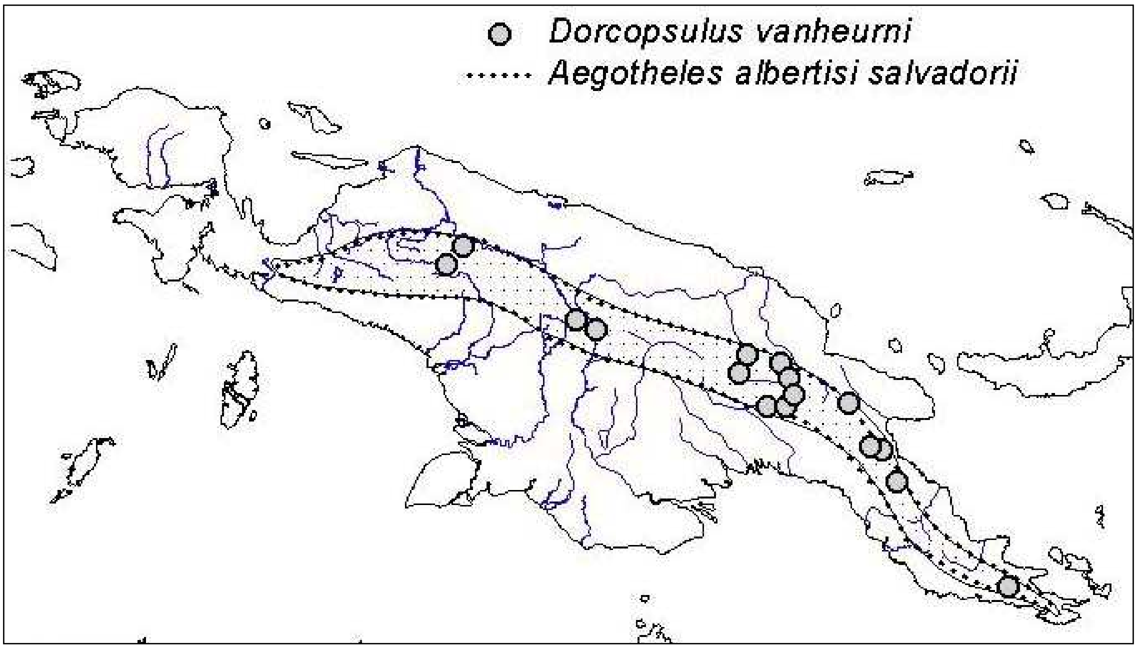


Figure 4.73 The Central Cordillera sub-endemic centre (stipples)

At least three divisions can be separated from each other within this sub-endemic centre, i.e. the Western Central Cordillera, the Eastern Central Cordillera, and the Southeastern Central Cordillera. The first division, i.e. **the Western Central Cordillera** (fig. 4.74), extends from the Weyland Range in the west to the upper Sepik-Fly rivers in the east. It can be defined by the ranges of *Austrochaperina brevicrus*, A. *kosarek* (Microhylidae – Genyophryninae); *Dendrolagus dorianus stellarum* (Macropodidae), *Antechinus naso naso* (Dasyuridae), *Pseudochirulus canescens dammermani* (Pseudocheiridae) and *Sericornis nouhuysi nouhuysi* (Acanthizidae). The occurrence of remarkably numerous endemic forms, which are noted as primary rainforest dwellers, on the upper Sepik-Fly rivers at the eastern end of this division suggests the natural existence of such habitat there. These endemic forms are for example *Litoria leucova* (Hylidae – Pelodryadinae), *Phalanger matanim* (Phalangeridae) and *Pogonomys championi* (Muridae – Uromyini). Similar to this is the Weyland Range in the western end of this area. It harbours also a number of endemic forms, such as *Phascolosorex dorsalis brevicaudata* (Dasyuridae).

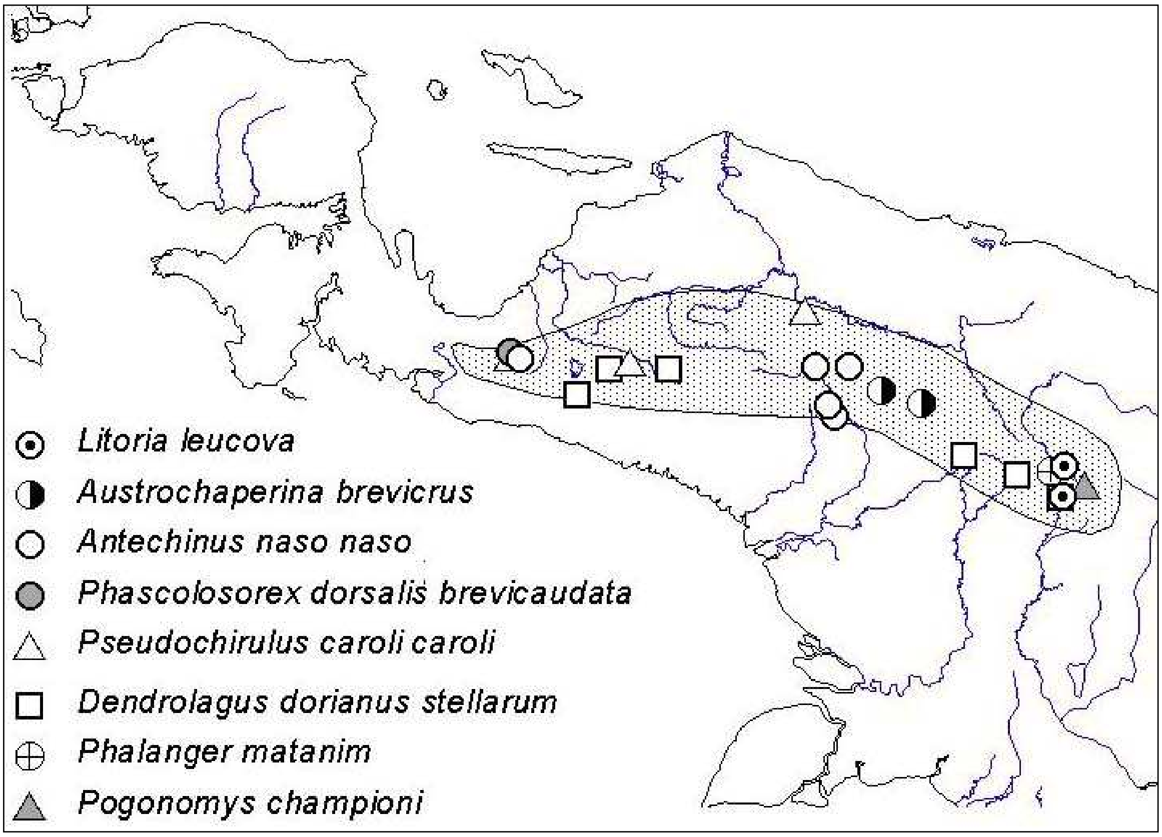


Figure 4.74 Type distribution of faunal elements of the Western Central Cordillera sub-endemic centre. The upper Sepik-Fly rivers on the eastern end has remarkably high levels of endemism.

The second division, i.e **the Eastern Central Cordillera** (Fig. 4.75), begins from the upper Strickland River to the mountains in the vicinity of Wau. It has a drier regional climate than the western one as indicated by the occurrence of *Dendrolagus goodfellowi buergersi* (Macropodidae). This taxon inhabits primarily mid-montane oak forests – a zone which experiences less rainfall (Flannery, 1995). Its occurrence on the upper Sepik-Fly rivers in the Western Central Cordillera sub-endemic centre (see account thereof) indicates the replacement of rainforest in that area by drier oak forests. Similar replacement has also been undergone on the upper Ramu River. Its previously natural rainforest is indicated by the occurrence of the endemic rainforest inhabitant, *Austrochaperina archboldi* (Microhylidae – Genyophryninae), there. Also found here are for example *Liophryne allisoni* (Microhylidae – Genyophryninae), *Antechinus naso tafa*, *A. n. misim* (Dasyuridae), *Dendrolagus dorianus notatus* (Macropodidae), *Phalanger sericeus sericeus* (Phalangeridae), *Pseudochirulus canescens canescens* (Pseudocheiridae), and *Crossomys moncktoni* (Muridae – Hydromyini).

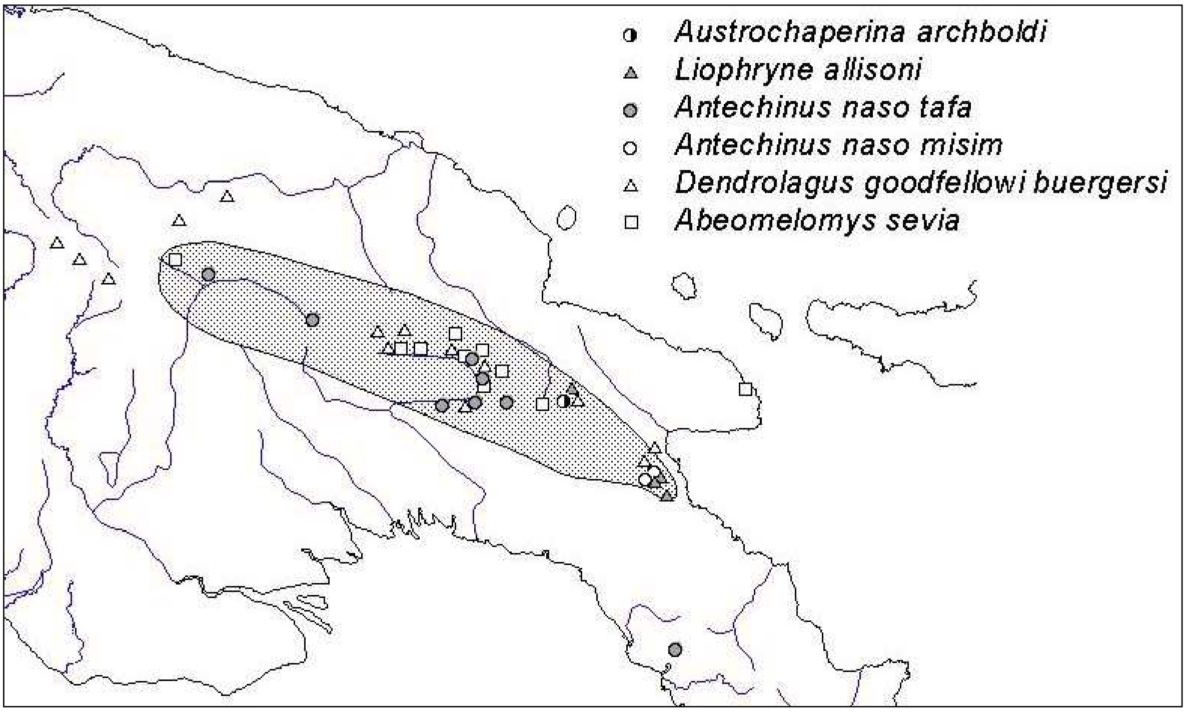


Fig. 4.75 The ranges of six faunal elements of the Eastern Central Cordillera sub-endemic centre (stipples).

Finally, the third division, i.e. **the Southeastern Central Cordillera** (Fig. 4.76), stretchs from the mountains southward of the vicinity of Wau to the Mt. Dayman in the southeast peninsula. The Myola area, lying on the upper Mambare River draining to the east coasts and and on the upper Brown River draining to the west coasts, harbours a numerous endemic amphibians. They are for example these three genyophrynine microhylids, i.e. *Aphantophryne sabini, Cophixalus verecundus and Liophryne similis.* It seems that this upper rivers has once been replaced by drier vegetation and leaving rainforest inhabitants to be isolated on the upper rivers as also once being occurred on the upper Sepik-Fly rivers and the upper Ramu River.

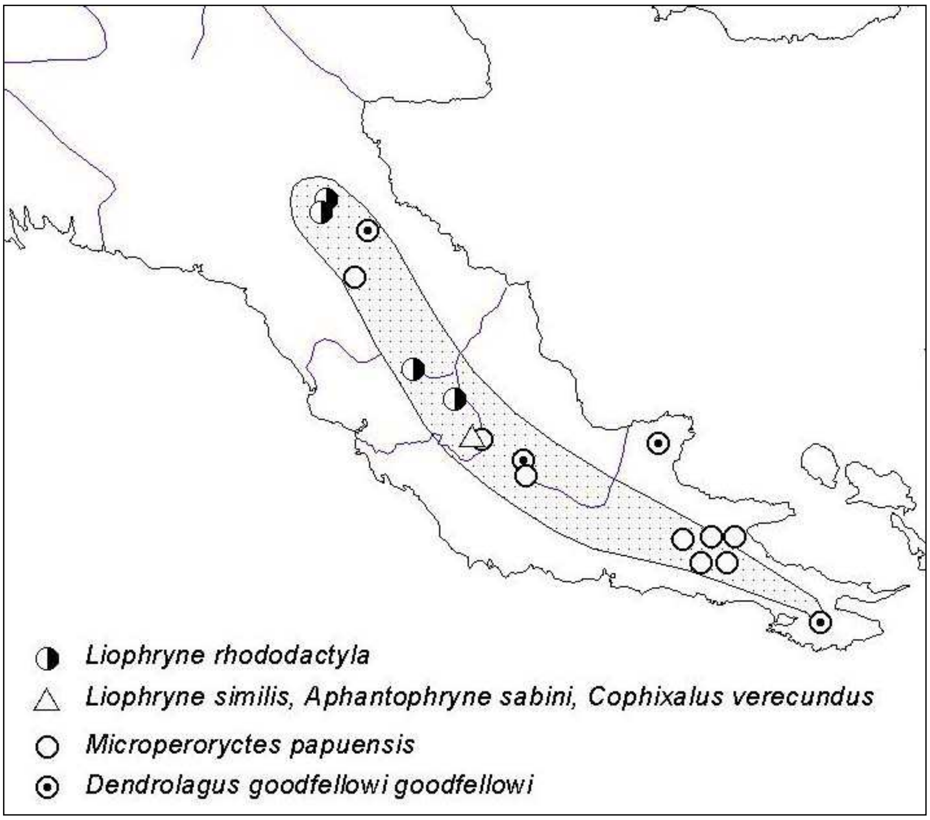


Fig. 4.76 Distribution in the Southeastern Central Cordillera sub-endemic centre (stipples). The upper Mambare and Brown rivers harbours remarkably numerous endemic forms.

14. The subalpine and alpine zones of the Central Cordillera

The sub-endemic centre (Fig 4.59, no. 14; Fig. 4.77) includes subalpine grasslands and alpine scrub. In New Guinea, such habitats are generally found from about 3,000 metres. There are currently at least three disjunct such habitats on the highest altitudes of the Central Cordillera, i.e on Snow Mountains in the Western Central Cordillera, on Central and Eastern Highlands in the Eastern Central Cordillera, and on Mt. Albert Edwards in the Southeastern Central Cordillera. The glacier itself remains today only on the highest peak of Mt. Jaya in the Snow Mountains (Peterson *et al.* 1973, Peterson & Peterson, 1994, van Ufford & Sedgwick, 1998). Faunal elements confined to this sub-endemic centre are for example *Dendrolagus mbaiso*, *Hydromys habbema* (Muridae – Hydromyini), *Mallomys gunung* (Muridae – Uromyini), *Stenomys omlichodes*, *S. richardsoni* (Muridae – Murinae) and *Thylogale calabyi* (Macropodidae). Of these taxa, only *T. calabyi* is found outside the Snow Mts. This species is recently restricted to patches of subalpine grasslands on Mt. Giluwe in the Eastern Central Cordillera and Mt. Albert Edward in the Southeastern Central Cordillera. Also found on alpine zone of Snow Mts. are for example *Anurophasis monorthonyx* (Phasianidae) and *Melidectes fuscus occidentalis* (Meliphagidae).

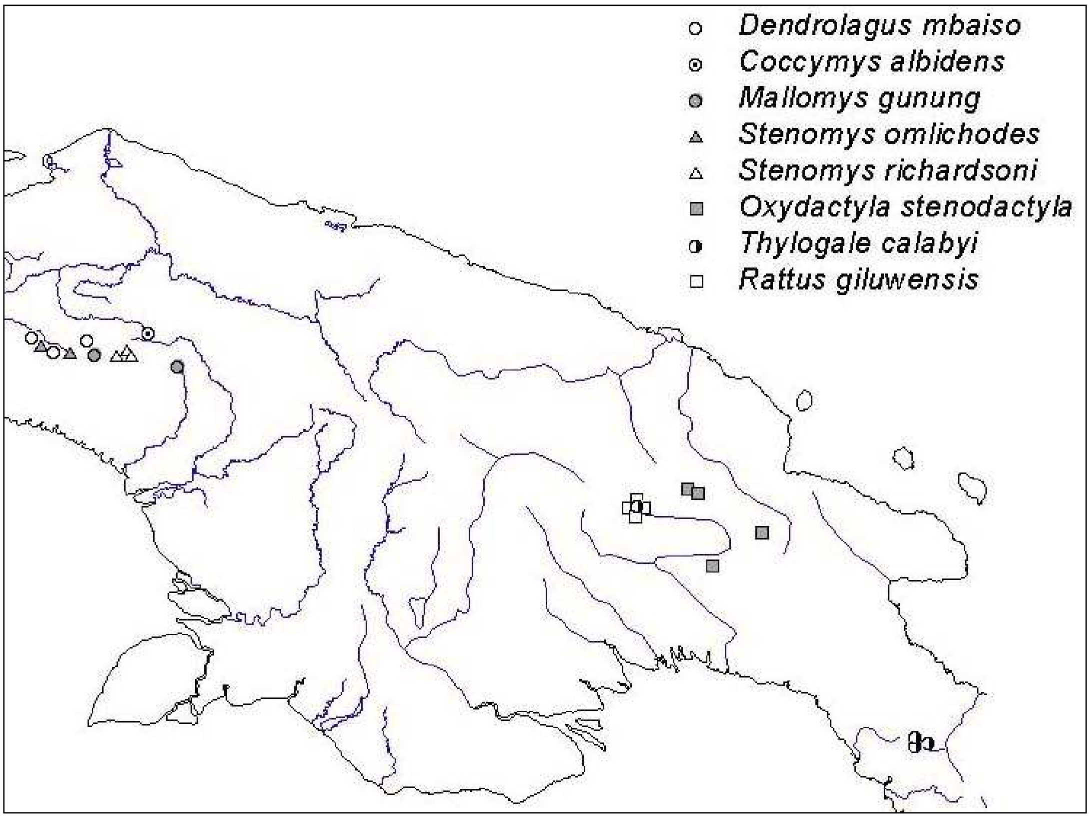


Figure 4.77 The recent distribution of subalpine and alpine zones in New Guinea with their faunal elements. The shared range of Thylogale calabyi on Mt. Giluwe in the Eastern Central Cordillera and Mt. Albert Edward in the Southeastern Central Cordillera indicates close affinity between the two divisions.

4.1.7 Lesser Sundas and Banda Arcs Endemic Centre

This endemic centre includes the western Lesser Sundas (excluding Bali Island) and the Banda Arcs as shown on Fig. 4.78 below.

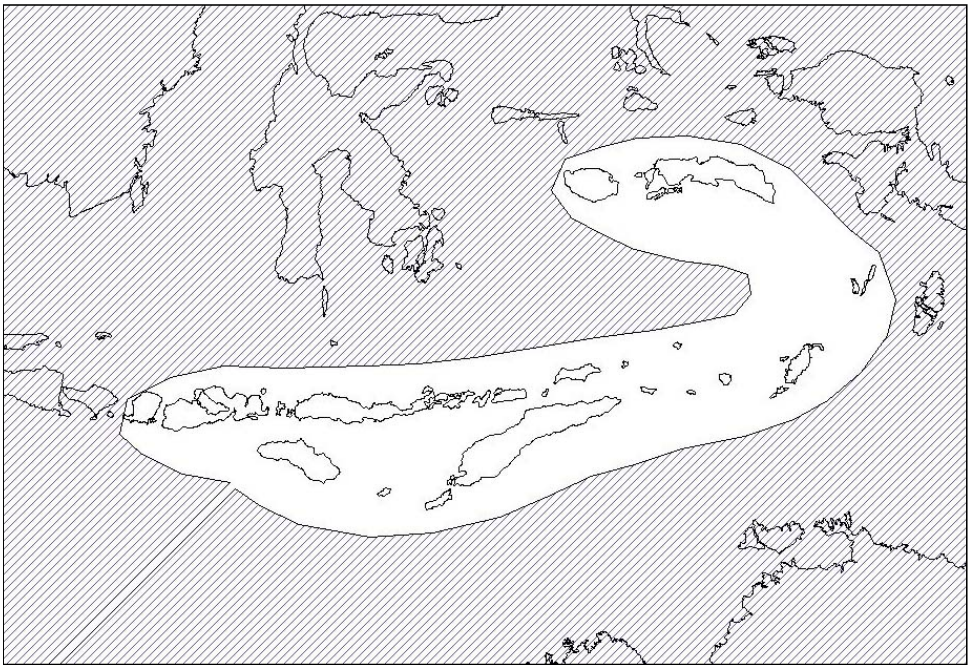


Figure 4.78 The Lesser Sundas and Banda Arcs Endemic Centre (unshaded)

4.1.7.1 Western Lesser Sunda Islands and the Inner Banda Arc

Endemism for all faunal groups in this region is considerably high. Amphibians reach the highest endemic levels with 40%; followed by birds (31.5%), mammals (27.3%) and reptiles (22.8%). These endemic forms are listed in Table 4.27.

While most amphibians and mammals could only disperse as far east as Flores Island, except for two amphibians, which are found on Wetar Island, reptiles and birds have been recorded on all the islands as far as the Banda Islands at the end of the Inner Banda Arc. This feature is simple to understand due to the readiness of both groups to disperse, namely birds through their flight capability and reptiles through their ability to passively disperse. However, the geographic positions of these islands, that are mostly separated from each other by deep marine barriers, are ideal for subspeciation in birds due to the tendency of the flightlessness and hence contributed much to its high endemism. On the other hand, such reduced dispersal ability, of course, does not apply to passive dispersers like reptiles.

Among islands, endemism seems to be only significant for a few islands. For amphibians and mammals, the only island, which supports endemic forms, is Flores Island.

Table 4.28 shows the comparison of the number of taxa and endemic taxa on different islands. The table is explained in full in the text.

Table 4.27 Endemic taxa of the Western Lesser Sundas and the Inner Banda Arc.

Family	Genera with number of endemic species (and endemic subspecies)
AMPHIBIAN	
Microhylidae - Genyophryninae	Oreophryne 2
Ranidae	Limnonectes 2, Occidozyga 1, Rana 1
REPTILES	
Gekkonidae	Cnemaspis 1, Cyrtodactylus 2, Gehyra 1, Lepidodactylus 2
Scincidae	Cryptoblepharus 3, Emoia 1, Sphenomorphus 1
Cylindrophiidae	Cylindrophis 1
Typhlopidae	Typhlops 1, Varanus 1
MAMMALS	
Soricidae	Suncus 1
Muridae – Murinae	Komodomys 1, Papagomys 2, Rattus 1, Spelaeomys 1
AVES	
Accipitridae	Accipiter (2), Spizaetus (1)
Alcedinidae	Caridonax 1
Apodidae	Aerodramus (1)
Campephagidae	Coracina (2), Pericrocotus 1(1)
Caprimulgidae	Caprimulgus (1)
Columbidae	Ducula (2), Ptilinopus (2), Treron 1
Corvidae	Corvus 1
Dicruridae	Dicrurus (2)
Estrildidae	Erythrura (1), Lonchura (1)
Meliphagidae	Lichmera 2, Myzomela 1(1)
Monarchidae	Monarcha 1(2)
Muscicapidae	Culicicapa (1), Cyornis (1), Rhinomyias (1)
Nectariniidae	Anthreptes (1), Cinnyris (1)
Oriolidae	Oriulus (1), Sphecotheres 1
Pachycephalidae	Pachycephala (5)
Paramythiidae	Dicaeum (6)
Picidae	Dendrocopos (1)
Psittacidae	Aprosmictus (1), Loriculus 1, Psitteuteles (1), Trichoglossus (3)
Rallidae	Gallirallus (1), Rallus (1)
Rhipiduridae	Rhipidura (3)
Strigidae	Ninox (1), Otus 2(2)
Sturnidae	Gracula (1)
Sylviidae	Phylloscopus (1), Tesia (2)
Turnicidae	Turnix (2)
Zosteropidae	Heleia 1, Lophozosterops (4), Zosterops (2)

Table 4.28 Taxa found on the Western Lesser Sunda Islands and the Inner Banda Arc

ISLANDS	**NO. OF TAXA & ENDEMIC TAXA**							
	Amphibians		**Reptiles**		**Mammals**		**Aves**	
Lombok	9	-	28	1	6	-	108	2
Sumbawa	7	-	25*	2	4	-	120	9
Flores	10	2	35	2	9	4	161	22
Lomblen	-	-	6	-	-	-	37	-
Pantar	-	-	1	-	-	-	18	-
Alor	-	-	9	-	-	-	62	2
Wetar	2	-	13	1	-	-	68	11
Romang	-	-	1	1	-	-	45	1
Damar	-	-	4	-	-	-	37	1
Teun	-	-	1	1	-	-	2	-
Nila	-	-	1	-	-	-	2	-
Banda Islands	-	-	6	-	1	-	14	2
All islands	**15**	**6**	**57**	**13**	**22**	**6**	**273**	**86**

Note:
* including the occurrence of *Dibamus taylori* on Sumbawa I.

4.1.7.1.2. Lombok Island

In contrast to Bali, Lombok Island has at least one non-volant endemic species, i.e. *Cnemaspis gordongekkoi* (Gekkonidae). Except *C. timoriensis* of Timor in the Outer Banda Arc far east from Lombok, the other relatives are confined to the Great Sunda Islands to the west. Other endemic taxa known from this island are two birds, i.e. *Pericrocotus flammeus exul* (Campephagidae) and *Dicaeum trochileum stresemanni* (Paramythiidae) whose relatives are also found on islands westwards. Thus the endemic forms, which can be found, are mostly the easternmost forms of the group mainly distributed on islands to the west. Closer affinities to islands lying westwards have also been indicated by mammals. Of 12 taxa, which can be certainly found, 5 of them share only with islands to the west, the other 6 taxa share both with islands to the west as well as to the east, while the last one taxon shares only with islands to the east.

Except in mammals, affinities suggested by other groups are slightly ordered to islands lying eastwards. For amphibians, of nine taxa recorded, two taxa, i.e. *Bufo biporcatus* (Bufonidae) and *Oreophryne monticola* (Microhylidae – Genyophryinae), share only with islands to the west, while three other taxa, i.e *Limnonectes dammermani*, *L. kadarsani* (Ranidae) and *Rana florensis* (Ranidae), share only with islands to the east. The other four taxa, i.e *Kaloula baleata baleata* (Microhylidae – Microhylinae); *Fejervarya cancrivora* and *F. limnocharis* (Ranidae) as well as *Polypedates leucomystax* (Rhacophoridae) occur both on islands to the west as well as to the east. Regarding reptiles, of the 28 taxa recorded, 12 taxa (42.9%) share with Bali to the west, 14 taxa (50%) share with Sumbawa to the east and the rest 2 taxa (7.1%) share with both Bali and Sumbawa. From108 birds recorded, 26 taxa

(24.1%) share with Bali to the west, 43 taxa (39.8%) share with Sumbawa to the east and the rest 39 taxa (36.1%) share with both Bali and Sumbawa.

The migration route from Sulawesi to the western Lesser Sundas, as has been indicated by *O. monticola* (Microhylidae – Genyophryninae) found on Bali Island, is also suggested by *Dibamus taylori* (Dibamidae). Currently it ranges probably throughout the Lesser Sundas, from Lombok eastwards via Sumba to Wetar Island. Its relatives are found on Sulawesi and the Great Sundas except Java. Such a range gives us a clue that Lombok Island was likely to have been the main "stepping stone" for fauna, which migrated, from Sulawesi.

4.1.7.1.3. Sumbawa Island

Sumbawa Island lies between Lombok Island to the west and Komodo Island of the Flores Group to the east. The shallow Alas Strait separates it from Lombok Island, while the deep Sape Strait separates it from Komodo Island. In regard to the deep marine barrier to the Flores Group, curiously its faunal elements show in general close affinities to those of this group. At least 72% of reptiles confined to share with the Flores group, while with Lombok to the west is only 64%. As regards, birds, about 99 taxa (82.5%) are also found on the Flores Group, while shared taxa with Lombok are only 82 taxa (68.3%).

Endemism on this island is relatively better represented than on Lombok Island. At least one reptile and 9 birds have been recorded to be endemic to this island. This corresponds to 7.7% and 11.8% of the total endemic taxa of each group.

4.1.7.1.4. The Flores Group

The Flores Group is comprised of the main Flores Island and several smaller islands lying within the 200m isobath. It includes the islands of Komodo, Padar and Rinca to the west as well as Solor, Adonara, Lomblen, Pantar and Alor to the east. The main Flores Island itself harbours the greatest number of taxa among others islands. There are at least 11 amphibians confined there, including the possibly introduced subspecies *Kaloula pulchra pulchra* (Microhylidae – Microhylinae); 35 reptiles of which 2 of them are endemic, 9 mammals with 4 endemic forms, and 161 birds with 22 endemic forms.

Although all islands within the group lie within the 200m line, most taxa are recorded to have their easternmost ranges on the Flores Island or for several taxa a few further extending to islands just east of Flores Island, like Solor or Adonara islands, or the farthest to the next Lomblen Island. Taxa with such distribution patterns are in common those derived from the Great Sunda Islands and the nearby islands to the west or those, which penetrated from the Sulawesian mainland to the north.

Among amphibians, even some of them failed to reach the eastern part of Flores Island, for example *Oreophryne jeffersoniana*, *O. rookmaakeri* (Microhylidae – Genyophryinae) and *Occidozyga floresianus* (Ranidae). The last two species are also known as endemic forms to Flores Island. Those that have their easternmost ranges on the Flores Island are for example *Kaloula baleata baleata* (Microhylidae – Microhylinae); *Fejevarya cancrivora*, *F. limnocharis*, *Limnonectes dammermani*, and *Rana florensis* (Ranidae). On the other hand, *Polypedates leucomystax* (Rhacophoridae) occurs on the Flores Island, but its range extends to Timor Island in the Outer Banda Arc. The occurrence of one subspecies, *Kaloula pulchra pulchra* (Microhylidae – Microhylinae), on Flores is reported by Iskandar (2000) as a result of introduction. The only amphibian known eastward from the Flores Island is *Limnonectes kadarsani* (Ranidae) from Adonara Island whose range to the west is well known as far as Lombok Island.

Also most of the mammals have their easternmost ranges on Flores Island. The only taxa recorded eastward from it, is *Cervus timorensis* (Cervidae), which has also been recorded from Adonara Island. The occurrence of numerous endemic mammals on Flores Island suggests the distinction of this island. These endemic forms are *Suncus mertensi* (Soricidae), *Papagomys armandvillei*, *P. theodorverhoeveni*, monotypic genus *Paulamys naso*, *Rattus hainwaldi*, and monotypic genus *Spelaeomys florensis* (Muridae – Murinae). Meanwhile, the only endemic form recorded outside Flores Island is the monotypic genus *Komodomys rintjanus* (Muridae – Murinae) from Rinca and Padar islands, but it is also known from subfossil material collected on Flores Island estimated to be 3,550 years old. Except *P. armandvillei* that is known both by living specimens and by subfossil fragments estimated to be 3,000-4,000 years old, most of the other endemic forms are certainly known from subfossil remains and hence mostly regarded as extinct. However, some scientists suspected that they may still live (Nowak, 1999).

Reptiles that are closely related to faunal elements to the west are for example *Draco volans boschmai* (Agamidae) and *Daboia russellii siamensis* (Viperidae). The only western form extending further east until Alor Island is *Naja sputatrix* (Elapidae), whose range recorded from Java to Alor, including Sulawesi. Those presumably derived from Sulawesian lineages are for example *Acrochordus granulatus* (Acrocordidae), *Python reticulatus reticulaus* (Boidae – Pytoninae); *Cerberus rynchops rynchops* (Colubridae); *Lamprolepis smaragdina smaragdina* (Scincidae); and *Ramphotyphlops braminus* (Typhlopidae).

An interesting phenomenon observed among reptiles is that those confined to islands in the eastern Flores group such as Alor and Pantar are normally also confined to Wetar Island to the east and to Timor Island to the south in the Outer Banda Arc. Even some of these taxa show close connections to New Guinea and northern Australia, or to islands far off eastern New Guinea. Since deep trenches separate most of these islands, only tectonic movements could be responsible for such distribution patterns. An exception shown by two eastern forms, *Cryptoblepharus leschenault* (Scincidae) and *Python timoriensis* (Boidae), that extends farther west beyond Alor Strait, lying between Lomblen and Pantar, as far as Flores. Taxa confined to the eastern Flores group with their distribution ranges are listed on Table 4.29.

Table 4.29 Examples of reptiles found on the Eastern Flores Group

Taxa	**Distribution**
Agamidae	
Draco volans timoriensis	**Alor**, Wetar, Timor, Semau, Roti.
Scincidae	
Cryptoblepharus leschenault	Flores, Besar, Ende, **Lomblen, Alor**, Wetar, Damar Islands, Timor, Semau, and Great Bastard Island
Lamprolepis smaragdina smaragdina	**Alor**, Wetar, Sumba, Savu, Timor, Roti; Halmahera and its nearby islands, New Guinea and its nearby islands, Buru, Seram and its nearby islands, Nusa Laut, Banda, Damar, Kai Islands, Tanimbar, Babar; Admiralty Islands, Marshall Islands, Solomon Islands.
Boidae	
Liasis mackloti mackloti	**Alor**, Wetar, Timor, Semau, Roti, New Guinea (Trans-Fly region); coastal N Australia.
Python timoriensis	Flores, **Lomblen**, Timor.
Colubridae	
Dendrelaphis inornatus timorensis	**Pantar, Alor**, Wetar, Timor, Semau, Roti.

Beside two distribution patterns, either confined to the western Flores group or the eastern one, several taxa show a combination of both. It means that they range until the western Flores group, then via Sumba and Timor islands of the Outer Banda Arc to the south, arrived on the eastern Flores group. Such taxa are listed on Table 4.30.

Table 4.30 Examples of reptiles found both on western and eastern Flores group

Taxa	**Distribution**
Dibamidae	
Dibamus taylori	Probably throughout the Lesser Sunda Islands from Lombok to Wetar.
Colubridae	
Elaphe subradiata subradiata	Lombok, Sumbawa, Komodo, Flores; Sumba, Roti, Semau, Timor, Alor, Wetar.
Lycodon capucinus	Sumatra, Java, Bali, Sumbawa, Komodo, Flores, Lomblen; Sumba, Sawu, Roti, Timor, Babar Islands, Alor, Wetar; Kalao, Salayar, Butung, Sulawesi. Also recorded from Maldives and Mascarenes to SE China, Philippines, and Australia.
Viperidae	
Trimeresurus albolabris insularis	Bali, Lombok, Sumbawa, Komodo, Padar, Rinca, Flores, Adonara; Sumba, Roti, Timor, Alor, Wetar, Romang.

In regard to the locomotive power of birds, it is not surprising that their ranges are only weakly affected by marine barriers. Thus their distribution is not limited by the Alor Strait, which affected reptile's distribution. Nevertheless, this does not mean that, such a barrier does not affect all birds. In fact, distribution patterns as occur among reptiles can be still found among several birds. The western forms whose ranges end on Flores Island or the islands of Adonara and Solor are about 53 taxa (37.3%).

The ranges of some birds have suggested the distinction of the eastern Flores group, for example, as listed in Table 4.31.

Table 4.31 Examples of birds restricted to the eastern Flores group and nearby islands to the east

Taxa	Distribution
Accipitridae	
Accipiter fasciatus hellmayri	Semau, Roti, Timor and **Alor**.
Apodidae	
Aerodramus esculenta perneglecta	Sawu, **Alor**, Wetar, Kisar, Romang, Damar and Tanimbar is.
Caprimulgidae	
Caprimulgus affinis timorensis	**Alor**, Roti, Timor, Kisar.
Monarchidae	
Myiagra ruficollis ruficollis	**Lomblen, Alor**, Sumba, Savu, Roti, Semau, Timor, Wetar, Romang, Damar and small islands in Flores Sea (Tanahjampea, Bonerate and Kalaotoa Islands)
Psittacidae	
Trichoglossus euteles	Timor and adjacent islands from **Lomblen** to Babar

4.1.7.1.5. Wetar Island

Wetar Island is an isolated island separated with Alor to the west and Romang to the east, as well as Timor to the south by deep trenches. In spite of this, it supports an array of taxa, including the non-volant forms. While mammals are absent from this island, at least two amphibians, *Fejevarya verruculosa* and *Rana elberti* (Ranidae), have been reported. The first taxon has also been reported from the New Guinea mainland, while the latter is also found on Timor Island.

Reptiles are represented by 13 taxa of which one of them is endemic to this island, i.e. *Cyrtodactylus wetariensis* (Gekkonidae). Close affinities to Timor and Alor are indicated by highly shared taxa (9). They are *Liasis mackloti* (Boidae); *Dendrelaphis inornatus timorensis*, *Elaphe subradiata subradiata*, *Lycodon capucinus* (Colubridae); *Trimeresurus albolabris insularis* (Viperidae); *Draco volans timoriensis* (Agamidae); *Dibamus taylori* (Dibamidae); *Cryptoblepharus leschenault*, and *Lamprolepis smaragdina smaragdina* (Scincidae). Only two taxa, i.e. *Cylindrophis boulengeri* (Cylindrophiidae) and *Cerberus rynchops rynchops* (Colubridae), are absent from Alor. In addition, *Varanus salvator* (Varanidae) is also not known from Alor and Timor.

There are about 68 birds recorded of which 11 of them (16.2%) are endemic forms. Three of these endemic forms are separated at species level, leading to the opinion of long isolation of this island. These endemic birds are *Ducula cineracea schistacea* (Columbidae), *Lichmera notabilis* and *Myzomela kuehni* (Meliphagidae), *Cyornis hyacinthinus kuehni* (Muscicapidae), *Cinnyris solaris exquisita* (Nectariniidae), *Oriolus melanotis finschi* and *Sphecotheres hypoleucus* (Oriolidae), *Aprosmictus jongquillaceus wetterensis* and *Psitteuteles iris wetterensis* (Psittacidae), *Rhipidura rufiventris pallidipes* (Rhipiduridae), *Otus magicus tempestatis* (Strigidae). Affinities suggested by birds are closely related to islands eastward of it, i.e. to Timor and Romang islands. The number of taxa shared with Timor is 51 taxa (75%) and with Romang are 30 taxa (44.12%).

4.1.7.1.6. The Eastern Inner Banda Arc

Eastward from Wetar Island, island size decreases. They are also totally isolated by deep trenches. These islands are Romang, Damar, Teun, Nila, Serua, Manuk and the Banda Islands. These islands are lacking amphibians and mammals. The only mammal recorded from the Banda Islands is *Cervus timorensis*, whose occurrence there is presumed to be as a result of ancient human introduction.

In contrast to this, reptiles are relatively well represented on these islands. There are about 12 taxa confined to these islands of which one of them, *Gehyra barea* (Gekkonidae) is endemic. Its close relative can be found mostly on the eastern Indonesian Archipelago. The only *Gehyra* found on the Great Sunda Islands to the west is *G. mutilata*, whose range is widespread from Madagascar to USA and Mexico and from Japan to Australia. At least three taxa share with the eastern Flores group, i.e. *Cryptoblepharus leschenault* and *Lamprolepis smaragdina smaragdina* (Scincidae); as well as *Ramphotyphlops braminus* (Typhlopidae). Regarding the broad and deep trenches between the Inner and Outer Banda arcs, surprisingly some reptiles share their ranges as shown by faunal elements listed in Table 4.32 and also in Table 4.29.

It seems likely that the Romang and Damar islands only recently emerged. This has been suggested by their relative high number of birds with 45 and 37 taxa respectively, but with only less endemic forms supported. Also Teun and Nila islands situated further east have perhaps only recently emerged, as they are inhabited by a relatively lesser amount of taxa.

Table 4.32 Reptiles found on the eastern Inner Banda Arc

Taxa	Distribution
Gekkonidae	
Lepidodactylus oortii	Damar, Tanimbar Is., Banda Is. Terra typica: Teun and Serua.
Scincidae	
Cryptoblepharus virgatus	Damar, Babar and Tanimbar Is., Southern New Guinea, Australia.
Sphenomorphus kuehnei	Kai Islands, Babar, Banda.
Boidae	
Candoia carinata carinata	New Guinea and nearby islands, Seram and nearby islands, Banda, Gorong, Tanimbar; Bismarck Archipelago.
Morelia amethistina	?S Philippine Islands; Halmahera, Bacan; New Guinea and nearby islands, Seram and nearby islands, Banda, Kai Is., Tanimbar Is., Aru Is.; Australia (NE Queensland), several Islands of Torres Strait; Umboi, Bismarck Archipelago.
Colubridae	
Oligodon forbesi	Damar, Babar Islands,. Tanimbar Islands.

4.1.7.2. The Outer Banda Arc

Endemicity on islands in this arc generally is much higher than those on the Western Lesser Sundas and the Inner Banda Arc, except surprisingly for amphibians. With 2 endemic species out of 9 species recorded, the endemism among amphibians only amounts to 22.2%. In contrast to this, the endemism in mammals, reptiles, and birds are obviously higher than those on the Western Lesser Sundas and the Inner Banda Arc with 45.5%, 30% and 53.1% respectively. The endemic taxa confined to islands in the Outer Banda Arc are listed in Table 4.33 below.

Table 4.33 Endemic taxa on the Outer Banda Arc. An asterisk marks the monotypic genera

Family	Genera with number of endemic species (and endemic subspecies)
AMPHIBIAN	
Hylidae – Pelodryadinae	Litoria 2
Ranidae	Limnonectes 1, Rana 1
REPTILES	
Agamidae	Calotes 1, Draco (2), Lophognathus 1
Boidae (Pythoninae)	Liasis (1), Morelia 1
Chelidae	Chelodina 1
Colubridae	Calamaria 1, Chrysopelea 1, Oligodon 1
Cylindrophiidae	Cylindrophis 1
Dibamidae	Dibamus 1
Gekkonidae	Cnemaspis 1, Lepidodactylus 1
Scincidae	Carlia 1, Cryptoblepharus 1(1), Glaphyromorphus 2, Tiliqua (2)
Typhlopidae	Typhlops 1
Varanidae	Varanus 2
MAMMALS	
Muridae – Murinae	Nesoromys* 1, Rattus 2
Muridae – Uromyini	Melomys 5
Peroryctidae	Rhynchomeles* 1
Soricidae	Crocidura 1
AVES	
Accipitridae	Accipiter (5), Aviceda (3)
Alaudidae	Mirafra (1)
Alcedinidae	Alcedo (1), Ceyx (2), Tanysiptera (3), Todirhamphus 1(1)
Apodidae	Aerodramus (2)
Artamidae	Artamus (1)
Bucerotidae	Aceros (1)
Cacatuidae	Cacatua 1
Campephagidae	Coracina 2(6), Lalage 1(1)
Columbidae	Ducula (2), Gymnophaps (2), Macropygia (3), Ptilinopus (1), Treron 1
Corvidae	Corvus (2)
Cuculidae	Centropus 1(1), Chrysococcyx (3), Eudynamis (1)
Dicruridae	Dicrurus (4)
Estrildidae	Erythrura (1), Lonchura (1), Padda 1
Megapodiidae	Megapodius 1(4)
Meliphagidae	Lichmera 3, Meliphaga 1, Myzomela 2(3), Philemon 3(2)
Monarchidae	Monarcha 4(5), Myiagra (5)
Motacillidae	Anthus (1)
Muscicapidae	Cyornis (1), Eumyias (1), Ficedula 1(7), Rhinomyias 1, Saxicola (3)
Nectariniidae	Cinnyris (3), Leptocoma (2)
Oriolidae	Oriolus 1(3), Sphecotheres (1)
Pachycephalidae	Pachycephala (11)

Table 4.33 (Cont.)

Family	Genera with number of endemic species (and endemic subspecies)
Paramythiidae	Dicaeum 1(5)
Petroicidae	Microeca 1
Pittidae	Pitta (3)
Podicipedidae	Tachybaptus (1)
Psittacidae	Alisterus (2), Aprosmictus (1), Eclectus (2), Eos 2(1), Geoffroyus (4), Lorius 1, Micropsitta (1), Prioniturus 1, Psitteuteles (2), Tanygnathus 1(3), Trichoglossus (1)
Pycnonotidae	Alophoixus (3)
Rhipiduridae	Rhipidura 4(8)
Strigidae	Ninox (7), Otus (2)
Sturnidae	Aplonis 1, Basilornis 1
Sylviidae	Bradypterus (3), Buettikoforella 1, Cettia 1, Megalurus (2), Phylloscopus (4), Urosphena (1)
Turdidae	Zoothera 2(3)
Turnicidae	Turnix (1)
Tytonidae	Tyto (2)
Zosteropidae	Heleia 1, Lophozosterops 1, Madanga 1, Tephrozosterops 1, Zosterops 4(2)

In contrast to the endemic pattern in the Western Lesser Sundas and the Inner Banda Arc, endemic forms of the non-volant group on this arc are distributed on several islands. Table 4.34 below shows the comparison of the number of taxa and endemic taxa on islands in the Outer Banda Arc.

Table 4.34 Taxa found on the Outer Banda Arc (excluding Sumba)

ISLANDS	NO. OF TAXA & ENDEMIC TAXA							
	Amphibians		Reptiles		Mammals		Aves	
Sawu Is.	1	-	4	1	-	-	34	2
Roti	-	-	11	2	-	-	64	2
Semau	-	-	7[b]	-	-	-	35	1
Timor	3	1	30	4	8	2	148	19
Kisar	-	-	-	-	-	-	28	-
Leti Is.	-	-	-	-	1	-	41	1
Sermata	-	-	2	-	-	-	28	-
Babar Is.	1[a]	-	6	-	-	-	49	6
Tanimbar Is.	2[a]	1	15	4	1	1	87	27
Kai Is.[f]	-	-	20	1	9	1	87	22
Watubela Is.	-	-	-	-	1	-	28	1
Nusa Laut Is.	-	-	5	-	-	-	42	1
Ceram group	5	-	34[c]	6	12	6	133	45
Buru	-	-	7	1	3	-	114	40
All Islands	**9**[a]	**2**	**83**[d]	**25**	**22**[e]	**10**	**420**	**223**

Note:
[a] = including the occurrence of Rana elberti (Ranidae) on Babar and Tanimbar islands.
[b] = including the occurrence of Stegonotus florensis (Colubridae) on Semau I.
[c] = including the occurrence of Boiga drapiezii (Colubridae) on Ambon I.
[d] = involves [b] and [c]
[e] = excluding Cervus timorensis (Cervidae)
[f] = including Tayandu Is. to the west

4.1.7.2.1. Sawu Islands

The westernmost island in this arc, Sawu Island, lies between Sumba to the west and Timor to the east. It includes the islands of Sawu and Raijua to the southwest. Its faunal elements are relatively poor in non-volant groups, with one amphibian, four reptiles of which one of them is an endemic form, and no mammals. Volant birds reach the highest number of taxa with 34 taxa of which two of them are endemic forms.

The only amphibian recorded from this island is *Litoria everetti* of *L. peronii* group (Hylidae – Pelodryadinae) whose range is shared with Sumba and Timor. Its close relatives are found to the east on islands from Ceram, Ambon and Kei Island eastwards to New Guinea and Australia.

Of the four reptiles found, most of them seem to have penetrated via the Inner Banda Arc. This has been shown by three taxa, i.e. *Lamprolepis smaragdina smaragdina* (Scincidae), and *Lycodon capucinus* as well as *Dendrelaphis inornatus inornatus* (Colubridae). The only reptile, which definitely arrived on Sawu Island via the eastern Outer Banda Arc, is the endemic *Liasis mackloti savuensis* (Boidae – Pythoninae). Its close relative, subspecies *L. m. mackloti*, is confined to islands to the east, i.e. to Roti, Semau, Timor of the Outer Banda Arc; Alor and Wetar of the Inner Banda Arc; South New Guinea and coastal North Australia as well as Samoa in the east.

There are about 34 birds recorded from Sawu Island of which two of them are endemic forms, i.e. *Accipiter fasciatus savu* (Accipitridae) and *Turnix maculosa savuensis* (Turnicidae). The close relatives of the first taxon are found from islands on the Flores Sea and Lombok Island to Solomon Island, while the latter from Sulawesi and Sumbawa to the Louisiade Archipelago. The other taxa are mostly restricted to the Wallacean region, from Sulawesi and Lombok in the west to the northern Moluccas and the Outer Banda Arc in the east. At least 18 taxa (52.9%) are restricted to this region. These taxa are listed below:

Gerygone inornata (Acanthizidae)
Aerodramus esculenta perneglecta (Apodidae)
Caprimulgus affinis kasuidori (Caprimulgidae)
Centropus bengalensis sarasinorum (Cuculidae)
Lonchura punctulata blasii (Estrildidae)
Hirundo tahitica javanica (Hirundinae)
Myiagra ruficollis ruficollis (Monarchidae)
Saxicola caprata pyrrhonota (Muscicapidae)
Coturnix ypsilophora pallidior (Phasianidae)
Mirafra javanica timorensis (Alaudidae)
Aerodramus fuciphagus micans (Apodidae)
Ptilinopus regina flavicollis (Columbidae)
Lonchura pallida pallida (Estrildidae)
Taeniopygia guttata (Estrildidae)
Philemon buceroides buceroides (Meliphagidae)
Anthus rufulus medius (Motacillidae)
Dicaeum maugei maugei (Paramythiidae)
Zosterops citrinellus citrinellus (Zosteropidae)

4.1.7.2.2. The Timor Group

The Timor Group includes Timor Island and the nearby Semau and Roti islands to the southwest. Within this group, the non-volant amphibians and mammals occur only on Timor Island, while reptiles and aves have been recorded from all islands.

The three amphibians recorded from Timor Island are *Litoria everetti* of *L. peronii* group (Hylidae – Pelodryadinae), an endemic *Limnonectes timorensis* and *Rana elberti* (Ranidae). The two non-endemic taxa share their ranges with other islands, i.e. *L. everetti* with Sawu and Sumba to the west and *R. elberti* with Wetar Island of the Inner Banda Arc to the north (see the accounts thereof).

Most mammals confined to Timor Island are of oriental lineages whose occurrence there is often presumed as a result of human introduction, for example *Paradoxurus hermaphroditus* (Viverridae); *Crocidura maxi*, *Suncus murinus* (Soricidae); *Macaca fascicularis* (Cercopithecidae); and *Rattus argentiventer* (Muridae – Murinae). However, the occurrence of endemic forms, *Crocidura tenuis* (Soricidae) and *Rattus timorensis* (Muridae – Murinae), suggests that their arrival on Timor Island might have been natural. The last taxon, *Phalanger orientalis orientalis* (Phalangeridae), is an Australian lineage whose wide ranges are also considered mostly to be as a result of human introduction. Its range includes Leti Island, Kai Island, Gorong, Seram, Ambon, Saparua, Buru, Sanana, Northern New Guinea, Karkar Island, Schouten Island, Japen, Su Mios, Waigeo, Batanta, Salawati, and Misool. It occurs also on the Banda Island of the Inner Banda Arc.

Of reptiles, about 30 taxa are confined to Timor Island of which 8 and 5 of them are also found on Roti and Semau islands respectively. Roti itself harbours three taxa, which are not confined to Timor, i.e. *Chelodina novaeguinea* and the endemic *C. mccordi* (Chelidae) as well as the endemic *Varanus auffenbergi* (Varanidae). The first taxon, *C. novaeguineae* (Chelidae), has also been recorded from the Trans-Fly region in South New Guinea and from North Australia. On the other hand, Semau Island is home to *Stegonotus modestus* and possibly *S. florensis* (Colubridae). The *Stegonotus* has a range from Philippines eastwards to the Bismarck Archipelago and North Australia. The only records known beyond this range are *S. borneensis* from Sarawak, Borneo and *S. florensis* from Flores Island in the Inner Banda Arc. This *S. florensis* has been known with certainty from the Flores Island, but records on Sumba and possibly Semau have been mentioned by some scientists. In regard to a relative continuous range of *S. modestus* along the eastern Outer Banda Arc, from Kai Island to Buru Island, its absence on the intervening Tanimbar and Timor islands is enigmatic.

This taxon has also been recorded from Halmahera and the nearby Ternate Island, Salawati, New Guinea and Aru Island.

While endemism in amphibians and mammals are quite high with 33.3% and 25% respectively, that among reptiles is much lower with only 4 endemic forms (13.3%). They are *Cnemaspis timoriensis* (Gekkonidae), *Cryptoblepharus boutonii schlegelianus*, *Glaphyromorphus antoniorum* and *G. timorensis* (Scincidae). The relatives of *C. timoriensis* in the Indonesian Archipelago occur on islands to the west, i.e. on Lombok, Sumatra and Borneo. In contrast to this, those of the next two genera are mostly found on islands to the east. The range of genus *Glaphyromorphus* is centred on Australia and extends to Southern New Guinea, Timor and Sumba. On the other hand, members of genus *Cryptoblepharus* do extend to the Lesser Sundas as far as Bali Island, or possibly as far as East Java, Karimun Jawa Island, and Kangean Island where populations on the last three places are mostly considered as human introduction. However, the other members found on the Indonesian Archipelago are all confined to islands in the east, extending westernmost as far as Gag and Gebe islands in the north, and Buru Island in the Outer Banda Arc.

Beyond the endemic forms, reptiles of Timor Island show close affinities mainly to those on Flores Islands in the Inner Banda Arc with 13 shared taxa and then to Wetar Island, still in the Inner Banda Arc as well as the New Guinea mainland each with 11 shared taxa. In addition, about ten taxa are restricted to the Wallacean region. They are *Draco lineatus beccarii*, *D. volans timoriensis* (Agamidae); *Python timoriensis* (Boidae – Pythoninae); *Dendrelaphis inornatus timoriensis*, *Elaphe subradiata subradiata* (Colubridae); *Cylindrophis boulengeri* (Cylindrophiidae); *Dibamus taylori* (Dibamidae); *Carlia schlegelii*, *Cryptoblepharus boutonii*, and *C. leschenault* (Scincidae). One taxon, *Trimeresurus albolabris insularis* (Viperidae) is also occurs on Bali Island. Except *D. l. beccarii* and *C. schlegelii*, all taxa above share with islands on the Inner Banda Arc. *D. l. beccarii* itself shares with Sula Islands and southern Sulawesi and *C. schlegelii* with Ambon Island.

Timor Island has the highest number of birds compared to other islands on the Outer Banda Arc with 148 taxa of which 19 of them (12.8%) are endemic forms. Furthermore, of these 19 endemic forms, 6 of them are separated at species level, indicating a long isolation of this island. The nineteen endemic forms are *Ducula cineracea cineracea* (Columbidae); *Centropus phasianus mui*, *Chrysococcyx minutillus ssp*. (Cuculidae); *Lichmera flavicans*, *Myzomela vulnerata*, *Philemon inornatus* (Meliphagidae); *Ficedula hyperythra clarae*, *Ficedula timorensis* (Muscicapidae); *Dicaeum sanguinolentum hanieli* (Paramythiidae); *Tachybaptus novaehollandiae timorensis* (Podicipedidae); *Psitteuteles iris iris*, *Psitteuteles* *iris rubripileum*, *Trichoglossus haematodus capistratus* (Psittacidae); *Ninox boobook fusca* (Strigidae); *Bradypterus seebohmi timoriensis*, *Buettikoforella bivittata*, *Megalurus timoriensis timoriensis*, *Phylloscopus presbytes presbytes* (Sylviidae); and *Heleia muelleri* (Zosteropidae).. Additionally, the distinction of western and eastern parts of the island has been suggested by *P. i. iris* (W Timor) and *P. i. rubripileum* (E Timor) as well as *H. muelleri* (W Timor).

4.1.7.2.3. Kisar, Leti and Sermata islands

Islands lying eastward from Timor Island, i.e. Kisar, Leti Island, and Sermata, are in general poor in faunal elements. Except for one mammal, *Phalanger orientalis orientalis* (Phalangeridae), that occurs on Leti Island and also on Timor Island (see account thereof), other faunal elements confined to these islands are only birds. Kisar and Sermata islands have each 28 birds without endemic forms, while Leti Island is home to 41 birds of which one of them is an endemic form, i.e. *Pachycephala pectoralis compar* (Pachycephalidae). Its close relatives occur from eastern Java in the west to Fiji Islands in the east, and from the Northern Moluccas in the north to Tasmania in the south.

Close connections suggested by shared ranges of birds are all ordered to Timor Island with 22 taxa for Kisar Island, 25 taxa for Leti Island, and 23 taxa for Sermata Island. In addition, birds of Kisar are also closely related to those of Alor and Wetar on the Inner Banda Arc with 17 shared taxa to each island; birds of Leti Island to those of Wetar and Romang on the Inner Banda Arc with 20 and 23 shared taxa respectively; and finally birds of Sermata to those of Leti Island with 19 shared taxa.

4.1.7.2.3. Babar Islands

After an extreme lack of fauna on islands eastward of Timor Island, they are starting to recover on Babar Island in the west of Tanimbar Island. Reptiles and possibly amphibians have been recorded again and there is an increasing number of, either in number of taxa or endemic form. The possible amphibian confined to these islands is *Rana elberti* (Ranidae). Its occurrence has been definitely recorded from Timor and Wetar islands, but it is also possible that it occurs on Babar and Tanimbar Islands as mentioned by some authors.

About 8 reptiles are recorded on Babar Island. A possible migration through island drifts is strongly suggested by their ranges because they are mostly shared with islands separated by deep marine barriers. Some of them are shared with islands on the eastern Inner Banda Arc or islands on the Outer Banda Arc westward of this island so that their accounts can be seen thereof. They are for example *Oligodon forbesi* (Colubridae); *Cylindrophis boulengeri* (Cylindrophiidae); *Cryptoblepharus virgatus*, *Lamprolepis smaragdina smaragdina*, *Sphenomorphus kuehnei* (Scincidae); and *Lycodon capucinus* (Colubridae). The only taxa shared just with islands to the east are *Tiliqua scincoides chimaerea* (Scincidae) and *Dendrelaphis calligastra* (Colubridae). The first taxon shares with Tanimbar Island and the latter with Tanimbar, Kai, possibly Ambon, and Aru Islands and further east including New Guinea and nearby islands, islands of Torres Strait, and Eastern Cape York Peninsula.

Of 49 birds recorded from Babar Islands, 6 of them (12.25%) are endemic forms. They are *Chrysococcyx minutillus salvadorii* (Cuculidae); *Ficedula hyperythra audacis*, *Saxicola caprata cognata* (Muscicapidae); *Pachycephala pectoralis sharpei* (Pachycephalidae); *Ninox boobook cinnamomina* (Strigidae); and *Urosphena subulata advena* (Sylviidae). All are separated at subspecies level, which suggests only recent separation. Close connections showed by birds are in general to Tanimbar Island with 30 shared taxa and to Timor Island with 25 shared taxa.

4.1.7.2.4. Tanimbar Island

Fauna from all groups can be found again finally on Tanimbar Islands to the east of Babar Island. There are two amphibians of which one of them is an endemic form, fifteen reptiles with four endemic forms, an endemic mammal, and 87 birds with 27 endemic forms. The two amphibians recorded include the occurrence of *Rana elberti* (Ranidae) that, as already mentioned elsewhere above, has been definitely found on Sumba, Timor and Wetar Islands but it possibly also lives on the Babar and Tanimbar islands. The other amphibian found there is endemic *Litoria capitula* of *L. rubella* group (Hylidae – Pelodryadinae) whose relatives are found on the New Guinean mainland and on the nearby Yapen and Aru Islands as well as on Australia.

The only endemic mammal recorded on Tanimbar Island is *Melomys cooperae* (Muridae – Uromyini). This tribe is centered on New Guinea and its nearby islands and also occurs on Talaud Island off Northeast Sulawesi, North Moluccas, the Eastern Outer Banda Arc, New Britain, and possibly Australia.

Of fifteen reptiles recorded from Tanimbar Island, the four endemic forms are *Lophognathus maculilabris* (Agamidae); *Morelia nauta* (Boidae – Pythoninae); *Oligodon unicolor* (Colubridae); and *Cylindrophis yamdena* (Cylindrophiidae). Separation at species level of all taxa from their relatives, suggest a long enough isolation on this islands. However in general close affinities with each 5 shared taxa are ordered to Babar Island to the west, Ceram group to the north, New Guinea mainland to the east and also to Banda Islands in the Inner Banda Arc. Close affinities are also showed to Damar Island in the Inner Banda Arc.

Endemism among birds for Tanimbar Island is quite high with 27 endemic forms (31%). Rather different with reptiles, the closest affinity shown by birds is ordered to Kai Island to the north with 31 shared taxa, then to Babar and Timor islands to the west each with 30 shared taxa.

4.1.7.2.5. Kai and Tayandu islands

The much smaller Kai and Tayandu islands to the north of Tanimbar Island surprisingly have more reptiles, mammals and at least the same number of birds but fewer endemic forms rather than Tanimbar Islands. Regarding the occurrence of numerous mammals on these islands, the absence of amphibians there is enigmatic. Of the twenty reptiles recorded, only one endemic form is known, i.e. *Draco lineatus ochropterus* (Agamidae) whose relatives are found on Malaysia and are relatively widespread in Indonesia and Philippines. Close connections suggested by reptiles are ordered to the New Guinean mainland with 13 shared taxa and to Seram group with 10 shared taxa.

Kai Island is the most oceanic island that supports a high number of mammals, even one taxon more than the much bigger Timor Island. Similar to reptiles, only one endemic form of this group is recorded from these islands, i.e. *Melomys bannisteri* (Muridae – Uromyini) of which one of its relatives occurs on Tanimbar Island (see account thereof). The other eight mammals recorded on these islands are *Thylogale brunii* (Macropodidae); *Echymipera rufescens rufescens* (Peroryctidae); *Petaurus breviceps papuanus* (Petauridae); *Phalanger orientalis orientalis*, *Spilocuscus maculatus chrysorrhous* (Phalangeridae); *Uromys caudimaculatus multiplicatus* (Muridae – Uromyini); *Suncus murinus* (Soricidae); and *Paradoxurus hermaphroditus* (Viverridae). The first five taxa are of Australian lineage whose ranges are centered on the New Guinean mainland. Their relatives are well represented there and also on the nearby islands. On the other hand, *U. c. multiplicatus* is oriental lineage whose ranges is also centered on the New Guinean mainland. Its relatives occur on the New Guinean mainland and the nearby islands and extend to Northeast Queensland. The last two taxa are also oriental lineages whose ranges extend widely to islands in the East Indies. In regard to the isolated position of Kai Islands by deep trenches, the occurrence of non-volant mammals there is mostly considered as a result of human introduction.

The number of birds on Kai Island is similar to that of Tanimbar Island with 87 taxa, but Kai Island supports fewer endemic forms with 22 taxa. Similar to mammals and reptiles, close connections suggested by birds are ordered to New Guinea with 41 shared taxa and Seram group with 39 shared taxa.

4.1.7.2.6. Watubela Islands and Gorong Islands

Northward of Kai Island, Watubela and Gorong islands experience the lack of fauna again although not so poor as on islands eastward of Timor. At least one mammal, *Spilocuscus maculatus chrysorrhous* (Phalangeridae), occurs on Tioor Island of Watubela Islands and five reptiles on Seram Laut Islands. They are *Candoia carinata carinata* (Boidae); *Brachyorrhos albus*, *Cerberus rynchops rynchops*, *Stegonotus modestus* (Colubridae); and *Lamprolepis smaragdina smaragdina* (Scincidae). All occur also on the Seram group to the north and on the New Guinean mainland to the east.

Watubela Islands and Gorong Islands support each an endemic bird, i.e. *Rhipidura rufiventris perneglecta* (Rhipiduridae) and *Geoffroyus geoffroyi explorator* (Psittacidae) respectively. Relatives of the first taxon occur from the eastern Inner and Outer Banda Arc, northern Moluccas, eastwards to Admiralty Islands and Bismarck Archiepelago as well as northern Australia, while the latter from Lombok Island in the western Lesser Sundas and northern Moluccas to Louisiade Archipelago off Southeast New Guinea and North Queensland. (hubungan yang lain).

4.1.7.2.7. The Seram Group

The Seram Group supports the highest number of taxa for all faunal groups among islands in the Outer Banda Arc, except birds whose number is surpassed by Timor Island. This island group is comprised of the main Seram Island and the nearby Boano, Kelang, Maniapa, Ambon, Haruku and Saparua. There are five amphibians, 35 reptiles with 6 endemic forms, 12 mammals with only 6 endemic forms, and finally 133 birds with 45 endemic forms. Reptiles includes the probable occurrence of *Boiga drapiezii* (Colubridae) and *Dendrelaphis calligastra* (Colubridae) on Ambon Island dan also *Emoia reimschisseli* (Scincidae).

While endemism in each group is considerably high with 17.1% for reptiles, 50% for mammals, and 33.8% for birds, there are surprisingly not any endemic forms of amphibians recorded. An asterophryne microhylid, *Callulops fuscus*, shares with Batanta Island off Northwest New Guinea. The other four taxa are ranids whose ranges share with islands separated from each other by deep trenches. *Limnonectes grunniens* has been recorded in this region from Seram, Ambon, Haruku and Saparua, but it also occurs on Sulawesi, Bacan, New Guinea, and possibly Java. Its relative, *L. modestus*, has a few restricted ranges, including only Sulawesi, Moluccas and Seram. *Rana sanguinea* occurs from Palawan Island on the Philippines, via Sulawesi to the Moluccas and Seram. Eastward of this, it is replaced by R. grisea that is found on New Guinea and Seram. Mammals confined to the Seram group are *Paradoxurus hermaphroditus* (Viverridae); *Crocidura maxi*, *Suncus murinus* (Soricidae); *Phalanger orientalis orientalis*, *Spilocuscus maculatus chrysorrhous* (Phalangeridae); *Rattus nitidus* (Muridae – Murinae); the endemic forms *Rattus feliceus* (Muridae – Murinae), *Melomys aerosus*, *M. fraterculus* and *M. fulgens* (Muridae – Uromyini) and two monotypic genera forms, i.e *Rhynchomeles prattorum* (Peroryctidae) and *Nesoromys ceramicus* (Muridae – Murinae).

Of reptiles, the six endemic forms recorded are *Calotes nigriplicatus* (Agamidae); *Morelia clastolepis* (Boidae – Pythoninae); *Calamaria ceramensis*, *Chrysopelea rhodopleuron* (Colubridae); *Dibamus seramensis* (Dibamidae); and *Varanus cerambonensis* (Varanidae). With an absence on large intervening areas, curiously relatives of *C. nigriplicatus* can be found on Sabah in Borneo and Sumatra. Along with the endemic *Morelia nauta* of Tanimbar Island and the endemic *M. trachyae* of Halmahera Island, *M. clastolepis* of Seram group is considered to be closely related to *M. amethistina* whose ranges are broadly recorded from the northern Moluccas, eastwards to the Bismarck Archipelago and southwards to Northeast Queensland. This includes the eastern Outer Banda Arc from the Seram group in the north, southwards to Tanimbar Island and also to Banda Island of the Inner Banda Arc in the south of the Seram group. In addition, *M. amethistina* occurs also possibly on the South Philippines Islands. Other than the endemic forms, the closest connections suggested by reptiles on the New Guinean mainland with 15 shared taxa if the occurrence of *Draco lineatus amboinensis* on Misool Island off western New Guinea is considered.

Although the number of birds in the Seram Group, are surpassed by those on Timor Island, the second highest number of endemic taxa is found in this island group with 45 endemic taxa (33.8%). The closest affinity suggested is on Buru Island to the west with 66-shared taxa. Close affinities are also suggested on the Northern Moluccas with 48-shared taxa and to New Guinea with 44-shared taxa.

4.1.7.2.8. Buru Island

Buru Island is the westernmost island of the Outer Banda Arc in the north. The birds of Buru Island have the highest endemicity among islands within the Outer Banda Arc with 35.1% . In contrast, non-volant forms are only poorly represented here. There are no amphibians and this island supports only three mammals whose occurrence have also been recorded from the Seram group to the east, i.e. *Phalanger orientalis orientalis* and *Spilocuscus maculatus chrysorrhous* (Phalangeridae) as well as *Suncus murinus* (Soricidae). Even reptiles, which have been richly recorded from the neighbouring Seram group, are only represented by 8 taxa here, if the occurrence of *Tropidonophis elongatus* (Colubridae) is included. *Draco lineatus bourouniensis* (Agamidae) is the only endemic form confined to this island whose relatives are found on the Philippines, Sulawesi, westwards via Java to Enggano Island off Southwest Sumatra; eastwards via Sula Islands off East Sulawesi to the Outer Banda Arc as far as Timor. It occurs also on Misool Island off Northwest New Guinea and perhaps Borneo. About three non-endemic reptiles, which are found, are the widespread forms, i.e. *Python reticulatus reticulatus* (Boidae – Pythoninae), *Cerberus rynchops rynchops* (Colubridae) and *Ramphotyphlops braminus* (Typhlopidae), while the other three taxa are those whose ranges are restricted to the eastern Indonesian Archipelago. They are *Stegonotus modestus* (Colubridae), *Crytoblepharus keiensis* and *Pseudemoia baudnii* (Scincidae). All share with Seram group to the west.

4.1.7.3. Sumba Island

Sumba Island lies westward from Sawu Island and it is excluded from the Banda Arc. However, the distinction of this island has been indicated by high endemism among reptiles (18.75%) and among birds (25.7%). Its faunal elements, especially reptiles and birds, are more closely related to those on islands to the north rather than to Sawu Island and Timor Island to the east. This is not surprising in regard to the passive dispersal ability of reptiles and the locomotive power of birds because the distance to the islands in the north is less than to those in the east. On the other hand, connections showed by amphibians are found to be with islands to the east. The only two amphibians recorded from this island, *Litoria everetti* (Hylidae) and *Rana elberti* (Ranidae), share their ranges with Sawu and Timor for *L. everetti* and with Timor, Wetar of the Inner Banda Arc, and perhaps Babar and Tanimbar far eastward for *R. elberti*.

Mammals confined to this island are mostly of oriental lineages whose occurrence here are often considered as the result of human introduction, such as *Paradoxurus hermaphroditus* (Viverridae); *Crocidura maxi* and *Suncus murinus* (Soricidae); possibly *Macaca fascicularis* (Trachypithecidae); and *Rattus argentiventer* (Muridae – Murinae).

Regarding reptiles, from 16 taxa recorded, 13 of them (81.2%), are also confined to the western Lesser Sunda Islands to the north. One taxon, *Stegonotus florensis* (Colubridae), is certainly confined to the Flores Island, but its occurrence on this island and possibly on Semau off Southwest Timor Island has been mentioned by some authors. The three taxa missing on the western Lesser Sunda Islands are endemic forms to Sumba Island, all members of Scincidae, i.e. *Emoia kitcheneri*, *Glaphyromorphus butlerorum* and *G. emigrans*. A relative of *E. kitcheneri* is still found on islands to the north, i.e. *E. similis* from Komodo, Padar, Rinca and Flores, but the two latter taxa are absent at all there.

Emoia is the genus whose ranges encompass areas from the Philippines and East Indonesia (including Sulawesi and the western Inner Banda Arc) to tropical pacific islands. The only members, which extend beyond these areas, are *E. laobaoense* of Vietnam and *E. atrocostata atrocostata*. This *E. a. atrocostata* has a wide distribution; being recorded from Ryukyu Archipelago of Japan, South Taiwan, Philippines (Palawan, Calamian Island, Panay etc.); westwards to Indo-Malayan Archipelago (Borneo, Java, Sumatra), West Malaysia (Pulau Pinang, Johor, Negeri Sembilan, Pulau Tioman) and Christmas Island off southern Java; eastwards to Palau Islands, New Guinea and islands of Torres Strait, Bismarck Archipelago, and Micronesia. Its close relatives are found on Cape York Peninsula (*E. a. australis*) and on Solomon Island as well as on Vanuatu (*E. a. freycineti*).

The other genus, *Glaphyromorphus*, is centred on Australia. Besides two endemic forms on Sumba Island as mentioned above, the other endemic forms known outside Australia are *G. antoniorum* and *G. timorensis* from Timor Island. With the absence on intervening areas, the next records come from South New Guinea, i.e. *G. nigricaudis* and *G. pardalis*. These two taxa share their ranges with North Australia and thus suggest early migration from that continent in the last Pleistocene Glacial Maxima.

Birds confined to this island are rich in number with 105 taxa recorded of which 28 of them (26.7%) are endemic forms as listed in Table 4.35. Long isolation on this island suggested by birds is showed by a high number of taxa separated at species level, namely with 9 taxa (32.14%) endemic forms. Beyond the endemic scope, close connections are ordered to Flores Island on the Inner Banda Arc with 58 shared taxa and to Timor Island on the Outer Banda Arc with 57 shared taxa of which 43 taxa are intersected.

Table 4.35 Endemic birds of Sumba Island

Family	Endemic Taxa
Accipitridae	*Accipiter fasciatus tjendanae*
Bucerotidae	*Aceros everetti*
Cacatuidae	*Cacatua sulphurea citrinocristata*
Campephagidae	*Coracina personata sumbensis*
Columbidae	*Ptilinopus dohertyi*
	Treron teysmannii
Dicruridae	*Dicrurus densus sumbae*
Estrildidae	*Lonchura punctulata sumbae*
Meliphagidae	*Myzomela dammermani*
Monarchidae	*Terpsiphone paradisi sumbaensis*
Muscicapidae	*Culicicapa ceylonensis connectens*
	Ficedula harterti
	Muscicapa segregata
	Rhinomyias oscillans stresemanni
	Saxicola caprata francki
Nectariniidae	*Anthreptes malacensis rubrigena*
	Cinnyris buettikoferi
Pachycephalidae	*Pachycephala pectoralis fulviventris*
Paramythiidae	*Dicaeum sanguinolentum wilhelminae*
Psittacidae	*Eclectus roratus cornelia**
	Tanygnathus megalorychos sumbensis
	Trichoglossus haematodus fortis
Rhipiduridae	*Rhipidura rufifrons sumbensis*
Strigidae	*Ninox rudolfi*
Sylviidae	*Megalurus timoriensis inquirendus*
Turnicidae	*Turnix everetti*
	Turnix maculosa sumbana
Tytonidae	*Tyto alba sumbaensis*

4.2 The affinities of the Indonesian Endemic Centres

For the reason of phylogenetic concern, Müller (1973, 1980) mainly used the polytypic and polycentric species in order to find out the affinity between two or more dispersal centres in the neo-tropical realm. The affinity depends on the phylogeny of the faunal elements ascribed to them. Further, he suggested that the supraspecific units, i.e. the ranges of genera or families should not be considered because such groups are often phylogenetically very old and the individual taxa within them had time to adapt to very different biotopes.

His dispersal centres could be more or less compared to the endemic centre that I use in this work and therefore I follow his work and use the subspecific forms to find out the affinities between the endemic centres in the Indonesian region. Below is eleven different examples used for this purpose.

1. *Kaloula baleata* (Microhylidae – Microhylinae) – the flowerpot toad or brown bullfrog – usually burrowing under ground. Its natural habitat includes primary and secondary forest as well as secondary clearings. Three sub-species are known, i.e. *K. b. baleata* (Southern Thailand, Malaysia, Sumatra, Borneo, Java, Bali and the Lesser Sundas as far as Flores and Sulawesi), *K. b. kalingensis* (Luzon Island in North Philippines) and *K. b. ghoshi* (Andaman Islands).
2. *Hytrix javanica* (Hystricidae) – the Javan porcupine – is a polytypic species of two extant members of subgenus Achanthion. It is found on Java, Madura, Bali, Lombok, Sumbawa, Rinca, Flores, Tanah Jampea, and considered as human introduction on southwestern Sulawesi. Its relative, *H. brachyura*, ranges from Nepal to Southeast China and to the nearby Hainan Island and southwards, with its absence on most of Thailand, to the Malay Peninsula, Sumatra and Borneo. In Sumatra, *H. brachyu*ra is restricted to the northeast and western Sumatra region
3. *Litoria infrafrenata* (Hylidae – Pelodryadinae) – the white-lipped tree frog – inhabits the coastal lowlands and extends into the highlands to a maximum altitude of slightly less than 3,500 ft. (Tyler, 1968). Two subspecies are known, i.e *L. i. infrafrenata* (New Guinea, westwards as far as Talaud Islands off Northeast Sulawesi, and Timor Island in the Outer Banda Arc, and extends to Queensland in North Australia) and *L. i. militaria* (Bismarck Archipelago).
4. *Phalanger orientalis* (Phalangeridae) – the northern common Cuscus – is a polytypic species, which is common in old gardens and primary forest. Two subspecies are known,

i.e. *P. o. orientalis* (New Guinea, including Batanta and Waigeo, and extends as far west to Sanana Island and Timor Island) and *P. o. breviceps* (Bismarck Archipelago and Solomon Islands).

5. The langur or leaf monkey genus *Presbytis* (Cercopithecidae) is endemic to the Great Sundas up the south Isthmus of Kra. This arboreal forest dweller is represented each by three endemic species on Borneo and Sumatra regions as well as one endemic form on Java. The monocentric subspecies of polytypic *P. femoralis* is currently disjuncted on West Borneo (*P. f. chrysomelas*), North Natuna Island (*P. f. natunae*), Riau Arch. (*P. f. rhionis*), East-central Sumatra (*P. f. catemana, P. f. paenulata, and P. f. percura*) and the Malay Peninsula including South Thailand (*P. f. ssp.*).
6. *Ratufa bicolor* (Sciuridae) – the Black Giant Squirrel – is a polytypic species that is strictly adapted to primary forests. Of nine extant subspecies, two of them are found on Sumatra including the nearby Batu Island (*R. b. palliata*) and on Java as well as Bali (*R. b. bicolor*). The other seven nominal forms are found northwards up to Nepal and Indochina.
7. The polytypic species *Trimeresurus popeiorum* (Viperidae) – the Popes Bambusotter – is a typical montane forest inhabitant that is usually found first at 800m. above sea level, mostly nearby the water courses. Two subspecies that are confined to Indonesia are *T. p. barati* (Sumatra and the nearby Mentawai Arch.) and *T. p. sabahi* (Borneo). Other subspecies, *T. p. popeiorum*, are found from India to Indochina and the Malay Peninsula, including Singapore.
8. *Megalaima australia* (Capitonidae) – the Blue-eared Barbet – is a polytypic species with seven subspecies. Two of them are found from the Hilamayas to Indochina (*M. a. cyanotis*) and on Peninsular Myanmar and Thailand (*M. a. stuarti*). The other five subspecies occur southwards, i.e. *M. a. duvaucelii* (Malay Peninsula, Sumatra, Bangka Island, Borneo), *M. a. gigantorhinus* (Nias Island off Northwest Sumatra), *M. a. tanamassae* (Batu Islands off West Sumatra), *M. a. australis* (Java), and *M. a. hebereri* (Bali).
9. *Litoria bicolor* (Hylidae – Pelodryadinae) is a polycentric group of the swamp-breeding amphibians. It forms a super-species complex of seven hemispecies (Tyler & Davies, 1978). While each three hemispecies are restricted to New Guinea (*L. longicrus, L. mystax, L. costrastens*) and Australia (*L. cooloolensis, L. olongburensis, L. fallax*) respectively, one hemispecies (*L. bicolor*) shares its range for those two regions, including Aru Island.

10. *Sminthopsis virginiae* – the Red-cheeked Dunnart – is a polytypic dasyurid, which is strictly adapted to monsoonal grassland and woodland. A sub-species confined to the New Guinea region (*S. v. rufigenis*) is a polycentric form. It occurs on the Trans-Fly region in South New Guinea, on the Port Moresby area in Southeast New Guinea and on Aru Island off Southwest New Guinea. Two other subspecies are found on Queensland (*S. v. virginiae*) and Northwest Australia (*S. v. nitela*).
11. The monotypic genus *Probosciger aterrimus* (Cacatuidae) – the Palm Cockatoo – inhabits rainforests, gallery forests, and forest edges. Three extant subspecies known are *P. a stenolophus* (Yapen Island and Northwest New Guinea), *P. a. goliath* (W Papuan Islands; West and Central New Guinea) and *P. a. aterrimus* (Aru Island, Misool Island, Trans-Fly of South New Guinea and Northeast Australia).

The affinities among endemic centres suggested by examples given above are interesting because they tend to be clustered into two groups. The first group, which is arranged from the first four species, has divided Indonesia into three biogeographical regions. They are:

1. Borneo, Sumatra, Java, Sulawesi and the Lesser Sundas as far as Flores.
2. Talaud Island and Sangihe Island, Northern Moluccas, Sanana Island, the Outer Banda Arc as far as Timor, and New Guinea.
3. Wallacea region

The second group arranged from the rest of the species has divided Indonesia into the same three biogeographic regions as the first group did, but there are obviously some differences of the borders for each region. The three regions are:

1. The Great Sundas and Bali
2. New Guinea (including Aru Island to the southwest as well as Waigeo and Batanta to the northwest) and Northern Australia.
3. Wallacea region

While the separation of the Indonesian archipelago shown by the second group concurs with Wallace' Line (1863 -1880) and Lydecker' Line (1896) fitted to 200m isobath of the Sunda and Sahul shelves today, the other made by the first group is very interesting because it completely disregarded broad marine barriers, which currently separate the

Wallacean region from islands on the Sunda and Sahul shelves. The Wallacean region formed by the first group was much smaller than it is today.

In the last Pleistocene Glacial Maxima, the lowering sea level is well-known to have facilitated faunal exchanges between fauna on the mainland with offshore islands lying within 200m isobath. In regard to this, faunal distribution patterns shown by the first group might have reflected the Indonesian Archipelago much earlier than the Pleistocene Period.

Thus, the affinities between Indonesian endemic centres show that there is a shift of biogeograpical lines in the Indonesian region. Now, the question is what kind of factors have affected it and how it had happened? Do they reflect a different time of evolution?

4.3 Biogeographic Evolution of the Indonesian Region

4.3.1 Palaeo-Biogeography of the Indonesian Region

The present day distribution of Indonesian fauna shows that, migration of oriental lineages from Asia to the Indonesian Archipelago happened much earlier than was previously thought. The most important thing is that these oriental lineages might have arrived first on the Archipelago through island drifts driven by tectonic movements. The docking region itself was mainly in what now is known as Northeast Borneo, North Sulawesi, North Moluccas, and Northeast New Guinea. This is contrary to what until now was widely believed that oriental lineages reached the Indonesian Archipelago from Southeast Asia mainly through a land bridge, which existed in the Pleistocene Period as a result of the lowering of the sea level. Considering such a land bridge, therefore the occurrence of some taxa beyond the Sunda Shelf is thus mostly regarded as the result of human introduction.

High endemism of all Bornean fauna except for birds, is obviously the result of a long duration of isolation. The question is how this island could be so isolated. Monk *et al.* (1997) stated that sea level changes in Indonesia show that there were several deep drops in the sea level below its present levels. These drops occurred in the late Oligocene (about 29 million years ago (-250m)), in the Pliocene (about 6.6. Ma years ago (-220m)), and at least twice during the Pleistocene, by Riss Glacial about 170 thousand years ago (-200m) and by Wurm/Wisconsin Glacial about 18,750 years ago (-130 to 175m). Of these lowering sea levels, at least the last one in the Pleistocene Period was well known to connect islands of the Great Sundas with an extension to Southeast Asia, while most of the others seem to have let Borneo remain isolated resulting in high endemicity on that island. The only explanation for this case is perhaps because Borneo at that time was still positioned far lower than it is now.

The present-day distribution ranges of *Turdus poliocephalus* (Turdidae) - the island thrush - a polytypic taxon that is commonly found locally in heather and other semi-open scrub vegetation at high altitudes, indicates that Northeast Borneo emerged a long time ago. It is considered as a part of Gondwana fragments, which had rifted between the mid-Jurassic and Cretaceous (Burret et al. 1990 in MacKinnon, 1997). Today high elevations of Mt. Kinabalu and the nearby Mt. Trus Madi in Northeast Borneo are homes to a subspecies *T. p. seebohmi*. Other than on these mountains, this taxon does not exist elsewhere in Borneo, although other peaks, which are higher than Mt. Trus Madi currently occur in Borneo, for example Mt. Makita (2,987m) in Central Borneo. In contrast to this, this species is well represented by two subspecies on Sumatra and diversely by five subspecies on Java. Albeit this high diversity on Java, it is absent on the nearby Mt. Rinjani (3,726m) of Lombok Island, whose peak height surpasses those of all mountains on Sumatra and Java, except Mt. Kerinci (3,805m) in Southwest Sumatra. Although it is absent on the West Lesser Sundas, curiously it occurs again on Timor Island, where two subspecies are confined to Mt. Mutis (2,427m) in the western part and Mt. Ramelan (2,960m) in the eastern part. On Sulawesi, two subspecies are native to Mt. Lompobatang (2,871m) in the southwestern part and Latimojong Mts. in the south-central part. There are no other records elsewhere although Sulawesi has currently several other high mountains whose peak heights are over that of Lompobatang, for example Mt. Soroako (3,016m) in the east of the Latimojong Mts. and Mt. Lokilalaki (3,311m) in north-central Sulawesi. On Ceram Island, one subspecies is endemic to Mt. Binaia (3,019m). Finally the high elevations of Central Cordillera in New Guinea and the nearby Goodenough Island to the southeast are homes to five subspecies. All records mentioned above in turn suggest that their ranges do not reveal the current highest altitudes, where the taxa could possibly have occurred. What they do show is basically emergent lands at that time. Their initial colonisation was obviously not after the time when those habitats came about, but far earlier when those high altitudes were much lower than today. Hence, it is now clear that while Sumatra and Java had emerged, most of Borneo remained submerged at that time. The only emergent region was the northeastern part from Mt. Kinabalu to the Mt. Trus Madi areas. This concurs with the fact of remarkably high endemism on the Mt. Kinabalu division in the sub-endemic area of the Mountains of Central Borneo.

Furthermore, the occurrence of polytypic *Aerodramus linchi* (Apodidae) suggests that most of Borneo still remained submerged even as Lesser Sundas began later to emerge. Of four subspecies recognized in *A. linchi*, its occurrence on Borneo is only represented by subspecies *A. l. dodgei* from high elevations of Mt. Kinabalu though *A. linchi* is actually common in hills and mountain forest habitats is the case of its close relatives on other islands from Sumatra to Lombok. This indicates that the raise of Mt. Kinabalu (recently the highest peak in Borneo mainland), was definitely younger than mountains and/or highlands along Sumatra to the Lesser Sundas.

The next initial raising of Borneo may have began first in the eastern part, as suggested by the ranges of *Chrysococcyx minutillus* (the little or Malayan bronze cuckoo), a polytypic cuculid preferring lowlands (Beehler et al., 1986). This species is highly differentiated into fourteen nominal forms. Two subspecies confined to Borneo are *C. m. cleis* of the northern and eastern Borneo and *C. m. aheneus* of Southeast Borneo and South

Philippines. Their absence on the other Bornean lowlands show that other lowlands were still submerged at that time. The separation between *C. m. cleis* and *C. m. aheneus* is obviously through an altitudinal difference because the southeastern part was clearly much lower than the northern and eastern parts that emerged earlier.

The emergence of East Borneo obviously was important for early faunal migration from Borneo to Java. Although Burrett et al. (1991 in MacKinnon, 1997) noted that by the Oligocene (30 Ma) Borneo was part of a landmass including West Sulawesi, faunal remains show that any land bridge apparently occurred much later in the Pliocene period and it connected only Borneo, Java and West Sulawesi. The oldest mammal remains from Java, date from the Pliocene and are of a species similar to those found in the Siwalik Hills of India, i.e. a primitive elephant-like mastodon *Trilophodon bumiajuensis*, a hippopotamus *Hexaprotodon*, and deer. These all date from 1.5 – 3 million years ago (Groves 1985 in Whitten et al., 1986). They represent obviously early immigrants, which moved to Java in the Pliocene by the lowering of the sea levels.

Indications of a land bridge connecting Java and Sulawesi in the Pliocene period are evident as seen by shared ranges of badly dispersed amphibians on Java and Sulawesi (see accounts thereof). Such a land bridge has been supported by the finding of fossils of large oriental lineages in Southwest Sulawesi, such as a Sulawesi elephant (*Elephas celebensis*), a pygmys stegodont (*Stegodon sompoensis*) as well as the larger stegodont (*S. trigonocephalus*), an anoa (*Bubalus depressicornis*), and two kinds of pig, i.e. a giant pig (*Celebochoerus heekereni*) and a Sulawesi pig (*Sus celebensis*). Additionally, fossils of a giant tortoise (*Geochelone atlas*) and a Celebes crocodile (*Crocodylus sp.*) have also been recorded. Those fossil remains are known from one of the only two sites on Sulawesi, i.e. river sediments near Sompoh, Beru and Celeko in Soppeng district about 100km northeast of Ujung Pandang in which animals found there, called the Cabenge fauna, are thought to date between the upper Pliocene and early Pleistocene (Whitten, 1987; Barstra, 1997 and Sartono, 1979 in Whitmore, 1987). Like the anoa and *Sus celebensis*, the probiscidians and *Celebochoerus* represent an old fauna related to species known by fossils from Pliocene beds of the Siwaliks in India and middle to earlier Pleistocene strata on Java (Thenius 1970; Hooijer 1975; Groves 1976 in Whittmore (Ed.), 1987).

In contrast to direct faunal migration from Borneo to Java, such migration apparently did not occur to Sumatra. The most submerged region of Borneo was the western part and this had apparently hindered the existence of any land bridge between Borneo and Sumatra before the Pleistocene period. Any contact between both islands apparently first existed as the northern part of Borneo (Sarawak region) began to emerge much later. Similar to Sulawesi, Sumatra however received Bornean lineages through Java, which migrated in the Pliocene Period as Sumatra apparently was still connected to Nicobar Island and Weh Island.

However, evidence from faunal records show that most of Sumatra was submerged after it received Bornean lineages which migrated through Java. The ranges of a polytypic *Macropygia emiliana borneensis* (Columbidae) show that, while subspecies *M. e. emiliana* occurs on Krakatau, Java, Lombok, Sumbawa, Flores and on the nearby Palu Island and hence suggests the emergence of these islands, populations on Sumatra are only represented on islands off the western coast, i.e. on Simeuleu Island (*M. e. hypopercna*), on Nias Island (*M. e. modiglianii*), Mentawai Island (*M. e. elassa*), and Enggano Island (*M. e. cinnamomea*). Evidence found on the Sumatran mainland from Mt. Kerinci at 2,500m and Palembang Residency, which are considered as stragglers from Java (*M. e. emiliana*), support the submergence of Sumatra. This submergence might have occurred as the sea level rose to +140m asl. in the Pliocene Period about 5.2 millions years B.P. (Monk *et al.* 1997). While most of Sumatra was submerged, the occurrence of subspecies *M. e. megala* on Kangean Island and subspecies *M. e. borneensis* on North Borneo suggests that a probable land bridge connected Borneo and Java was also submerged.

The submergence of most of Sumatra explains odd separations of some taxa from Borneo and Sumatra. These separations are for example between populations of *Kalophrynus punctatus* (Microhylidae – Microhylinae) on Mentawai Is. and on Borneo and also between two cercopithecids, i.e. *Simias concolor* on Mentawai Island and genus *Nasalis larvatus* on Borneo. Additionally, their absence on Java Island in turn suggests that perhaps most of this island was also submerged, except the higher southern part as indicated by the occurrence of endemic *M. e. emiliana* (Columbidae) described above. Furthermore, the occurrence of *Paradoxurus hermaphroditus* (Viverridae) on the mainland and on the islands off West Sumatra except Mentawai Island (because there it is replaced by its relative, *P. lignicolor*), shows the retreat of the increased sea level so that Sumatra Island was inhabitable again. Nevertheless, the current disjunct population of *Chiropodomys gliroides* (Muridae) on Nias Island off the western coast of Sumatra, separated from the mainland population that occurs only on the southern tip, suggests a submergence of Sumatra again. From the former submergence itself, *C. gliroides* seems to have derived *C. karlkoopmani*, which is today endemic to Mentawai Island. Hence, it is now clear that Sumatra has undergone more than one submergence. The sea level changes in Indonesia show that several major rise in the sea level occurred in the Pleistocene Period (Monk *et al.* 1997). These relatively recent events concur with the remainder of the populations of *C. gliroides* (Muridae) on Nias Island and on the mainland in the same taxonomical level.

While West Sulawesi was still close to Java, North Sulawesi was beginning to emerge as suggested by the range of a polytypic columbid *Ducula pickeringii*. The three extant subspecies show emergent islands in the northern region, i.e. small islands off North and Northeast Borneo and Sulu Archipelago (*D. p. pickeringii*); and North Sulawesi (*D. pickeringii ssp*); and Miangas and Talaud Islands (*D. p. palmasensis*). As a result of this rising, oriental lineages could then drift further east to North Sulawesi. The occurrence of oriental lineages, such as genyophryne and asterophryne microhylids as well as ranid *Platymantis* on the Northern Moluccas and New Guinea and even up as far as to the Bismarck Island and Solomon Arch. show furthermore that tectonic movement had drifted oriental lineages not only to Borneo and Sulawesi, but a lot further east to those islands. Nonetheless, a break off of the landmass into independent smaller islands obviously occurred during these movements, which highlights the absence of large oriental lineages there.

On the other hand, the occurrence of non-volant Australian lineages on the Talaud and Sangihe Islands and on the Northern Moluccas, suggests a westward back drifting of tectonic movements. Otherwise those Australian lineages could not reach those islands that recently became separated broadly by marine barriers with New Guinea. Of amphibians they are all represented by pelodryadine hylids, i.e. *Litoria infrafrenata infrafrenata* on Talaud, Halmahera, Ternate, Bacan, Morotai, Gebe and Biak-Supiori; *L. nigropunctata* on Gebe Island; and *Nyctimystes rueppelli* on Halmahera and Morotai. Of mammals, they are composed by phalangerids and petaurid. The phalangerids are *Ailurops ursinus melanotis* on Talaud Island; *Strigocuscus celebensis sangirensis* on Sangihe Island; *Phalanger ornatus* on Halmahera, Ternate, Tidore, Bacan and possibly Morotai; *P. rothschildi* on Obi and Bisa; *P. alexandrae* on Gebe Island; and *P. orientalis orientalis* on Waigeo and Batanta, while the only petaurid reckoned is *Petaurus breviceps papuanus* on Halmahera, Bacan, and Gebe. In regard to the current location of these islands relative to New Guinea, it seems that tectonic movement was not linear westwards but somehow resembles a curve. These biogeographical results concur with geological records. Based on these records, Hall (2001) was able to show that multiple arc systems extended early to middle Oligocene (35-30 million years ago) from the Sundaland margin into the west Pacific, including the East Philippines-Halmahera arc, the Izu-Bonin-Mariana arc, and the South Caroline arc. By the end of the Oligocene about 25 million years ago, the leading edge of the east Philippine-Halmahera-South Caroline arc collided with the New Guinea passive margin, causing in turn the clockwise rotation of the Philippine Sea-Caroline plate with the Pacific.

The drifting of Australian lineages westwards on the other hand, indicates that in contrast to Borneo, New Guinea was populated by modern non-volant animals before the arrival of oriental lineages. Nonetheless, recent high diversity of oriental lineages there, such as genyophryne and asterophryne microhylids or hydromyine and uromyine murids suggest that there still are enough niches for those immigrants in spite of the earlier occurrence of Australian lineages there.

The arrival of Australian lineages on New Guinea itself apparently also occurred by tectonic movements. Close affinities of faunal elements on the Vogelkop Peninsula with those which inhabited sub-endemic areas either in North or South New Guinea as well as those in Central Cordillera show that this peninsula might be one of the origin centres of New Guinean fauna. The ranges of some taxa show clearly that they have their origins on this peninsula. Of mammals, they are monotypic genus *Zaglossus bruijni* (Tachyglossidae); monotypic genus *Myoictis melas*, *Antechinus melanurus*, perhaps *Dasyurus albopunctatus* (Dasyuridae); *Echymipera kalubu* (Peroryctidae); *Dendrolagus inustus*, *Dorcopsis muelleri* (Macropodidae); *Phalanger orientalis* & *Spilocuscus maculatus* (Phalangeridae); *Petaurus breviceps* (Petauridae); *Pseudochirops albertisii* & *Pseudochirulus canescens* (Pseudocheiridae). Of amphibians, they are among other *Litoria infafrenata* and *Nyctimystes pulchra* (Hylidae– Pelodryadinae) while *Casuarius unappendicullatus* (Casuariidae) is an example of a bird found.

The occurrence of numerous taxa of different families in Australian lineages, having their origin on the Bird's Head indicate that this peninsula must be a part of Australia which drifted and collided with New Guinea. It might have been within a close distance of Australia so that it could receive many taxa before it moved towards New Guinea. In addition, it must be big enough to harbour various taxa, but on the other hand, its extent seems to have remained unchanged so that its faunal elements were only poorly differentiated in comparison to oriental lineages, which drifted towards New Guinea.

The assumption of an early separation of Australian lineages which drifted on to the Bird's Head from their ancestors in Australia is supported by biochemical studies suggesting that New Guinean species previously placed in the genus *Antechinus* are not closely related to the Australian species of *Antechinus*, and so must be assigned to a separate genus (Krajewski et al. 1993; Kirsch & Springer 1993).

The closer affinity between the sub-endemic area of the Bird's Head with that of Northern North Coastal Range indicates the longer existence of faunal exchanges between the two sub-endemic areas, rather than with South Papua. This may have resulted from the existence of the Central Cordillera, which acted as a natural barrier to South Papua. The Bird's Head must have collided only with North New Guinea, but not with South New Guinea so that fauna originating on the Bird's Head, which are mainly lowland to mid-elevation inhabitants, could not disperse to the south due to the existence of higher elevations of the Central Cordillera. This in turn gives us some clues as to how the Bird's Head collided with Sepik-Papuan ophiolites and even earlier, how the Sepik-Papuan ophiolites collided with the New Guinea passive margin.

The New Guinea passive margin is well known as a northern part of the Australian plate. As this passive margin collided with the Pacific intra-oceanic island arcs causing the emplacement of the Sepik-Papuan ophiolites, the island arcs apparently did not cover perfectly the passive margin, but somehow went over it, forming such peninsulas on both ends. On the western end, it formed the Wandammen Peninsula and on the eastern end, it formed a peninsula between Goodenough and Milne bays. The Bird's Head with Australian lineages thereon apparently moved in a Southwest-Northeast direction towards New Guinea and docked in the Wandammen Peninsula. This thin peninsula could not hold the push of the Bird's Head so that it was bent and along with the Bird's Head moved further clockwise with the Wandammen Peninsula as its axis. However, such a clockwise rotation likely did not cause the Birds' Head to become directly abutted against Northern New Guinea, as proposed by Charlton (1998), regarding high endemism on the Bird's Neck sub-endemic area. As a result of this collision, a migrate way from the Bird's Head to the northern slopes of the Central Cordillera existed through the Bird's Neck, while to the southern one there was nothing due to the existence of a higher elevation barrier of the Central Cordillera.

On the other hand, tectonic movements drifted multiple island arcs with oriental lineages thereon towards New Guinea where they docked in the early Miocene about 20 million years ago (Hall, 2001). As the result of this docking, Australian lineages migrated to those island arcs and moved along westwards. The westernmost occurrence of Australian lineages *Litoria infrafrenata infrafrenata* (Hylidae – Pelodryadinae) and monotypic genus *Ailurops ursinus melanotis* (Phalangeridae) on Talaud Islands, as well as *Strigocuscus celebensis sangirensis* (Phalangeridae) on Sangihe Islands suggest that those islands were apparently the first ones which docked in New Guinea followed by the Northern Moluccas and islands off North New Guinea lying outside the 200m line such as Batanta, Waigeo, Numfoor and Biak-Supiori and other outside 200m lying islands eastwards as indicated by the occurrence of Australian lineages there, as already mentioned elsewhere above. The part of multiple arcs, which docked in New Guinea in the early Miocene about 20 millions years B.P., geologically well known as the New Guinea Terranes, which is thought to have been formed in the South Caroline arc (Hall, 2001).

The docking of multiple island arcs in New Guinea clearly did not only facilitate the migration of Australian lineages to this island arc, but also it facilitated the movement of oriental lineages to New Guinea. Mammals are only represented by murids including *Rattus praetor*, *R. steini*, *Stenomys verecundus*, *Melomys rufescens*, *M. platyops*, *Uromys caudimaculatus*, and *Hydromys chrysogaster*. The amphibians are mainly composed of genyophryne and asterophryne microhylids such as *Oreophryne biroi*, *Cophixalus biroi*, *Choerophryne rostellifer* and *C. proboscidea*, *Copiula tyleri*, and monotypic genus *Sphenophryne cornuta*, but ranids have also been recorded for example *Platymantis papuensis papuensis*. As it can be seen, the composition of oriental lineages, which drifted to New Guinea, are mainly made up of small fauna, which are highly differentiated, in contrast to Australian lineages, which drifted on to the Bird's Head. The independent smaller islands, which were formed after the break of bigger landmasses, not only hindered a drifting of large fauna but also undoubtedly accelerated the evolution rate. This explains why those oriental lineages, which drifted to New Guinea are much more differentiated within families in comparison to Australian lineages which drifted on to the Bird's Head.

The occurrence of Australian lineages on the Bismarck or even on the Solomon islands supports the westward back motion of tectonic movements, which pulled these islands westwards. As the New Guinea Terranes docked in New Guinea, these islands obviously collided with islands lying westward of them shortly before they bounced back away as a reaction to that resistance. Thus, albeit the Solomon had apparently never come into contact with New Guinea, Australian lineages could migrate to Solomon through the Bismarck, as the Bismarck first collided with New Guinea through a westward motion, and then collided with the Solomon through an eastward motion. The Australian lineages which migrated to the Bismarck and Solomon archipelagos are for example *Litoria infrafrenata militaria* and *L. thesaurensis* (Hylidae – Pelodryadinae); *Echymipera kalubu cockerelli* (Peroryctidae); *Dendrolagus matschiei*, perhaps *Macropus agilis papuanus* (Macropodidae); *Phalanger orientalis breviceps*, *Spilocuscus maculatus maculatus*, *S. kraemeri* (Phalangeridae); and *Petaurus breviceps papuanus* (Petauridae).

In the Pliocene period, there are evidences of numerous extinction in New Guinea. Flannery (1995) recorded that the oldest mammal remains from the New Guinean mainland date from the Pliocene Period. These were recovered from sediments now known as the Otibanda Formation found on Wiganda Creek, a tributary of the Watut River near the present-day town of Wau. The fossils thought to be no older than 3.1 million years represent large diprotodontids, '*Kolopsis' watutense*, *Kolopsis rotundus*, and *Kolopsoides cultridens*; the macropodids, *Watutia novaeguineae*, *Protemnodon otibandus*, *P. buloloensis*, and one similar to the species of *Dorcopsis*; a dasyurid assigned to genus *Myoictis*; a murid; and a thylacinid assigned to genus *Thylacinus*. The only other fossil mammal of possible Pliocene age is from the Awe Formation found near Mogorafugwa, Southern Highland Province, which appears to represent *Protemnodon otibandus*. Although the Pliocene sediments of the Awe Formation lie at an elevation of over 1,000 metres today, both geological evidence and the occurrence of remains of lowland species such as crocodiles show that they did accumulate at lower elevations. Except for the undetermined Murid, all taxa are considered to be lowland inhabitants. Hence, it can be concluded that the New Guinea mainland remained much lower than it is today towards the end of the Pliocene Period, some three million years ago. This even perhaps remained so until the Pleistocene as suggested by Löffler (1976). Based on geological records, he was able to show that the formation of major volcanics in the Eastern Central Cordillera are considered to be Pleistocene in age, ranging from 1.1 to 0.202 million years ago.

Please also remember that current high elevations of the Central Cordillera as the result of Sepik-Papuan ophiolites emplacement, was first much lower than it is today as indicated by the range of *Turdus poliocephalus* (Turdidae). The ranges of five subspecies show clearly which parts of New Guinea had emerged by such emplacement at that time, i.e. Jayawijaya Mts. (*T. p. versteegi*), Bismarck Mts. (*T. p. carbonarius*), Saruwaged Mts. on the Huon Peninsula (*T. p. keysseri*), mountains of Southeast New Guinea (*T. p. papuensis*), and Goodenough I. (*T. p. canescens*).

Pliocene fossils from New Guinea thus show that southern New Guinea was still submerged towards the end of the Pliocene period or even up the Pleistocene period. This in turn indicates that a land bridge connecting New Guinea and Australia must be first existed in the Pleistocene period and not earlier, for example as the sea level lowered in the early Pliocene period. The rising of southern New Guinea itself began apparently on the Papuan Plateau as indicated by the occurrence of endemic *Dendrolagus spadix* (Macropodidae) there. This plateau is a large area of elevated limestone, which lies along the southern flanks of the

Central Cordillera, north of the Gulf of Papua. The southwestern part must have emerged not long thereafter and interestingly, some of its faunal elements, such as *Echymipera rufescens rufescens* (Peroryctidae) and *Spilocuscus maculatus chrysorrhous* (Phalangeridae) have disjunct populations on the southern Moluccas in spite of deep trenches between. While such ranges were obviously driven by tectonic movements, it shows that tectonic movements still occurred in the Pleistocene Period. In order to understand how populations on the southern Moluccas and southern New Guinea could be closely related, we must look their ranges more closely and the result shows that, it is caused by the counter-clockwise motion of the Bird's Head.

As a result of the westward movement of the New Guinea Terranes in a wide left-lateral strike-slip zone, Japen Island apparently became detached from northern New Guinea to the Geelvink Bay. This island lies within the 200m line and may have connected to the New Guinean mainland by a lowering sea level in the last Pleistocene Glacial Maxima so that its faunal elements are closely related to those on the New Guinean mainland. Nonetheless, the occurrence of some endemic forms, such as *Hylophorbus nigrinus* (Microhylidae – Asterophryinae), indicates that not all taxa reached this island through such a land bridge, but some other may have drifted on the detached Japen Island to its current position as it was pushed by a left-lateral movement of the New Guinea Terranes. The possible dispersal through such a drift would also explain the enigmatic range of *Pseudochirops albertisii* (Pseudocheiridae). Currently, this species is found only in montane forest above 1,000 metres and its range encompasses widely separately blocks of this habitat: the Arfak Mountains and the Weyland Range (P. a. albertisii), Japen Island (P. a. japeni), and the North Coast Ranges (P. a. schultzei) (Flannery, 1995). Given this evidence, this species must have penetrated Japen Island very early, as it was still attached to New Guinea. Geologically, Japen Island should mark the southern limit of the left-lateral zone where the New Guinea Terranes moved.

Furthermore, the left-lateral movement of the New Guinea Terranes not only caused the detachment of Japen Island, but it also pushed the Bird's Head to rotate counter-clockwise so that it collided with South New Guinea. Such a rotation occurred because in contrast to the stable New Guinea passive margin, the Bird's Head was only attached to the narrow Wandammen Peninsula. The clockwise rotation of the Philippine Sea-Caroline plate with the Pacific caused the New Guinea Terranes to push the Bird's Head in such a direction. The thin Wandammen Peninsula could not hold the push of the New Guinea Terranes so that it rotated counter-clockwise, causing a collision with South New Guinea.

This counter-clockwise movement was also suggested by Charlton (1988). It is predicted to have taken place approximately in the last 3 million years B.P. He interpreted however that the Bird's Head, along with Japen Island, directly abutted against North New Guinea (i.e. Mamberamo area and the Van Rees Mts.) so that faunal interchange is expected. This unfortunately does not concur with this work as suggested by high levels of endemism on the Bird's Neck sub-endemic area. Anyway, what the most important from such a counter-clockwise movement of the Bird's Head is its effect.

As the Bird's Head rotated counter-clockwise to its current position, it closed the Southern New Guinea from the wet monsoon winds blows from Asia. The Bird's Head itself was closed by Halmahera Island because this island moved also to its current position as a result of the clockwise rotation of the Philippine Sea-Caroline plate with the Pacific. On the other hand, the close relationships of new guinean fauna with moluccan fauna indicate once that there was land connection among these regions. Such land connection is supported by no endemic form of amphibians on Seram Island, a case that is very odd regarding the strong isolation of this island recently by deep marine barrier. Taxa with such disjunct distribution are for example *Callulops fuscus* (Microhylidae – Asterophryinae), monotypic group *Litoria vagabunda* (Hylidae – Pelodryadinae), and *Rana grisea* (Ranidae). The first taxon, *C. fuscus* has been recorded from Batanta Island and Seram Island as well as from the nearby Ambon Island. The second, L. vagabunda is only known from the Sorong area on the eastern coasts of the Bird's Head and a disjunct population on Seram Island. Also *Rana grisea* (Ranidae) occurs only on New Guinea and Seram Island.

Such close affinities can be simply explained as follows. The Outer Banda Arc, along with Sanana Island of the Sula Islands and Buru Island to the west, might not be as curvy as it is today and the leading edge of this arc were once lying to the west of Batanta Island. As the result of westward motion, Batanta collided with Sanana Island. The occurrence of *Platymantis papuensis occidentalis* (Ranidae – Cornuferinae) and *Phalanger orientalis orientalis* (Phalangeridae) on Sanana Island in the Sula Islands with disjunct populations among others on Batanta Island suggest that Sanana Island was the first island, which collided with Batanta Island. Additionally, the endemic *Callulops kopsteini* (Microhlyidae – Asterophryinae) on Sanana Island is apparently closely related to *C. fuscus*, which occurs on Batanta, Seram and Ambon islands. Both resemble each other in having shorter legs. This in turn shows that after Batanta collided with Sanana, the clockwise rotation of the Philippine Sea-Caroline plate with the Pacific caused Batanta to move clockwise and this in turn pushed Sanana, Buru and the Outer Banda Arc counter-clockwise.

The push to these islands was also accentuated by the clockwise movement of the Halmahera arc. A relative continuous range of *Litoria infrafrenata infrafrenata* (Hylidae – Pelodryadinae) from Buru, Ceram, Ambon, and further south via Kai and Tanimbar, to Timor shows that these islands were moved back along the arc and temporarily collided with each other as the result of the push of Batanta, but Timor was likely to have remained fixed on its position so that it apparently only rotated clockwise instead of moving away. The resistance of Timor caused islands to the north to curve. As the push became stronger, Batanta moved closer to the Bird's Head. This resulted in Sanana, Buru and Seram each colliding with Batanta and moving further westwards. Through this process, fauna gradually migrated from Batanta to Sanana, Buru and Seram. The earlier they migrated, the further west immigrants will be found today.

The curvy process of the Outer Banda arc also forced Kai Island to collide with the Aru Islands and facilitated faunal migration from Kai Island to Aru Islands, for example *L. i. infrafrenata* and *Spilocuscus maculatus chrysorrhous* (Phalangeridae). On the other hand, populations already settled on Aru Islands, such as *Echymipera rufescens rufescens* (Peroryctidae), could migrate to Kai Island by such a collision. This explains why populations of some taxa confined to New Guinea and Aru Island are much more closely related to those of the Southern Moluccas than to those of Northern Australia.

Other than to facilitate faunal exchanges, the movement of the Outer Banda Arc to its current position had apparently also closed Southern New Guinea from the wet monsoon winds blow from the Indian Ocean. The closure of Southern New Guinea from the wet monsoon winds blow from the Asian Continent, as already mentioned elsewhere above, and from the Indian Ocean might resulted in a more arid regional climate in Southern New Guinea. This in turn seems to be responsible for numerous faunal extinction on New Guinea in the Pliocene period. The thought of pliocene fossil age in New Guinea of no older than 3 million years ago fits to the period of the counter-clockwise rotation of the Bird's Head. Given this evidence, it seems that the pliocene extinction on Java might also have resulted from the regional climate change due to the closure of this island from the wet Northeast Trade Winds as North Sulawesi collided with Southern Sulawesi.

The collision between the New Guinea Terranes with the Bird's Head took place on the northern tip of the Bird's Head, causing the raising of the Tamrau and Arfak mountains. In regard to this raising, that occurred much later than the Central Cordillera's emergence, it is now clear why *Turdus poliocephalus* (Turdidae), whose ranges reflect Palaeolands, is absent on the highlands of the Bird's Head although it has been well recorded from the highlands on Ceram and the Central Cordillera. Furthermore, the collision between the Bird's Head with South New Guinea formed the migrate way from the Bird's Head and the North Bird's Neck respectively to South New Guinea and vice versa. This much later faunal exchanges explain why the affinity between the Bird's Head with South Papua is more distantly compared to Northern New Guinea.

By a clockwise rotation of Timor, Sawu and Sumba islands, lying to the west, also moved clockwise, with Timor as an axis, far westwards right next to the border of the Inner Banda Arc. In contrast to faunal migration along the Outer Banda Arc by a land collision, such migration was likely not to have happened to faunal elements of Sawu and Sumba because the fixed Timor did not move to collide with Sawu and thus, Sawu did not collide with Sumba. This explains why most taxa, which dispersed through the Outer Banda Arc, have their westernmost ranges on Timor.

On the Sula Islands off eastern Sulawesi, *Platymantis papuensis occidentalis* (Ranidae), *Callulops kopsteini* (Microhylidae – Asterophryinae), and *Phalanger orientalis orientalis* (Phalangeridae) were restricted to Sanana Island and did not extend to nearby Mangole and Taliabu or further west to Banggai Islands. This is interesting because currently those islands are all situated within the 200m line and might be connected among others by the lowering of the sea level in the Pleistocene Glacial Maxima. A plausible explanation for such odd ranges comes from the ranges of *Orthothomus cuculatus* (Sylviidae), a polytypic taxon that is strictly adapted to lower and montane forests at 1,000 – 2,500m. Currently subspecies *O. c. riedeli* is confined to North Sulawesi, *O. c. meisei* to Latimojong Mts. in south-central Sulawesi, and *O. c. hedymeles* to Mt. Lompobatang in South Sulawesi and Taliabu Island of Sula Islands. On the other hand, subspecies *O. c. stentor* is restricted to North-central and Southeast Sulawesi. While the occurrence of subspecies *riedeli*, *meisei*, and *hedymeles* reflect clearly emergent lands at that time, the occurrence of subspecies *stentor* may indicate a submerged region. Otherwise *O. c. hedymeles* would not extend to Taliabu Island without touching populations in the intermediate area. Additionally, this evidence shows that Taliabu Island that is currently close to the Moluccas was formerly much closer to the southwestern peninsula. This is supported by the occurrence of other sub-species on Buru and Seram in the southern Moluccas (*O. c. dumasi*), as well as the mountains of Bacan Island in the northern Moluccas (*O. c. batjanensis*). Furthermore, the occurrence of subspecies *O. c. cinereicollis* on mountains of Northeast Borneo suggests that the raising of Taliabu Island was earlier than the raising of the rest of Borneo.

While the eastern and southeastern peninsulas were still submerged, northern Sulawesi collided with the western peninsula but left a former sea between to be what is now Lake Lindu in West-central Sulawesi. Positive evidence for that collision comes from the restriction of a snail, *Oncomelania hupensis*, an intermediate host of a blood-fluke or trematode flatworm *Schistosoma japonicum*, only to the Lake Lindu area and none has been found in other water courses or at elevations lower than 1,000 – 1,200m. In the Philippines, this snail is found near sea level and is known from 900m above sea level in one province of Mindanao (Whitten *et al*., 1987). Such distribution patterns show that tectonic movements had drifted its ancestor southwards from the Philippines to North Sulawesi. This southward motion of tectonic movements drifted North Sulawesi further south to collide with West Sulawesi, which at that time was still close to the Sundaland. Based on mollusc fauna analysis on an island in Lake Lindu, it was concluded that the lake was formed during the Pliocene, between 5.0 and 1.6 million years ago (Sarasin & Sarasin, 1905 & Bloembergen, 1940 in Whitten, 1987).

Furthermore, the current position of Lake Lindu at 1000m asl. suggests the continual raising of the islands. North to Southwest Sulawesi was then connected so that its faunal elements could disperse easily throughout the region as suggested by their present-day distribution ranges including the entire mainland, except the east-central and southeastern peninsulas. They are for example *Crocidura rhoditis* (Sciuridae) and monotypic genus *Lenomys mayeri* (Muridae). There are some other taxa not having such a range, but they seem to have also migrated at that time, for example genus *Oreophryne* (Microhylidae – Genyophryninae). However, the less successful Sulawesian non-volant migrants to arrive on Java, in contrast to Bornean migrants, suggest that any land bridge connecting both islands, as occurred by the lowered sea level in the Pliocene Period, do not exist anymore. *Limnonectes grunniens* (Ranidae), which is detected as the only amphibian to migrate from Sulawesi, but apparently did not directly move to Java, but moved through the western Lesser Sundas.

The knowledge of the later collision between North and South Sulawesi also explains why fossils of large fauna *Stegodon-Celebochoerus-Geochelone* are only found in the South Sulawesi and nowhere else. This is likely not because they were not preserved or had not yet been discovered in other places, but because they were already extinct as a more seasonal climate existed as a result of the closure of the Moluccan Sea in the Pliocene. Please remember that Southwest Sulawesi received the dry southeast trade winds, which must have been drier in the Pliocene Glacial time. Thus, the extinction of these fauna is not the result of competition with Sulawesian fauna which migrated from the northern part as Musser (1987) suspected, but it is more as the result of the climate changes. As the east and southeast peninsulas were still submerged, they apparently collided with each other but left the ocean between to become Lake Matano, Lake Mataloha, and Lake Towuti. The clockwise rotation of the Philippine Sea-Caroline plate with the Pacific caused the Halmahera arc to push Sanana and Buru islands as well as the Outer Banda Arc, but pulled the Taliabu and east-southeast peninsulas to move clockwise so that it collided with the West-central Sulawesi, but again, leaving the sea region, which became Lake Poso. The docking of east and southeast peninsulas caused the counter-clockwise movement of Sulawesi so that it moved away from the Sundaland blocks. Sulawesi began to be isolated since this time.

After the collision with West-central Sulawesi, the southeast peninsula was apparently emerged, but in contrast with the east peninsula it remained submerged. This at least has been indicated by the absence of polytypic *Lophozosterops squamiceps* (Zosteropidae) on mountains of east Sulawesi though there is a high mountain whose peak surpasses those on other regions, for example Mt. Tokala (2,630m asl). Meanwhile, Mengkoka Mts. in Southeast Sulawesi is home to the subspecies *L. s. analogus*. Also other mountains of Sulawesi are well inhabited, i.e. *L. s. heinrichi* on Tentolo-Matinan Mts. in Northwest Sulawesi, *L. s. stresemanni* on mountains of Northeast Sulawesi, *L. s. striaticeps* on mountains of north-central Sulawesi, *L. s. stachyrinus* on south-central Sulawesi (Latimojong Mts.), and *L. s. squamiceps* on South Sulawesi (Lompobatang Massif). The only very recently emerged east peninsula also explains why populations of a monkey genus *Macaca* there is currently not yet differentiated from those on the west-central. There are also evidences from geological records. Deposits collected around Lake Matano indicate its formation of about 1.6 million years ago (B. Wahyu, pers. comm. in Whitten et al. 1987). Further, Miocene-age limestone on its southern boundary suggests that the area was under ocean water during the later Tertiary and early Quaternary (Whitten et al. 1987).

The counter-clockwise rotation of Sulawesi, accentuated by the clockwise rotation of Sulu Archipelago, caused Borneo and the Sundaland blocks to rotate counter-clockwise (Hall, 2001). As a result, Borneo moved away from Java to its current position, Sumatra was separated from Nicobar Islands and Weh Island, and Java pushed the western Lesser Sundas eastwards. Additionally, the counter-clockwise rotation of Borneo pushed in turn Sulawesi back eastwards.

Bornean fauna migrated to the Sulu Archipelago as it collided with Borneo. These taxa are for example *Microhyla annectens* (Microhylidae – Microhylinae), which migrated to Tawitawi Island, and *Sus barbatus* (Suidae) whose range is shared with the Sibutu and

Tawitawi Islands in the Sulu Archipelago. On the other hand, the separation of the Sumatra mainland from Nicobar Islands as well as from Weh Island and from Enggano Island had terminated an intermittent gene flow, which occurred when sea level lowered, as deep marine barriers then existed between them.

As a result of the eastward motion,which resulted from the push of Borneo, Sulawesi collided with Banggai and Sula islands (excluding Sanana Island). This complex island moved eastwards and collided with Sanana Island. As a result of this colision, Sulawesian fauna migrated to Peleng Island of Banggai Islands, but not further eastwards due to the marine barriers. Sulawesian fauna, which migrated to Peleng Island, are for example *Sus celebensis* (Suidae), *Ailurops ursinus ursinus*, *Strigocuscus pelengensis pelengensis* (Phalangeridae), *Tarsius spectrum* (Tarsiidae), *Rattus koopmani* and *R. pelurus* (Muridae – Murinae). Contrastly, fauna occur on Sanana Island, such as *Callulops kopsteini* (Microhylidae – Asterophryinae), *Platymantis papuensis occidentalis* (Ranidae – Cornuferinae) and *Phalanger orientalis orientalis* (Phalangeridae), could not move to Mangole Island. These features suggest that Mangole Island, lying between Taliabu Island and Sanana Island, might have still been submerged so that a possible land connection could not be used for faunal exchanges.

Similar to the migration process from Sulawesi to Banggai and Sula islands, faunal elements from Java and Bali migrated to the Lesser Sundas and vice versa as Java and Bali pushed the Lesser Sundas. Thus, *Oreophryne monticola* (Microhylidae – Genyophryninae) from Lombok Island migrated to Bali and *O. jeffersoniana* arrived on Sumbawa, Komodo, Rinca and West Flores. Its absence on the eastern part of Flores Island and other islands to the east indicated that although the western part of the Lesser Sunda Islands were emerged at that time, most of the eastern parts were still submerged. Going further east, especially east of Alor Island, the ocean floor is much deeper. Islands in this region could hardly have been emerged. Even a collision connecting those islands could not be used for faunal migration because it was under the ocean. The Ombai Strait between Alor Island in the west and Wetar Island in the east remains as a strong deep marine barrier until now.

By the eastward motion of the Lesser Sundas, Sumba that was situated very close to the border of the Inner Banda Arc, was pushed to move back towards Timor, firstly facilitating faunal migration from the Inner Banda Arc to the Outer Banda Arc through Sumba Island but only as far as Timor Island because this fixed island did not move away from its position but once again rotated, this time counter-clockwise, so that it collided with Alor and Wetar islands of the Inner Banda Arc to the north. This assumption has been well proven by the ranges of *Draco volans boschmai* and its relative, *D. v. timoriensis* (Agamidae). The first taxa is confined to the islands of Sulawesi, Lombok, Sumbawa, Komodo, Rinca, Flores, Adonara and Sumba, while the latter occurs on Roti, Semau, Timor, Alor and Wetar. On the other hand, the ability of *D. v. timoriensis* to colonise Alor and Wetar suggests that these islands were among the few islands, which were emerged in the eastern Lesser Sundas. Another taxon, which migrated by this time from Timor to Wetar is for example *Rana elberti* (Ranidae), while from Timor to Sawu and Sumba is *Litoria everetti* of *L. peronii* group (Hylidae – Pelodryadinae). Migration route from Flores, via Sumba to Timor are also well represented by fossil records of stegodon and a giant land-tortoise, i.e. *Stegodon trigonocephalus florensis* on Flores and Timor; *S. sumbaensis* on Sumba; and *S. sompoensis* on Flores and Timor. Thus, close before the last Pleistocene Glacial Maxima, islands on the Indonesian Archipelago have been in their current position, but some of them still remained submerged.

4.3.2 Pleistocene Glaciation, Eustatic Sea Level Changes and their Biogeographic Dynamics

4.3.2.1 Sunda Shelf

The emergence of West Borneo possibly towards the end of the Pleistocene Period resulted in most of the Sunda platform becoming exposed, as sea levels lowered during the glacial period in the Pleistocene. The maximum fall in Southeast Asia was about 150m below present levels (Whitten *et al*. 1987). This connected the islands of the Great Sundas with an extension to Southeast Asia. A migration corridor existed from Borneo to Sumatra as well as to the Malay Peninsula and hence facilitated their faunal exchanges. This corridor included the Natuna and Anambas Islands off the northwestern coast of Borneo. Fauna, which presumably migrated through this corridor, are for example *Presbytis femoralis* (Cercopithecidae), *Callosciurus prevostii* (Sciuridae), *Pongo pygmaeus* (Pongidae), and *Tupaia tana* (Tupaiidae).

Presbytis femoralis (Cercopithecidae) is detected as a recent migrant from Borneo to Sumatra. Its ranges in the mangrove forests on the eastern coast of Sumatra show that this species was apparently the first lineage of *Presbytis*, to arrive on Sumatra. Nevertheless, its absence in the mangroves of Southeast Sumatra gives us a clue that this region, probably along with Southwest Borneo and Northwest Java, were likely to still have been submerged at that time. Hence, the form of the Sunda Shelf at the beginning of the Pleistocene Glaciation might have resembled a bowl with the lowest area being where today Bangka, Belitung, Southwest Borneo and Northwest Java are. Only after this lowest region emerged, did another migration corridor exist, i.e. via Bangka and the Belitung Islands. Bornean fauna, which presumably migrated to Sumatra via this corridor, is for example *Hylobates agilis* (Hylobatidae). Currently it occurs both on Southwest Borneo and Southeast Sumatra as well as on offshore islands in between.

The recent rising of the lowest Sunda platform contributed, in turn, to the massive ancient river system in the Great Sundas because the drainage areas had grown. Some large rivers were formed (see Figure 4.79), serving as an effective barrier to faunal distribution, for example the westernmost record of *Leptobrachella* (Megophryidae) comes from Bunguran Besar on the Natuna Islands, showing a break in distribution at the Kampar River. As a result of the change of this river system, the Natuna Islands, which previously were an important migration corridor, became more isolated. This explains the occurrence of numerous endemic taxa on this island, for example *Kalophrynus bunguranus* (Microhylidae – Microhylinae) and *Leptobrachela natunae* (Megophryidae).

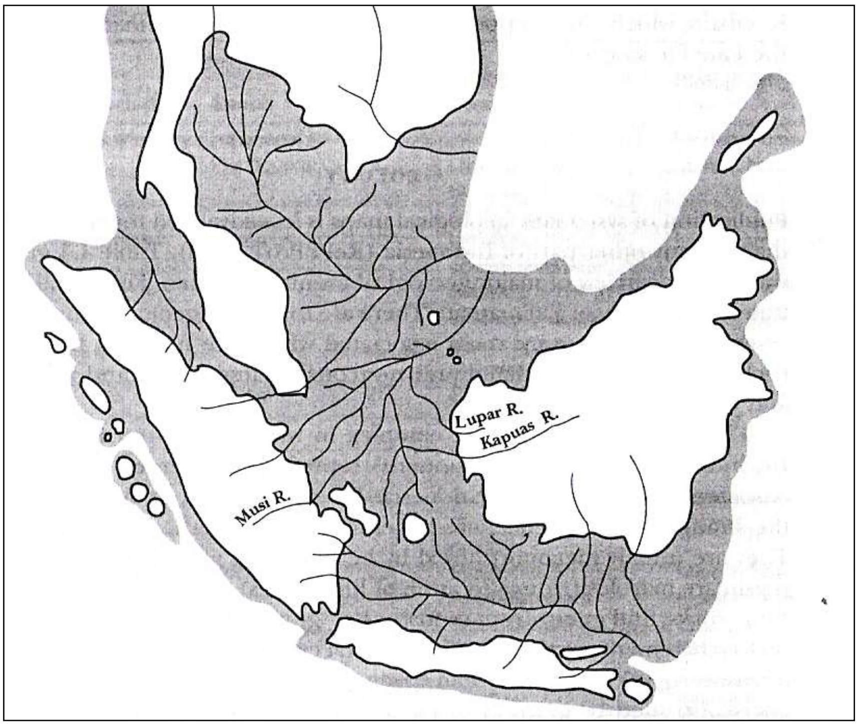


Figure 4.79 The Sunda Shelf showing present coastlines (unshaded), the area of Sundaland exposed at times of lowest sea level (dark shade) during the last glacial about 12,000 years ago, and past and present river systems (After Tjia 1980 in MacKinnon 1997).

A large river existed between Borneo and Java towards the Strait of Makasar, which also served as a strong natural barrier between both islands. This agrees closely with the faunal records indicating no direct faunal exchange between the two islands. Taxa, which are recognised as recent immigrants to Java in the Pleistocene Period, shared their ranges commonly with Borneo, Sumatra and Java. The only few taxa, whose ranges are shared only between Borneo and Java are recognised as immigrants which arrived on Java earlier than the Pleistocene Period, such as the wild *Bos javanicus* (Bovidae).

The reduction in sea levels resulted in a more seasonal climate because more water remained in ice-form on the mountain peaks. The regional climate was probably only 2^0-4^0C cooler in the Quaternary and Pleistocene than it is today, but conditions were often more arid (Morley and Flenley 1987 in MacKinnon 1997). The tree line was lowered by about 350-500m in Sumatra (Whitten, 1987) and apparently by more or less a similar amount on the other Great Sunda Islands. As most migration routes on the mainland in the Great Sundas include corridors on the upper rivers in the mountain region, the lowering of the tree line mostly caused the blocking of these corridors, leading to isolation of fauna.

The block of the headwaters of Barito separated, for example, *Hylobates agilis* and *H. muelleri* (Hylobatidae). The retreat of the tree line to its current position re-opened the gene flow between these two populations. They interbred, producing hybrids.

On the other hand, the lowering of the tree level facilitated montane fauna to disperse across lower elevations, which previously acted as barriers for them. This explains the occurrence of disjunct populations of some upper montane forest dwellers currently on the highest peaks in Borneo, Sumatra, and Java, for example *Pelophryne brevipes* (Bufonidae), *Crocidura baluensis* and *C. paradoxura* (Sciuridae).

Although the evidence shows that West Indonesia was affected also by the drier Pleistocene Glacial climate, however B.M. Barmawidjaja *et al.* (1993), based on palynological records, suggested that the Pleistocene climate in West Indonesia was much wetter rather than in the eastern part. This also concurs with faunal records. The wetter climate in West Indonesia during the glacial period resulted in fauna confined there, becoming more adapted to a wetter climate. Only a few taxa that migrated in this period to Java could successfully extend further to East Java, which is much drier than the western part because it received the dry southeasterly winds from Australia. An example of such taxa is *Callosciurus nigrovittatus* (Sciuridae). Currently, its two subspecies are faunal elements of Northwest Java sub-endemic area (*C. n. bantamensis*) and of Mt. Muria sub-endemic area (*C. n. madsoedi*). Both are likely to be isolated as sea levels rose during the warm period in the Holocene period (see Figure 4.80), resulting in the contraction of savannah forests and the expansion of lowland rainforests. For areas such as the Mt. Muria region, lying on a delta of a big river, the rising sea levels caused a complete geographic isolation.

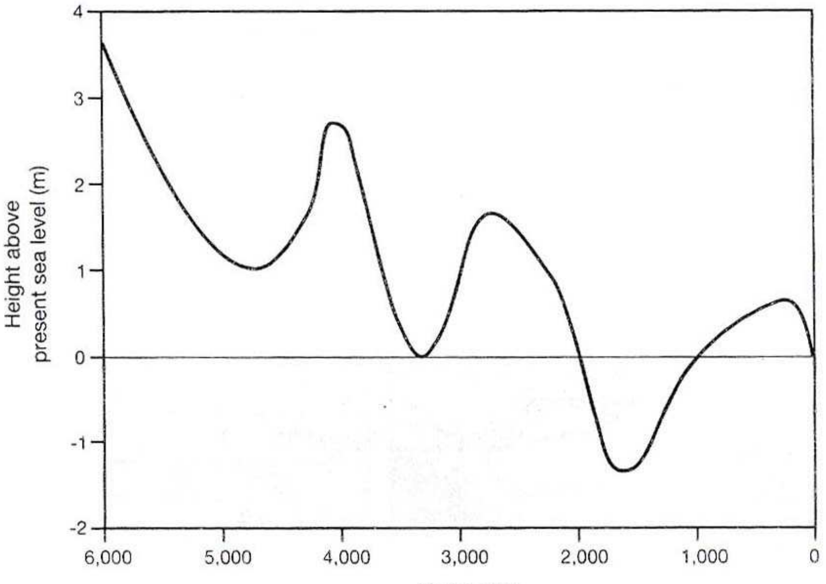


Figure 4.80 Changes in sea level on the Sunda Shelf during the last 6,000 years (After Tjia 1980 in MacKinnon et al 1997).

Such a geographic isolation as in the Mt. Muria region is mostly found on West Borneo, but there is also one found in Northeast Borneo. This study recognises at least three sub-endemic areas, which existed as a result of such isolation, i.e. Mt. Poi sub-endemic area in Western Sarawak, Kapuas delta sub-endemic area in West Kalimantan and Padas delta sub-endemic area in Northeast Borneo.

The emergence of Southwest Borneo in the last glacial time resulted in its natural habitats being dominated by drier vegetation as indicated currently by the occurrence of endemic taxa restricted to dry habitats, such as *Lonchura atricapillla obscura* and *L. a. selimbaue* (Estrilididae) in the Sampit and Pontianak regions respectively as well as *L. leucogastra smythiesi* in the Kuching region. Their separation at subspecific level apparently occurred as sea levels rose in the post Glacial (see Figure 4.80). The inundation of coastal areas resulted in the fragmentation of their habitats, leading to isolation of these fragmented populations and the invasion of rainforest.

On the Sumatran mainland, the most peculiar zoogeographic boundary is that which runs SW/NE north of Lake Toba as it is obviously not caused by physical barriers such as rivers or mountains. Some scientists (for example Whitten *et al.* 1993) thought that the wide barrier of bare, volcanic material resulting from the huge eruption, which occurred 75,000 years ago, possibly causes this. Faunal records show, however, that northern Sumatra is drier than the southern part. The habitats of *Mus caroli* (Muridae – Murinae) include rice and hay fields as well as grassy areas in deciduous forests. It is represented in Indonesia by two widely disjunct populations, i.e. on North Sumatra and on East Java (see Fig. 4.81). Similar to this is the range of *M. Cervicolor*.

In North Sumatra, there are some breaks in the mountain range (see Fig. 4.82), so that southwesterly monsoon winds are channeled and wind speed may be greatly increased. One of such winds is Angin Bohorok, a föhn wind moving to the east of the Barisan Range, which draws air into itself from the west of the range. The air ascends the western slopes, clouds form and there is heavy rain. When it reaches the eastern slopes, the air is still warm, but it has lost most of its moisture, so it blows down as a very warm, dry wind. It starts in the Karo highlands and is funneled into the upper Langkat and upper Deli Serdang regions through the Bohorok depression. This concurs with the arbitrary border separating North Sumatra from South Sumatra.

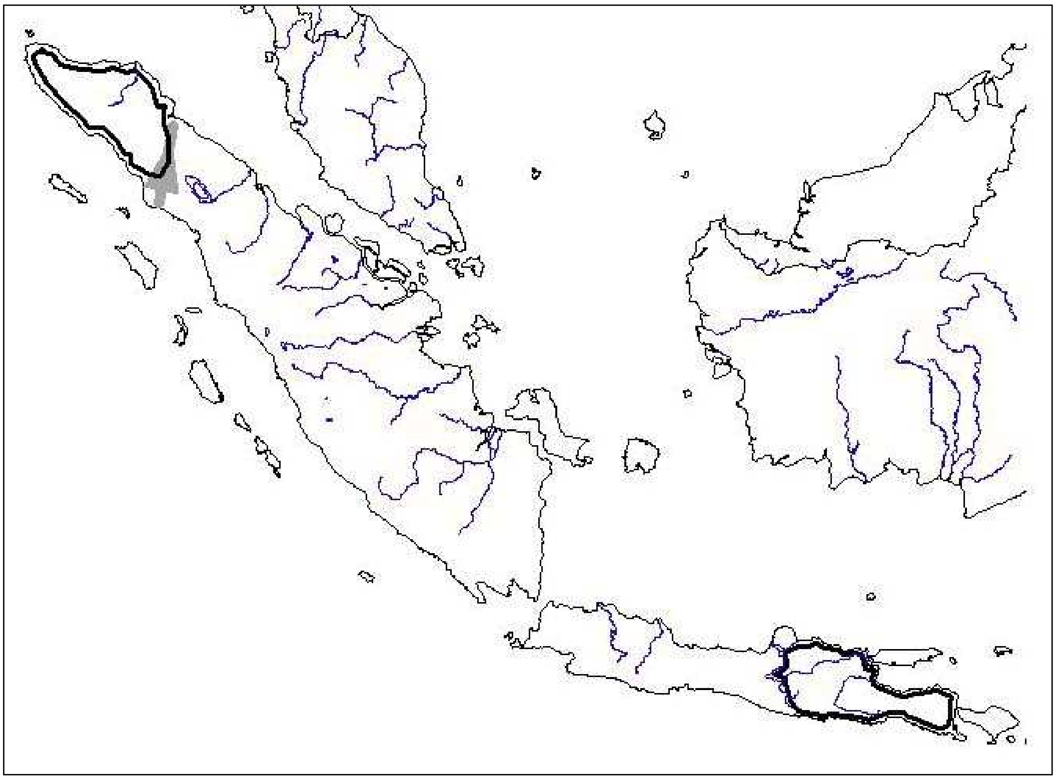


Figure 4.81 The ranges of *Mus caroli* (thick line), showing disjunct populations on North Sumatra and East Java. The grey arrow shows the Angin Bohorok.

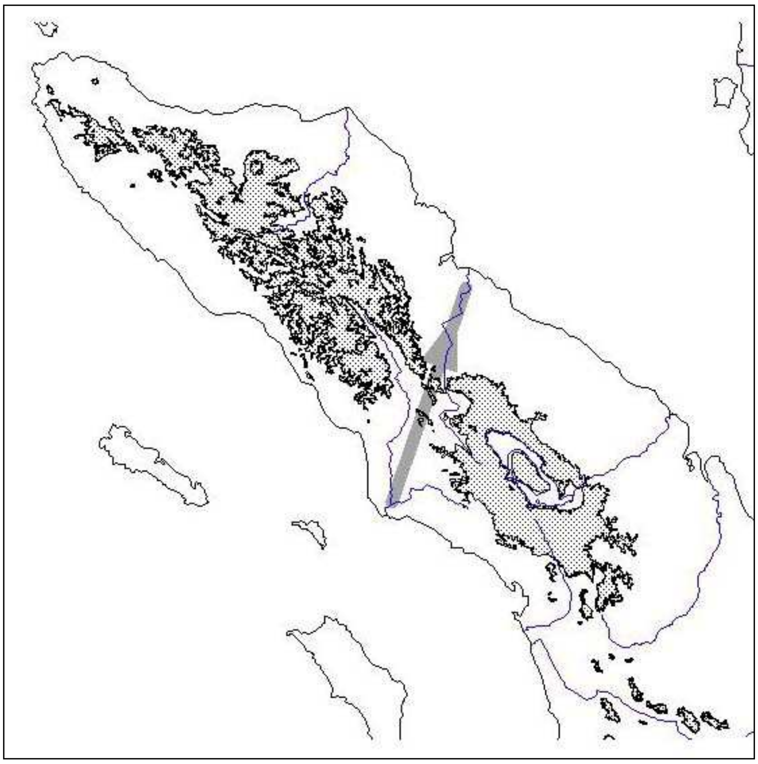


Figure 4.82 The break in the mountain range (stipples) caused the southwesterly winds (grey arrow) to be funnelled through and acted as a natural boundary for faunal distribution.

In regard to the existence of such a barrier, fauna restricted to North Sumatra, for example *Presbytis thomasii* (Cercopithecidae), apparently reached this region not from the southern part, but they penetrated this region through the exposed Sunda Shelf from the Malay Peninsula. As the land bridge appeared in the post Glacial, they then became isolated there. The penetration of *Presbytis melalophos* and *P. thomasii* inland suggests the retreat of the tree line as the climate warmed up. Their separation at subspecific level later was much affected by physical barriers of 1,000m contour lines and rivers.

Palynological evidence from Lake Kerinci and Lake Toba shows that, up to 16,500 years ago, a mosaic of sub-alpine and upper montane forest probably existed on the Siborong-borong Plateau, south of Lake Toba (Maloney, 1980 in Whitten, 1987). Oak forest became established about 16,500 years ago and persisted until ± 12,000 years ago, which led to the lowering of the vegetation zones by 350-500m (Maloney, 1983 in Whitten, 1987). The climate began to warm about 8,000-9,000 years ago, so the upper montane species retreated up the mountains (Whitten et al., 1993). Montane taxa such as *Chimarrogale phaeura* and *Crocidura baluensis* (Soricidae) are currently disjuncted on the mountaintops of Borneo, Sumatra and the Malay Peninsula.

On the Javan mainland, disjunct populations of *Presbytis comata fredericae* (Trachypithecidae) that inhabits Mt. Slamet from its close relative, *P. c. comata*, in the western part show that Glaciation lowered the tree line so that *P. c. fredericae* could disperse to Mt. Slamet. Its absence eastward of this is certainly due to a habitat change, to a much drier region, which was caused by the dry southeast trade winds. Lowlands in East Java therefore experience the driest climate among the islands. The rainforest habitats exist only on montane regions at high elevations. Thus, it is not surprising if its faunal elements are more represented by volant fauna, such as *Turdus poliocephalus whiteheadi* (Turdidae).

4.3.2.2 Sahul Shelf

In the Pleistocene period, there was rapid uplift of the New Guinea mainland as suggested by Löffler (1976). This physiographic change in turn affected the regional climate. The raising of the North Coast Ranges in Northern New Guinea and the Adelbert Range in Northeastern New Guinea resulted in the formation of rain shadow deserts on the leeward side because the wet Northeast Trade Winds loss their moisture after they drop heavy rain on the windward side. Therefore, the leeward side experiences warm and dry winds.

In the last Pleistocene glaciation, the regional climate got more seasonal. Based on pollen analyses, it is known that the lowering of the sea level reached its maximum approximately around 18,000 years B.P. and the tropical lowland forests were largely replaced by the lower montane oak forests (van der Kaars, 1991) (see Fig. 4.83). For fauna restricted to such habitats, the lowering of these forests had facilitated them to disperse across lower elevations. Some of such taxa is for example *Dendrolagus goodfellowi* (Macropodidae). Currently the occurence of three subspecies show clearly how their ranges were once connected each other by migration corridors of such forests. They are *D. g. pulcherrimus* on the Northern North Coastal Range sub-endemic area, *D. g. buergersi* on the Southern North Coastal Range sub-endemic area and the modest elevations of the Eastern Central Cordillera sub-endemic area and *D. g. goodfellowi* on the modest elevations of the Southeastern Central Cordillera sub-endemic area. The absence of this species from the Western Central Cordillera indicates that this region was much wetter than the Eastern and Southeastern Central Cordillera because it is situated outside the rain shadow deserts.

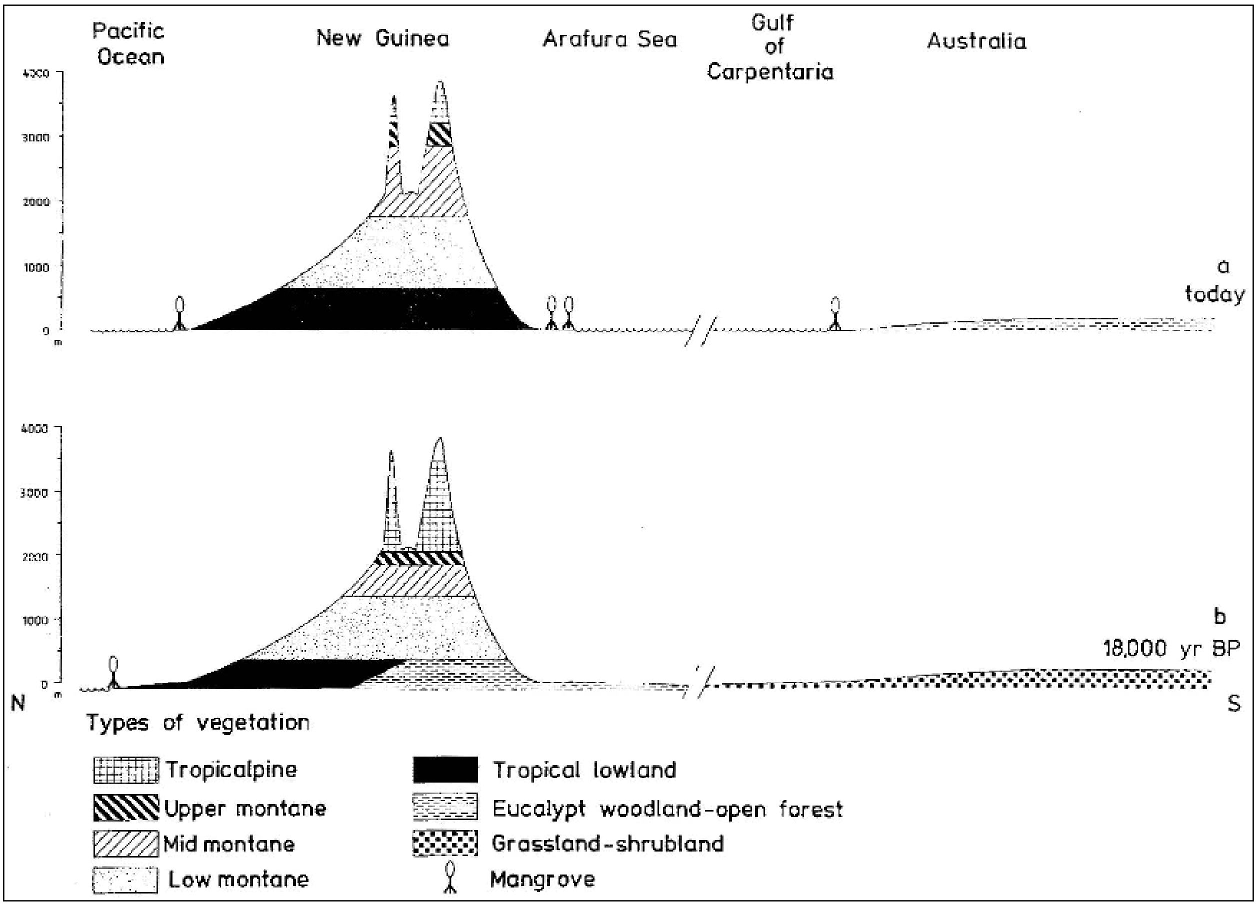


Fig. 4.83 Idealised vegetational cross section of New Guinea and northern Australia along longitude 137^{0}E. Comparing present-day situation (a) with a tentative reconstruction for the last glacial maximum (b) (from van der Kaars, 1991).

By the expansion of these lower montane oak forests, the natural vegetation lying on the migration corridors had been contracted. This can be well observed at the upper Sepik-Fly rivers and Ramu-Markham rivers by the occurrence of endemic rainforest dwellers there. Endemic forms restricted to the former rivers are for example monotypic group *L. Leucova*, *L. havina* and *L. majikthise* of *L. iris* species group, *Nyctimystes zweifeli* (Hylidae – Pelodryadinae); possibly *Callulops sagittatus* (Microhylidae – Asterophryinae); *Albericus rhenaurum* (Microhylidae – Genyophryninae); *Phalanger matanim* (Phalangeridae) and *Pogonomys championi* (Muridae – Uromyini). On the other hand, endemic forms restricted to the latter is for example *Mantophryne infulata* (Microhylidae – Asterophryinae).

The dispersal of montane taxa across lower elevations, which has been facilitated basically by the descent of the tree line, has also been proposed by Pasveer and Aplin (1988). Based on vertebrate remains from archaeological cave deposits, they recorded numerous montane taxa, which migrated down as far as about 350 – 400m above sea level on the Bird's Head in the Last Glacial Maxima. As a result of this lower tree line, highland forms on the Bird's Head and the Central Cordillera were interchanged.

The close relationship between alpine zone of the Eastern Highlands and of Mt. Albert Edward in the Southeastern Central Cordillera also makes sense only if the lowering of the tree line had occurred during the Quaternary. Geological records from Mt. Giluwe (4,365 m) and Mt. Wilhelm (4,509 m) in the Eastern Central Cordillera show that the last glaciation on these mountains was contemporaneous with the last glaciation of the northern hemisphere. The recession of the ice began at about 12,000 year B.P. and by 9,000 years B.P., the mountain peaks of Papua New Guinea were completely free of ice (Löffler, 1976). Thus, the separation of their faunal elements, for example *Thylogale calabyi* (Macropodidae), can be suspected to had undergone at this time. In contrast to this, the mountain peak of Mt. Jaya (5,030 m) in the Western Central Cordillera is still covered by ice field until today despite the steady retreat of its glaciers (Peterson *et al*. 1973; Peterson & Peterson, 1994; van Ufford & Sedgwick, 1998). Therefore, it is only distantly related to the alpine zone of the Eastern and Southeastern Central Cordillera.

Other than facilitating migration corridors for some montane fauna, an interesting phenomenon found in this period is that the lowering of the tree line seems to had caused at the same time the extinction of some other montane fauna (see Table 4.36). The Table show clearly two patterns of the extinct marsupials in New Guinea, i.e. 1) the Pliocene fossils correlated to the lowlands browser and 2) the Pleistocene-Holocene fossils correlated to the browsers on the higher elevations. These two patterns are relatively simply to explain. The regional climate change in the mid-Pliocene period, which resulted from the closure of New Guinea from the wet monsoon winds, was much affected the lowland inhabitants because New Guinea still lying much lower at that time. The regional climate change in the Pleistocene glaciation period was contrastly much affected fauna living on higher elevations because New Guinea mainland had been raised rapidly in the Pleistocene period.

Table 4.36 Summary of the extinct Plio-Pleistocene and Holocene marsupials of New Guinea (from Flannery, 1995)

Taxon	Age	Ecology
THYLACINIDAE		
Thylacinus sp.	Pleistocene-Holocene	carnivore
MACROPODIDAE		
Dendrolagus noibano	Pleistocene	Mid-montane browser
Protemnodon buloloensis	Pliocene	Lowlands browser
Protemnodon hopei	Pleistocene	Subalpine browser
Protemnodon nombe	Pleistocene	Mid-montane browser
Protemnodon otibandus	Pliocene	Lowlands browser
Protemnodon tumbuna	Pleistocene	Mid-montane browser
Thylogale christenseni	Pleistocene-Holocene	Subalpine grassland
Thylogale sp.	Pleistocene-Holocene	Subalpine grassland
Watutia novaeguineae	Pliocene	Lowland browser
DIPROTODONTIDAE		
Hulitherium thomasettii	Pleistocene	Mid-montane browser
Kolopsis rotundus	Pliocene	Lowlands browser
'Kolopsis' watutense	Plio-Pleistocene	Lowlands browser
'Kolopsoides' cultridens	Pliocene	Lowlands browser
Maokopia ronaldi	Pleistocene	Subalpine browser

On the other hand, for lowland inhabitants, the expansion of montane vegetation resulted in the break up of the gene-flow in some places. An example for such a case is the isolation of rainforest dwellers in the Northern North Coast Ranges from their relatives, commonly in the Bird's Head. Other example is the separation of *Talegalla fuscirostris meyeri* (Megapodiidae) on the Bird's Neck sub-endemic area from its close relatives on lowlands of Southern New Guinea. The hybridization in the Siriwo River between the two crowned-pigeon, which are strickly restricted to the undisturbed lowland forest, also reveal a former expansion of montane vegetation. They are *Goura cristata* (Columbidae), which is known as a faunal element of lowlands of the Bird's Head sub-endemic area, and *G. victoria* (Columbidae), which occurs in Japen and Biak islands and northern New Guinea.

In contrast to Northern North Coast Ranges, rainforest lowlands in the Northeastern New Guinea seems to be less isolated. Taxa found there, such as *Mantophryne infularis* (Microhylidae – Genyophryninae), extend their ranges generally further south through the upper Ramu and Markham rivers. In respect to the Northeast Trade Winds, the Northwest-

Southeast Adelbert Range does form the rain shadow deserts on the leeward side, but the occurrence of lowlands in both ends of the range has acted as migration corridors for fauna to disperse further south.

Other than replaced by the lower montane oak forests, the tropical lowland forests were also suffered from the expansion of drier vegetation, such as eucalypt woodlands, open forests, grasslands and shrublands (see fig. 4.83). The southern New Guinea was mainly affected by such expansion because it faces the Arafura Sea which was exposed by the lowering of sea level in the last glaciation. Thus, the lowland forests in Trans-Fly sub-endemic area and the Mambare-Anabunga sub-endemic area, which are situated in the southernmost of New Guinea, are mostly replaced by these drier vegetation. The existence of previously primary rainforests on these two sub-endemic areas has been indicated by the occurrence of endemic rainforest dwellers there, for example *Dorcopis luctuosa luctuosa* on the Mambare – Anabunga sub-endemic area and *D. l. phyllis* on the Trans-Fly sub-endemic area. The known hybrids between the two birds of paradise, which are strickly restricted to rainforests, in the Fly/Strickland rivers support a former expansion of drier vegetation in the Trans-Fly sub-endemic area. The two birds are *Paradisaea apoda* and *P. raggiana* (Paradisaeidae). The former occurs in southern New Guinea, from Mimika River in the west to the Fly River and perhaps Strickland River in the east. In East presumably overlaps with (hybrids known). *P. raggiana* itself inhabits area to the east with the western boundary on the Fly/Strickland rivers, but a western isolate populations inhabits relict rainforest in the Trans-Fly (at Morehead).

On the other hand, the close relationship between these two sub-endemic areas suggests the existence of the non-rainforest migration corridor in the intermediate area, undoubtedly on the exposed Arafura Sea. Later in the post-glacial period, the sea-level retreated to its current level and let populations on these two sub-endemic areas disjuncted. Their recent separation are shown as they generally still remain at the same taxonomical level, for example *Litoria congenita* (Hylidae – Pelodryadinae) and *Macropus agilis papuanus* (Macropodidae).

There contrastly might be an extension of rainforests lowlands in the Northern New Guinea as shown on Fig. 4.83. This in turn explains the close relationships of Northern North Coastal Range sub-endemic area with Japen Island to the west and rainforest lowlands in the Northeast New Guinea. Gene flow among these areas however must have been ended as the sea level retreated up in the post glacial period.

Furthermore, the exposure of the Arafura Sea in the last glacial maxima had facilitated faunal exchange between New Guinea and Australia. A landbridge existed between the two regions may have been the first migration corridor through such a land connection, contrastly to several possible land connection much longer before Pleistocene period as proposed by Flannery (1995).

4.3.2.3 Wallace's Region

Between the Sunda and Sahul shelves, there are currently islands isolated by broad deep marine barriers; being separated by Wallace's Line from islands on the Sunda shelf and by Lydekker's line from islands on the Sahul shelf. The region well known as Wallace's region or simply Wallacea thus includes Sulawesi and the nearby islands, the Moluccas and the Lesser Sundas (except Bali) and the Banda Arcs.

In Sulawesi, the lowered sea level in the last glacial maxima resulted in a more arid seasonal climate in the southwestern peninsula than the other regions because it was affected by the dry southeast trade winds. There was an ecological transition to the Central Sulawesi from the dry, low-elevation forest of the southwestern peninsula to the moister, mid- to high-elevation forest of Central Sulawesi (Supriatna, 1991; Supriatna et al. 1992 in Evans et al., 2000). This might have resulted in the separation of *Macaca maura* on the southwestern peninsula from *M. tonkeana* to the north.

Other than separation between species as undergone on *M. maura and M. tonkeana*, the more seasonal regional climate on the southwestern peninsula might have also caused the faunal extinction there. Beside the Cabenge fauna date from the Late Pliocene (more than 1 million years ago), other fossil remains of Sulawesi had been collected from various limestone caves near Maros in the southwest peninsula. The animals in the cave sites are known as the Toalian fauna and are of relatively very recent origin, dating from perhaps 30,000 years ago (Hooijer, 1950 in Whitten et al. 1987). They represent species, which are today still found on the mainland.

As in other mainland, the lowered tree line in the last glacial maxima can be detected from the formation of most sub-endemic areas in lowlands of Sulawesi, except those resulted from the inundation of Lake Tempe in the southwest peninsula and Lake Limboto in the northern peninsula. The expansion of lower montane forests had isolated one peninsula from another. On the other hand, for montane dwellers theirselves, such an expansion had facilitated their dispersal across lower elevations.

The most recent sea level maxima in the post glacial period detected off the southwest peninsula were 4,500 and 1,600 years ago when sea level was 5 and 2.5m higher respectively than at present (Figure 4.84) (de Klerk, 1983 in Whitten *et al.*, 1987). Evidence for this has been found in the vegetation record. The pollen remains taken from the swampy Lake Rawa Lampulung in the Lake Tempe region shows that at least part of the surrounding area was covered by mangrove vegetation, that is, it was inundated by sea, from about 7,100 to 2,600 years ago (Gremmen, in press in Whitten, 1987). This caused the separation of the blocks of land either side of the Tempe depression and in turn made the separation between *M. maura* and *M. tonkeana* get longer.

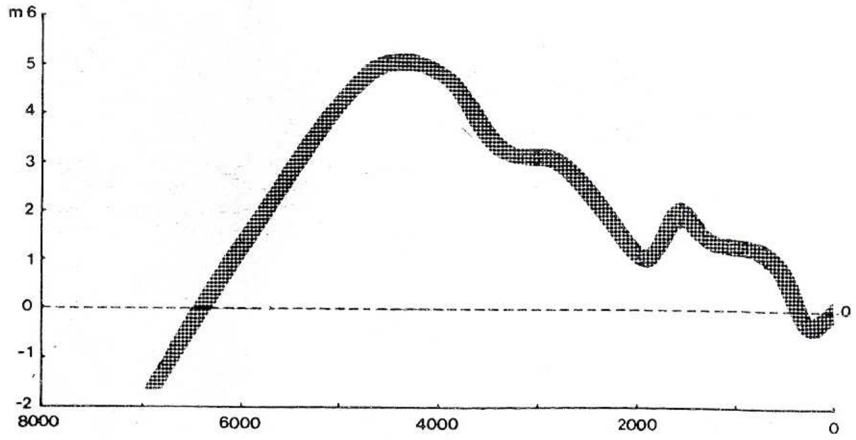


Figure 4.84 Changes in sea level over the last 7,000 years determined from a study on the southwest peninsula of Sulawesi (After de Klerk 1983 in Whitten *et al.* 1987).

The raising of sea level in the post glacial apparently also caused the separation of Lake Limboto in the northern peninsula and this might have resulted in the separation between *M. hecki* and *M. nigrescens*. The former itself was formerly considered as a subspecies of *M. nigra* on Northeast Sulawesi sub-endemic area, while the latter as a subspecies of *M. tonkeana* on Central Sulawesi.

Currently, *M. maura* and *M. tonkeana* is known to hybridize in the northern extent of the low-lying Tempe Depression. The mtDNA study conducted by Evans et al. (2001) suggests that *M. maura* females colonized this region since the last oceanic retreat. *M. maura* females is suspected to be better adapted to the lowland conditions of this region, more likely to disperse, or able to exclude *M. tonkeana* females. However, the current level of effective gene flow between *M. maura* and *M. tonkeana* itself is thought to be insufficient to homogenize their respective genomes in the future. From the biogeographical point of view, this shows that gene isolation since the last glacial maxima has been long enough time for speciation in these macaques

Islands of Banggai and Sula off eastern Sulawesi are currently connected by a 200m isobath. The lowering of the sea level in the Last Glacial Maxima connected these islands with each other so that some of their faunal elements could exchange. An exception in this case is Sanana Island. Although this island was lying very close to Mangole Island, there are no Sulawesian fauna that could migrate to this island. Therefore, *Strigocuscus pelengensis mendeni* (Phalangeridae) and *Rattus elaphinus* (Muridae – Murinae) successfully colonised Taliabu Island and Mangole Island, but did not extend to Sanana Island. In contrast, fauna confined to Sanana Island, such as *Callulops kopsteini* (Microhylidae – Asterophryinae), *Platymantis papuensis occidentalis* (Ranidae – Cornuferinae) and *Phalanger orientalis orientalis* (Phalangeridae) could not move to Mangole Island. This evidence leads to the assumption that the eastern part of Mangole Island was likely to have still been submerged in the Last Glacial time so that fauna of Mangole and Sanana remained separated.

It has been mentioned in the last section that the eastern part of Flores Island and other islands eastward from Flores Island, except Alor and Wetar, might have still been submerged as Java and Bali pushed the Lesser Sundas eastwards. Islands of the Flores group, from Komodo to Alor, are lying within the 200m isobath. Hence, they are suspected to have connected to each other by the lowered sea level in the Last Glacial Maxima. However, the only records of amphibian and mammal, i.e. *Limnonectes kadarsani* (Ranidae) and *Cervus timorensis* (Cervidae), on Adonara Island, just eastward from Flores Island, show that most islands eastward from Flores Island remained submerged in the Last Glacial period. Thus, it is now clear that the emergence of some islands in the Wallacea region occurred very recent and this in turn explains the absence of some taxa on certain islands.

Positive evidences also come from subfossil records. Based on those records, it is known that there was a numerous faunal extinction on Flores Island around 3,000-4,000 years B.P. This might have been as a result of the rise of the sea-levels in the post glacial maxima (see Fig. 4.84). Because Flores Island was still lying much lower than it is today, such rising of the sea-levels might have resulted in submergence of most of that island, following by extinction of numerous fauna live thereon.

4.3.3 Biogeography and Conservation

The recognition of biogeographic units, especially areas of endemism, in conservation work is the most important in order to ensure the establishment of each representative and to hinder ineffective protection efforts. Especially within the mainland, where endemism is partitioned, this would help much in determining areas with complementary, non-redundant diversity as the target for protection to attain the best preserve biodiversity (Vane-Wright et al. 1991; Brown & Lomolino, 1998).

The result of this study recognised, that some protected areas, which, already existed in Indonesia, are sometimes redundant, while the other more important areas with high endemicity are barely protected. Poorly regulated development and the non-sustainable harvesting of natural resources, especially timber, now threaten high endemism on Borneo. The other islands of the Great Sundas, i.e. Sumatra and Java experience similar conditions, especially in Java, where a real competition with human's need is the worst. New Guinea is suffering from one of the the world's largest producers of copper. Other islands are not better. Conflicts with human are the most environmental problems in the developing countries.

In Borneo, high efforts must be given to the Mt. Kinabalu region. Also eastern and southeastern Borneo as well as northern Borneo deserve high protection. The large southwestern Borneo on the other hand is only important in the region where Pleistocene dry relicts occur. In Java, the high mountains, especially those in the western and eastern parts, are important due to their high endemicity. The central part is important only in certain area, such as Mt. Lawu. Also the lowlands in the eastern part and the north coastal should be well preserved for their dry relicts. In Sumatra, the most important area to protect seems to be islands off the western coast of Sumatra that never had a land connection to the mainland since the Pliocene, such as the Mentawai Island. In Sulawesi, the southwestern and the northern peninsula are the most important. In New Guinea, the highlands of Tamrau and the Arfak mountains have been relatively well protected. However, other important area, such as the Bird's Head, is only poor protected. There is only one nature reserve there, i.e. Teluk Bintuni Nature Reserve, the object of which is to protect a wide lowland area on the Bird's Head, whereas in fact there are both lowland rainforests and dry form relicts. The Bird's Neck sub-endemic area is not protected at all. The same condition occurs on the Central Cordillera and the south-central part. The islands of Batanta, Japen, and Aru also do not have protection. Within Wallacea's region, Halmahera, Ceram, Timor and Flores are the first priority. Also Wetar must be considered within.

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