..let us take the great islands of Sumatra and Java. These approach so closely together and the chain of volcanoes that runs through them gives such an air of unity to the two, that the idea of their having been recently disjoined is immediately suggested. The natives of Java, however, go further than this; for they actually have a tradition of the catastrophe which broke them asunder, and fix its date at not much more than a thousand years ago.

The Malay Archipelago,
Alfred Russel Wallace

Mt. Bromo in East Java, one of the many volcanoes that shaped Indonesia.
Island South-East (SE) Asia (see Figs. 1.1 and 1.2) is one of the richest areas in the world in terms of its biodiversity (Sumardja 1997; Myers et al. 2000), with ca. 13% of all mammal species occurring on about 1% of the world’s land mass. This species richness is probably the result of the region’s dynamic geological past (Holloway & Hall 1998), and relatively stable environmental conditions, which resulted in many speciation opportunities and relatively few extinction events (e.g. Whitmore 1987). Its life forms are adapted to a climate characterized by uniform but not excessive heat, abundant moisture, and no marked departure from the average meteorological state, throughout the year. These conditions only occur in three widely separated regions of the world, island SE Asia, western Africa, and South America, which is probably why, for example, the tapir and trogons of Malaya should so closely resemble those of South America; and that the great apes and crested hornbills of western Africa should find their nearest relatives in Sumatra and Borneo (Wallace 1876).

Figure 1.1. Island SE Asia, a highly fragmented part of the world’s land mass.

In particular, the high geological activity of this highly fragmented region (see Fig. 1.1) has led to complex patterns of species diversity, and, as a consequence, the zoogeography of this region remains poorly understood (e.g. Heaney 1984, 1986; Ruedi 1996). One of the reasons for this is that limited information is available on palaeo-faunas and floras, as fossil finds are rare. Even when sites are found, the incompletely known nature of the biota inhibits clear interpretation of past environments from fossil evidence. This lack of a palaeoenvironmental background puts this region in a somewhat underprivileged position. In Africa, for instance, many authors have discussed patterns of mammalian distribution in a palaeoenvironmental
context (e.g. Rodgers et al. 1982; Kingdon 1990; Potts & Deino 1995; Gibernau & Montuire 1996; Bobe et al. 2002). Also, South and Central America have been the subject of much debate and a strong theoretical framework exists explaining biogeographic patterns (e.g. Haffer 1969; Brown 1987; Colinvaux et al. 1996; Haffer 1997; Colinvaux 1998; Colinvaux & De Oliveira 2000; Colinvaux et al. 2000; Cowling et al. 2001), although some of the theories remain contested. A substantial understanding of the evolutionary processes that took place in these two continents allow much more than in SE Asia the modelling of, for instance, species richness and bioregions, important in species conservation, or the interpretation of human evolution and dispersal.

Figure 1.2. Map of SE Asia, showing the Sundaic and Wallacean Subregions and country names. Solid line = Wallace's Line; dashed line = Huxley's Line.

There is therefore a considerable need for improving the palaeoenvironmental understanding of the SE Asian region and the related phylogenetic and biogeographic patterns of SE Asian species. To address this need there have recently been several
conferences specifically aiming to bring together the specialist knowledge of geologists, biogeographers, taxonomists, and evolutionary biologists: In 1996, “Biogeography and Geological Evolution of SE Asia” (Hall & Holloway 1998); in 1999, “Faunal and Floral Migration and Evolution in SE Asia-Australasia” (Metcalfe et al. 2001); and in 2000, “Leiden 2000: A Double Bill. Biogeography of Southeast Asia 2000”. These meetings showed that there is a rapid advance in understanding of the region’s geological evolution and phylogenetic and biogeographic patterns, although a coherent synthesis of the two is still required.

The biogeographical theory for the region dates back to the 19th century when scientists such as Müller in 1839, Earl in 1845, and Sclater in 1858 noted the faunal break between east and west Indonesia. In fact, Müller described a zoogeographic boundary in 1846, the formal description of which would lead to Wallace’s fame some 20 years later. This boundary separated Borneo, Sumatra, Java, and the lesser Sundas, on the one side, from Sulawesi, and other eastern islands on the other. Müller explained these patterns by the differences in climate and island area, and the related physiology of the species (Weber 1902). However, it was not until later, when Wallace mapped the zoogeographic boundary separating Sundaland in the west from Sulawesi and Lombok in the east, that a more solid theoretical framework was provided for the overall biogeographic patterns in the region.

Huxley (1868), who found greater biogeographic affinities between Palawan and Borneo than between Palawan and the Philippines, modified Wallace’s Line such that the greater proportion of the Philippines were excluded from Sundaland (Fig. 1.2). Since then, a large number of adaptations have been made to the basic model of Wallace and Huxley, which, often depending on the species group under consideration, shifted the zoogeographic boundaries across the regional map; still the Wallace’s Line retained its almost mythical status (see Keast 2001). Although these lines indicate to some extent the affinities of certain species groups with either the Asian or Australian continent, they rarely provide an explanation for how the species arrived and survived at their present locations. Neither of the large areas on either side of the Wallace/Huxley Lines, i.e. the islands of New Guinea and Borneo/Java, are connected to what are considered to be the source lands of their faunas, Australia and
mainland Asia respectively. The main question is therefore how non-volant land species arrived on these islands, and why, after having arrived there, they stopped at the boundary drawn by some 19th century scientists. A logical explanation is, of course, that both these islands have ‘better’ connections with their own source area, than with the areas across the Wallace’s/Huxley’s Lines. Charles Darwin imagined that isolation, brought about by subsidence of once-continuous lands, was critical in differentiation between species. In his notebook B, which began in the second half of 1837, he wrote: “….Species formed by subsidence. Java & Sumatra. Elevate & join keep distinct. two species made. elevation and subsidence continually forming species.” In searching for a solution to the relation of mammalian species in the archipelago, he looked to the depth of water between islands and the possibility of former land connections between them, pencilling in the phrase “relation of character of quadrupeds to soundings”. As part of his research, Darwin studied Dutch charts of the region that listed measurements of soundings between the islands of the archipelago. He made a list of especially deep places, three of which were located exactly on the line that Wallace later drew dividing the Asian and Australian biotic regions (Camarini 1994). Following a similar train of thought, Earl (1845, in Wallace 1869, p. 20) gave an explanation for changing island connections in a paper read to the Royal Geographical Society. He noted the shallow seas that connected Java, Sumatra, and Borneo to the Asian mainland, and a similar shallow sea connecting New Guinea and some of the adjacent islands to Australia. Both these seas connected islands with similar faunas. Wallace (1892) was one of the first to link these shallow seas to sea-level lowering during the Pleistocene glacial periods (for names of eras, epochs and periods see Table 2.1), while he also discussed the role of glacially induced environmental changes in shaping the region’s biogeography. Weber (1902), later followed by the better-known work of Molengraaff and Weber (1920), further refined this idea and added the influence of Pleistocene river courses on species distributions.

The Isthmus of Kra (Fig. 1.2) is another zoogeographic boundary in this region. Located on the Malay/Thai Peninsula it separates the Indochinese and Sundaic Subregions (Corbet & Hill 1992). It was initially recognized as an important floristic boundary (e.g., van Steenis 1950), but it also separates mammalian and avian faunas (e.g., Wallace 1876; Hughes et al. 2003). Wallace (1876, p. 315) drew a line between
the Indo-Chinese and Indo-Malayan (now named Sundaic) Subregions at about 13–14 °N, but now the boundary is generally considered to be further south between 11 and 13 °N (Hughes et al. 2003). Because this biogeographic boundary is diffuse it is probably better to refer to it as a transitional zone rather than a line.

Many authors (Beaufort 1926; Kahlke 1972; Banks 1980; von Koenigswald 1981; Heaney 1985b; MacKinnon et al. 1996) have characterised Sundaland as a system through which most species could freely move during glacial periods, up until approximately 10 thousand years ago (Kya) when higher sea-levels once more physically separated the islands. However, studies of the fossil faunas of Java, and to some extent Sulawesi, Flores, and Borneo, for instance, show that mammalian faunas in these areas date back much further than the Late Pleistocene (e.g. Stromer 1931; van der Maarel 1932; Brongersma 1935; von Koenigswald 1935b; Hooijer 1952, 1957, 1962; Dawson 1971; Hemmer 1971; Kahlke 1972; Schütt 1973; Aimi & Aziz 1985; van den Bergh et al. 1996, 2001; van den Bergh 1999; Zaim 1999). Furthermore, phylogenetic investigations of the region’s mammalian faunas using taxon-specific differences in DNA sequences also point to divergence times between species that date back hundreds of thousands or even millions of years (Myr) (e.g. Hayashi et al. 1995; Lan et al. 1995; Miththapala et al. 1995; Randi et al. 1996; Ruedi 1996; Ruedi & Fumagalli 1996; Zhi et al. 1996; Evans et al. 1999; Amato et al. 2000a; Warren et al. 2001). This indicates that mammals have been present in the region and undergone speciation for a long time.

Clearly, a biogeographic model that focuses on Late Pleistocene events alone misses out on the significant contribution of evolutionary processes before that time. Still, many biogeographers focus on the Last Glacial Maximum (LGM) and concomitant sea-level lowering in the explanation of biogeographic patterns in mammals (e.g. Kahlke 1972; von Koenigswald 1981; Brandon-Jones 1996a, 1998; Kitchener & Dugmore 2000). Others recognize that mammalian speciation in island SE Asia has taken place for much longer than the last 10 or 20 thousand years (Kyr), although they still consider Pleistocene sea-level changes as a major factors in species divergence (e.g., Cracraft et al. 1998; Bininda-Emonds et al. 1999). There are probably several reasons why this is happening. Firstly, there is a considerable lack of fossil finds,
especially from Sumatra and Borneo, which has made it difficult to develop a comprehensive biogeographic model for the region with sufficient time depth. Secondly, the region is tectonically very active and there have been many changes in land-sea distribution during the Tertiary and Quaternary, the majority of which are still poorly understood, and remain little investigated. Thirdly, I think that there is great attraction in the LGM model of a large exposed Sundaland mass, dissected by massive rivers, which then disappeared under the sea. This LGM model does explain many biogeographic patterns, especially those that focus on faunal similarities between the islands. It is the exceptions to the model, however, that show how incomplete it is.

A more complete biogeographic model for the region was first proposed by von Koenigswald (1935a; b), and later developed further by other palaeontologists (for an overview see van den Bergh et al. 2001). It relied primarily on similarities between fossil faunas from the Asian mainland, Java, Sulawesi, and Flores. Von Koenigwald hypothesized that mammals from the Indo-Malayan Region first colonized Java when it was an island in the Late Pliocene to Early Pleistocene (note that definitions of Pliocene and Pleistocene stages are continuously changing making it difficult to compare between different sources). During the late Early Pleistocene, a limited land connection came into existence between Java and the Asian continent, allowing more species, including *Homo erectus*, to enter Java. Von Koenigwald (1939 in Shutler & Braches 1986) considered the oldest fauna of Java to be entirely Siva-Malayan, i.e. of Indian origin. He proposed that the Sino-Malayan fauna with Chinese affinities joined the Siva-Malayan fauna on Java at a later time, implying that these faunas mixed on Java rather than on the continent. Towards the end of the Early Pleistocene and periodically during the Middle Pleistocene, more extensive land connections came into existence, allowing fully balanced mainland faunas to enter Java. Von Koenigwald (1935a; b) suggested that, during the Pleistocene, mammals migrated to Java via the Philippines and Borneo on the basis of the Chinese affinities of this fauna. This theory has been largely rejected (see, for example Shutler & Broches 1986; van den Bergh 1999; Tougard 2001), because the Philippines and Sulawesi have typical island faunas, which suggests that they were not part of a continuous land migration route. Also, it is doubted whether Java had an exclusively Siva-Malayan fauna, as the
faunal unit associated with this fauna is no longer acceptable (Shutler & Braches 1986). Instead, Shutler and Braches (1986) proposed the Burma-Nepal area as the likely place where the Chinese and Indian elements mixed before migrating to Java, rather than arriving separately and mixing on the island.

The possibility that Pleistocene faunal elements reached Java via Sumatra has also been abandoned because of the absence of Plio-Pleistocene fossils on the latter island (Shutler & Braches 1986), although Shutler and Broches (1986) suggested that instead these faunal elements could have reached Java via a route following the Andaman and Nicobar islands and the islands west of Sumatra. Muir et al. (2000) further speculated on the evolution of Sumatra’s mammals by suggesting that the explosion of the Toba volcano wiped out most of the island’s orang-utans, and presumably also many other species.

De Vos and Sondaar (1982) re-examined the Dubois collection of Javan fossils, and suggested that the use of guide fossils by von Koenigswald appeared to be of little use, because these guide fossils often represented isolated findings of very rare species. De Vos and Sondaar (1982) developed a new biostratigraphic scheme for Java which replaced the classical biozonation of von Koenigswald (van den Bergh, 1999). Although this new scheme appears to provide a good basis for the comparison of Javan faunas with those elsewhere, much of the details of the faunal succession and dating remain unresolved (van den Bergh, 1999; C.P. Groves, pers. comm.).

Medway (1971) presented some interesting new ecological insights in the biogeographic theory of the region. He suggested that since the Pliocene an ecological barrier existed that prevented certain continental faunal elements from reaching Java. Notable among this group are the true horses, the camel, giraffe, and a number of antelopes and other bovids. All these are adapted to arid or seasonal environments and Medway suggested that such vegetation types had to be absent from Pleistocene Sundaland. The large herbivores that did reach Java in the Early Pleistocene were forms that typically frequent riverine, forest edge, or forest habitats. In the Middle Pleistocene, the invading Sino-Malayan fauna contained a large number of forest-dwelling species, which to Medway suggested that, at one or more stages of the Middle Pleistocene, routes existed for the movement of forest-adapted mammals.
between continental SE Asia and Sundaland. Medway (1971) further suggested that, in the Pleistocene, internal barriers existed within Sundaland. On Borneo two continental proboscideans existed, one of which also occurred in Malaya, and neither of which were present on Java. He thought that the Bornean species might have reached Borneo by a north-western landbridge, along which other extant Bornean mammals like *Dendrogale*, *Dremomys*, and *Melogale* also spread from Indochina. At that same time, however, the Malayan Kinta Valley site and Java shared various ungulate species, showing that Java was probably not isolated from the rest of Sundaland.

Larick et al. (2000) linked basic geologic and faunal evidence to understand the biogeographic relationships between Java and mainland Asia. They suggested that as the Pliocene proceeded, a generally cooler global climate tied up enough sea water to forge Java’s first tenuous link with the mainland, which during the late Middle Pliocene allowed the colonization of Java by the Satir fauna. Next, the stronger cold spikes of the Late Pliocene would have further reduced sea-levels, which would be enough to firmly link Java with the mainland. The contemporary Ci Saat fauna still reflects somewhat isolated conditions, but its more advanced elephantids and bovids suggest a turn over. According to Larick et al., the Middle Pleistocene Trinil fauna still has relatively few species suggesting a mainland connection through a filtered corridor.

Tougard (2001) suggested that in the late Middle Pleistocene there was a northern fauna in SE Asia, biogeographically distinct from the southern one. The boundary between the two faunas was possibly located somewhere on the Malay Peninsular, probably south of the present boundary between the Sundaic and Indochinese faunas, i.e. the Isthmus of Kra. Finally, a tropical rainforest fauna of Chinese origin, including *Homo sapiens*, entered Java in the Late Pleistocene. During the Holocene break-up of the Sunda Shelf, the faunas on the various islands became impoverished in response to reduced land areas and changing climatic conditions (van den Bergh et al. 2001).

In Sulawesi, the first, still extant mammal genus to arrive was the Babirusa (*Babyrous* *babyrussa*) which is thought to have dispersed to the island in the Oligocene (Thenius 1970), or Miocene (Randi et al. 1996). The first clear wave of
species, which included elephants and stegodonts, appears to have had close affinities with the Siwalik faunas from Central Asia (Groves 1976; Cranbrook 1981; Musser 1987; van den Bergh 1999; van den Bergh et al. 2001). Van den Bergh et al. (2001) suggested that these species reached South Sulawesi from the Sunda Shelf during the Pliocene. A second wave of immigrants to South Sulawesi may have come from either the Philippines or Sundaland in the Middle Pleistocene. Finally, the origin of the fossil mammal faunas of the Lesser Sundan Islands is still under debate (van den Bergh et al. 2001). Groves (2001a) further discussed the origin and dispersal of Sulawesi’s mammalian fauna. He suggested that a land bridge may have existed between Sundaland and Sulawesi, as opposed to Cranbrook (1981), Musser (1987), and van den Bergh (1999; 2001) who considered the Sulawesi fauna to be depauperate and unbalanced, and suggested that it dispersed across the Borneo-Sulawesi sea barrier. According to Groves, the primates and viverrids that occur in Sulawesi can hardly be considered as part of a depauperate and unbalanced fauna. He suggested that possibly the first faunal wave (see above) may have come across a land bridge, while only the second wave might be derived from chance dispersal across the sea.

The biogeographic theory of Tertiary and Quaternary SE Asia has not only focussed on the presence and absence of land bridges between the islands, but many authors have also incorporated changes in vegetation into their models. Stresemann (1939) decided on the following working hypothesis. In the Early Pleistocene, during the first Dry Period (capitalization by Stresemann), the tropics were blanketed by grasslands, allowing for dispersal of grassland species from Burma and Malaysia to Sumatra and the lesser Sundas. Stresemann hypothesized another dispersal route from South China, via Taiwan to the Philippines, Sulawesi, and the lesser Sundas. This first Dry Period was followed by the first pluvial, and rain forest spread to the Malay Peninsula, North and West Borneo, the Philippines, and North Sulawesi. Savannah landscapes disappeared altogether along with the species that dependent on that vegetation for their survival. A second Dry Period followed, milder than the first one, which this time only opened the grassland corridor via Taiwan and the Philippines, as the other route was obstructed by rain forest. After this a second Pluvial followed. This model may be oversimplified, but, as will be suggested later, may hold a considerable grain of truth.
In summary, in spite of almost 200 years of investigation, the theoretical biogeographic framework for island SE Asia is still in its infancy. Even with recent advances in the field, there remain many gaps in our knowledge of palaeoenvironmental conditions and their relationship to mammalian evolution. Especially the biogeographic history of Borneo and Sumatra remains poorly understood, mainly because of an almost complete lack of fossil finds predating the Late Pleistocene. Also, most of the existing literature on the subject has addressed the Late Pleistocene and Holocene and little is known about what happened before that time. There is therefore a considerable need to further our knowledge of this subject, and to work towards a more complete biogeographic model.

In this research, I aim to combine palaeoenvironmental information from the literature with data on species evolution (either based on molecular data or on fossil finds). I believe that a thorough search of the literature will reveal data that have so far been overlooked by researchers working on this subject. Also, the linking of palaeoenvironmental information with data on the divergence of taxa, and the presentation of this in the form of maps will allow for a more advanced process of induction, hopefully revealing biogeographic and evolutionary patterns that have so far not been recognized. An improved biogeographic model will increase our understanding of the fundamental processes that have shaped the biodiversity in the region, invaluable knowledge in a time when much of this biodiversity is threatened with extinction. Many species are increasingly under pressure from a wide range of factors, and understanding the underlying forces shaping a species’ distribution can contribute to the preservation of species. Especially, in the Indonesian and Malaysian archipelago a good understanding of species’ biogeography is necessary to make wise decisions about which populations most need our conservation support.