

# Historical biogeography of *Spatholobus* (Leguminosae-Papilionoideae) and allies in SE Asia

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Key words: historical biogeography, phylogeny, Leguminosae, SE Asia

## Abstract

A phylogenetic analysis of *Spatholobus* and its allies (Leguminosae-Papilionoideae) is presented. The resulting phylogeny is used for a historical biogeographical analysis of SE Asia together with the phylogenies of three other genera: *Fordia* (Leguminosae-Papilionoideae), *Genianthus* (Asclepiadaceae), *Xanthophytum* (Rubiaceae). Areas of distribution, based on all species, are defined. The distribution areas coincide in large part with the tectonic terranes of SE Asia, and they are briefly discussed in connection with their possible geological history.

The result of the biogeographic analysis, a general area-cladogram of SE Asia, is compared with the available geological information. The general area-cladogram shows the existence of four major groups of areas: areas on continental SE Asia, areas around the Isthmus of Kra, areas on the Malay peninsula and areas on Borneo.

The first split in the cladogram is between the continental SE Asia group of areas (including the Isthmus of Kra) and the Sundaland groups. This can be interpreted in terms of varying sea levels between the mid-Eocene and the Pliocene.

The areas on the Malay peninsula do not show any tectonic event, because the areas were welded together long ago, before the development of the analyzed genera. The separation of areas on the peninsula are perhaps due to ecological factors.

The first four splits in the Borneo clade probably reflect uplift in the late Miocene-Pliocene of the areas of Meratus, SW Borneo, Semitau and NE Borneo. For other areas such as the Philippines and Sulawesi, not enough data were available.

The general area-cladogram is also used to reconstruct the biogeographical history of the genus *Spatholobus*. It is suggested that the genus came from around India, invaded the dry Sunda shelf during a period of low sea level, and speciated due to the isolation of the area after sea level rises. There were renewed invasions from the mainland into the Malesian archipelago during later periods of low sea level.

## Introduction

Although biogeographers have always had an interest in geology, this has been renewed since the broad acceptance of plate tectonic theory in geology and the introduction of cladistic methods in taxonomy. Taxonomists are not only interested in describing the flora and fauna, but also in discovering historical relationships, the phylogeny, within a group of taxa under study. When the phylogeny of a group is known, it is also possible to set up a hypothesis about the history of the group in space and time. In many cases speciation will be related to events concerning the area defined by the taxa, e.g., isolation. On the cladogram, distribution data of the taxa within the group can be plotted. By comparing and analysing the area-cladograms of different non-related groups, a general pattern will appear. This pattern, a general area-cladogram, may give information about the history of the areas, and thus be of interest to geologists.

*Spatholobus* consists of 29 species of lianas in SE Asia (Ridder-Numan and Wiriadinata, 1985; Ridder-Numan, 1992). The closely allied genera *Butea* and *Meizotropis* occur only on the mainland of SE Asia. Both genera are comprised of two species (Sanjappa, 1987). *Spatholobus* and its allies, *Butea* and *Meizotropis*, belong to the Leguminosae, subfamily Papilionoideae. As an outgroup for the phylogenetic analysis the genus *Kunstleria* has been chosen (Ridder-Numan and Kornet, 1994). This genus resembles *Spatholobus*, but differs in the amount of leaflets, the shape of the pod and the flower.

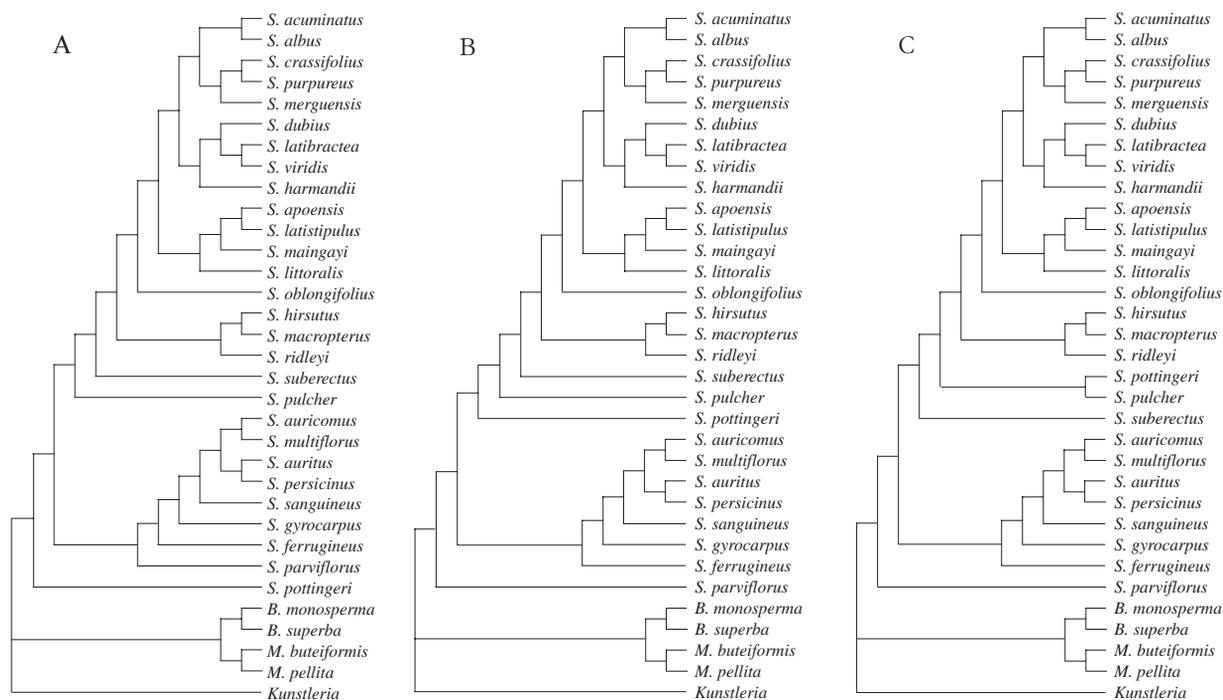


Fig. 1. Three most parsimonious trees found by using PAUP under the heuristic search option, 'stepwise addition sequence random', tree-bisection-reconnections (TBR); all characters analysed unordered, uninformative characters ignored and characters with multiple states treated as polymorphisms; length 589, CI 0.46.

## Phylogeny

The phylogenetic method is based primarily on the phylogenetic principles of Hennig (1966); the relationship between species can be found by looking for shared derived (apomorphic, homologous) characters, and not by overall similarities, which can arise through the sharing of common inherited 'primitive' characters (plesiomorphy). In this study, which is described in more detail in Ridder-Numan (1996), the phylogeny of the genus *Spatholobus* and allies and the cladistic biogeography of SE Asia are worked out. I will not add to the discussion on the methods and ideas behind phylogenetics, as there is a wealth of information on methodology and already many practical studies have been published (Brooks, 1990; Brooks and McLennan, 1991; Cracraft, 1983, 1988; Forey *et al.*, 1993; Nelson and Platnick, 1981; Page, 1988, 1990; Wiley, 1981, 1987; Zandee and Roos, 1987; for a recent overview: Morrison, 1996). Several computer programs have been developed to analyse the morphological or molecular data, *e.g.*, PAUP (Swofford, 1991, 1993), Hennig86 (Farris, 1988), PeeWee (Goloboff, 1993), and

CAFCA (Zandee, 1995).

For a phylogenetic treatment an existing group is used that is supposed to be monophyletic, although monophyly can never necessarily be assumed on beforehand. One of the purposes of cladistics is to find out if groups are monophyletic. In addition, it is necessary to include an outgroup, to polarise the character states used in the phylogenetic analysis.

## Data

A data matrix has been made for all species of *Spatholobus*, *Butea* and *Meizotropis*, which consists of 97 characters (relating to pollen morphology, leaf anatomy, and macromorphology). For details see Ridder-Numan (1996). The outgroup *Kunstleria* was considered a single taxon by coding the information on species as a combined column of data. Autapomorphic character states occurring in only one species were ignored, and any state occurring in the rest of the genus was taken as representative. Data for the matrix, as well as samples of pollen and leaves, were taken from herbarium specimens.

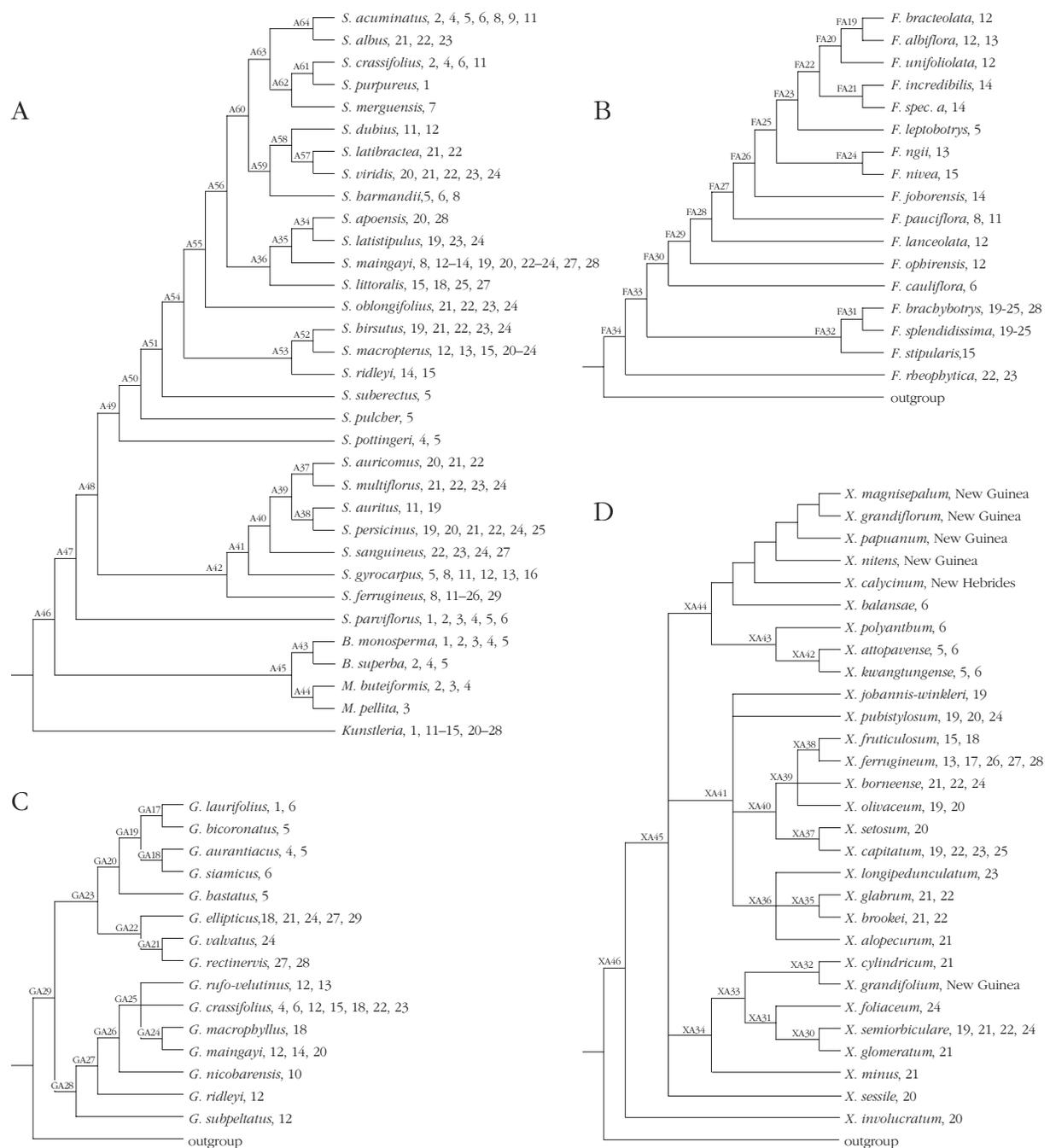


Fig. 2. Cladograms of A: *Butea*, *Meizotropis* and *Spatholobus*; B: *Fordia* (Schot, 1991); C: *Gentianthus* (Klackenberg, 1995); D: *Xanthophyllum* (Axelius, 1990). Numbers in the cladograms refer to the numbering of the ancestors used for compiling the area-taxon datamatrix. Numbers by species names refer to the areas shown in Fig. 5.

### Method of analysis

PAUP (Swofford, 1993) was used for the phylogenetic analysis. This program compares the data of all taxa in the data matrix with each other, and calculates cladograms. Out of the

possible cladograms the Most Parsimonious Tree (MPT) was chosen, *i.e.*, with fewest character state changes. The heuristic search option was used with a stepwise addition sequence set at random, and as branch-swapping method tree-bisection-reconnection (TBR). All charac-

ters were unordered, and uninformative characters, *e.g.*, autapomorphies, were ignored. Characters with multiple states were treated as polymorphic. To avoid homoplasy due to the increased variability by polymorphy, I kept the number of states for each character low, by re-evaluating each character state using MacClade (Maddison and Maddison, 1992), and recoding the characters where possible. In addition Pee-Wee (Goloboff, 1993) was used.

### Results

Following the phases of preliminary analyses, checking and rechecking data, coding and recoding characters, an eventual phylogenetic analysis was performed. The analysis with PAUP resulted in three most parsimonious trees (MPT) with a length of 589 steps, and a consistency index of 0.46 (Fig.1). The consistency index (CI) is, according to Sanderson and Donoghue (1989), within the expected ranges for analysis with this number of taxa involved. An evaluation of 10,000 random trees from the set of all possible trees with the same options as above was carried out to see if it was likely that the MPT's found were equal or within the range of randomly found trees. The three MPT's (length = 589 steps) were much shorter than the 805.6 steps of the random tree set, and it is very likely that the data set has more structure than would be expected by chance alone. The analysis with Pee-Wee resulted in a tree which made the genera paraphyletic, and with a length within the range of the random trees.

### The choice of the tree

The three MPT's show similar topologies. There are several ways to choose between equally parsimonious trees, including successive approximation weighting (Farris, 1969; Carpenter, 1988). Successive approximation weighting resulted in one most parsimonious tree slightly different from the set of three MPT's found as result of the initial analysis. This tree is 1 step longer than the original set of most parsimonious trees, and is nearly identical to the second of the three MPT's found without weighting (Fig.1B).

When taking into account the amount of support for the branches in the three different trees, differences are minor. Except for some other slight changes, the second tree has more sup-

port for the first branch leading to the genus *Spatholobus*. As two of the three equally MPT's are little different it may also be possible to give preference to one of the trees on morphological arguments, although implying subjective weighting criteria. *S. parviflorus* differs from the other species in *Spatholobus*, and more closely resembles *Butea*. Although it certainly belongs to *Spatholobus*, a place in the cladogram as close to *Butea* as possible would be expected. In the first cladogram *S. parviflorus* is included in the *S. ferrugineus* clade, in the other two it is placed at the base of the whole *Spatholobus* clade, which is preferable in my view. In addition, there are similar arguments for other species possible (Ridder-Numan, 1996). As a result of all these considerations tree 1 was discarded. There are no convincing arguments to choose between the remaining two, but I accepted tree 2 as a working hypothesis (Fig.1B).

### Cladistic biogeography

Considerable research has been undertaken to find appropriate methods for analysis of data provided by phylogenies of taxa and their distribution, *e.g.*, Bremer (1992, 1995), Brooks (1990), Brooks and McLennan (1991), Cracraft (1983, 1988), Morrone and Carpenter (1994), Nelson and Ladiges (1991), Page (1988, 1990), Turner (1995), Turner and Zandee (1995), Welzen (1992), Wiley (1981, 1987), and Zandee and Roos (1987). Many computer programs are helpful for analysing or comparing taxon-area cladograms, such as: PAUP (Swofford, 1991, 1993) and Hennig86 (Farris, 1988), CAFCA (Zandee, 1995), COMPONENT (Page, 1993), and TAS (Nelson and Ladiges, 1992).

Apart from limitations in the computer implementation, problems may occur when choosing taxa for the historical biogeographical analysis. In order to avoid comparing cladograms that reflect different time spans and different vicariance events, it is best to use groups of about the same age, *e.g.*, not an 'old' group known from the Cretaceous with a more 'recent' group. Different groups of taxa can also have a 'conflicting' distribution pattern. For instance, some taxa have migrated from SE Asia into the Malesian archipelago eastward, whereas others migrated from the east towards SE Asia. In comparing such patterns it is possible that in the analysis the patterns will cancel each other and reflect nothing. With these limitations in mind I used the results of the cladistic analysis of *Spatholobus* and al-

lies, and those of the other groups. As geological background I used Hamilton (1973, 1979, 1988), Hutchison (1989a, 1989b, 1992, 1996), Metcalfe (1988, 1990, 1991, 1994a, 1994b, 1996), Audley-Charles (1987), Dercourt *et al.* (1993), Rangin *et al.* (1990), Hall (1995, 1996).

#### *The data*

The data used for the biogeographical analysis were the phylogenies of the genera *Fordia* (Schot, 1991), *Genianthus* (Klackenberg, 1995), *Xanthophytum* (Axelius, 1990) and *Spatholobus* and allies (Fig.2). The genera occur in continental SE Asia and the West Malesian archipelago (Figs.3 and 4). A small monophyletic group in *Xanthophytum* occurs in New Guinea.

#### *The delimitation of the areas*

To facilitate comparison of the different area cladograms, areas were recognised from consideration of the distribution of all species (Fig.5). These are not exclusively areas of endemism, but areas of distribution as described by Axelius (1991). Some areas contain endemics (= only occurring in the chosen area) and would be considered areas of endemism, but others are composed of overlapping distributions of more widespread species. Some authors (Sosef, 1994), state that each area should at least contain one endemic, and that areas without endemics ('remnant areas') are not informative. In my opinion, however, species occurring in an area – endemic or not – will reflect their relation to species sets in other areas, and thus a solution for placement of 'remnant areas' is also possible. As a result of using these areas, however, it is possible that some end-branches in the general area cladogram will be empty, because the species present in that particular area, becomes optimised on a node lower in the cladogram, when it is occurring in more than one area in the clade.

The delimitation of the areas also depends on the number of species present in an area. Problems may arise during analysis when there are too few species in an area. Due to lack of data (many zeros in the area-taxon matrix), these areas often turn up at the base of a cladogram, especially when the program requires all zero outgroups. Furthermore, the size of the area can be important. When the size chosen is too large results concerning several parts of the area will

remain uninformative. It is clear that by adding other genera to the analysis, delimitation of areas has to be reviewed and changed wherever necessary.

An area-taxon matrix was based on the available cladograms and the distributions (Figs.2, 3, 4, 5). The area-taxon matrix gives the presence (or absence) in an area of each terminal node (= taxon) in the cladogram, as well as for all other (internal) nodes (= ancestors). In this way the structure of the cladogram is added to the matrix. The basic working hypothesis is that speciation results from passive allopatric speciation (vicariance), which implies no taxon-specific mechanisms. Therefore, it is assumed that the ancestor was present in the same areas as its descendants, thus excluding, *e.g.*, dispersal events. The coding of the ancestor nodes is thus not independent, and is in fact an imperfect and unlikely assumption. In the case of incongruencies, dispersal is one of the possibilities to explain these patterns. Dispersal events may be recognised by parallelisms. This factor, often described as 'ad hoc' explanation, has to be kept in mind, because dispersal is an important strategy for plants, often leading to widespread species. In the case of extinction or primitive absence in part of the area, this way of coding leads to reversals (= species from state present to state absent). And, as mentioned above, if only one taxon (or a few) is present in an area (a column with many zeros), the area may be placed artificially low in the area cladogram after analysis.

When one or more genera are absent in part of the total area, these missing data for areas (usually called 'missing areas') can be treated under different assumptions. Assumption 0 (Zandee and Roos, 1987) considers missing data as primitively absent (= the genus was never present). In this case missing data are coded as zero. However, under assumptions 1 and 2 (Nelson and Platnick, 1981) these missing data are treated as uninformative (unknown optimisation state), and coded as '?' (Nicobar Islands for *Spatholobus*). The latter two assumptions are less restrictive than the former method, but require some manipulation for areas. In this analysis missing taxa were treated both under assumption 0 and assumption 1. Widespread species were only treated under assumption 0, *i.e.*, the areas inhabited by the widespread species formed one single area in the past (monophyletic origin). The area-taxon matrices of the genera combined with an artificial (all-zero) outgroup into one large matrix were analysed with PAUP

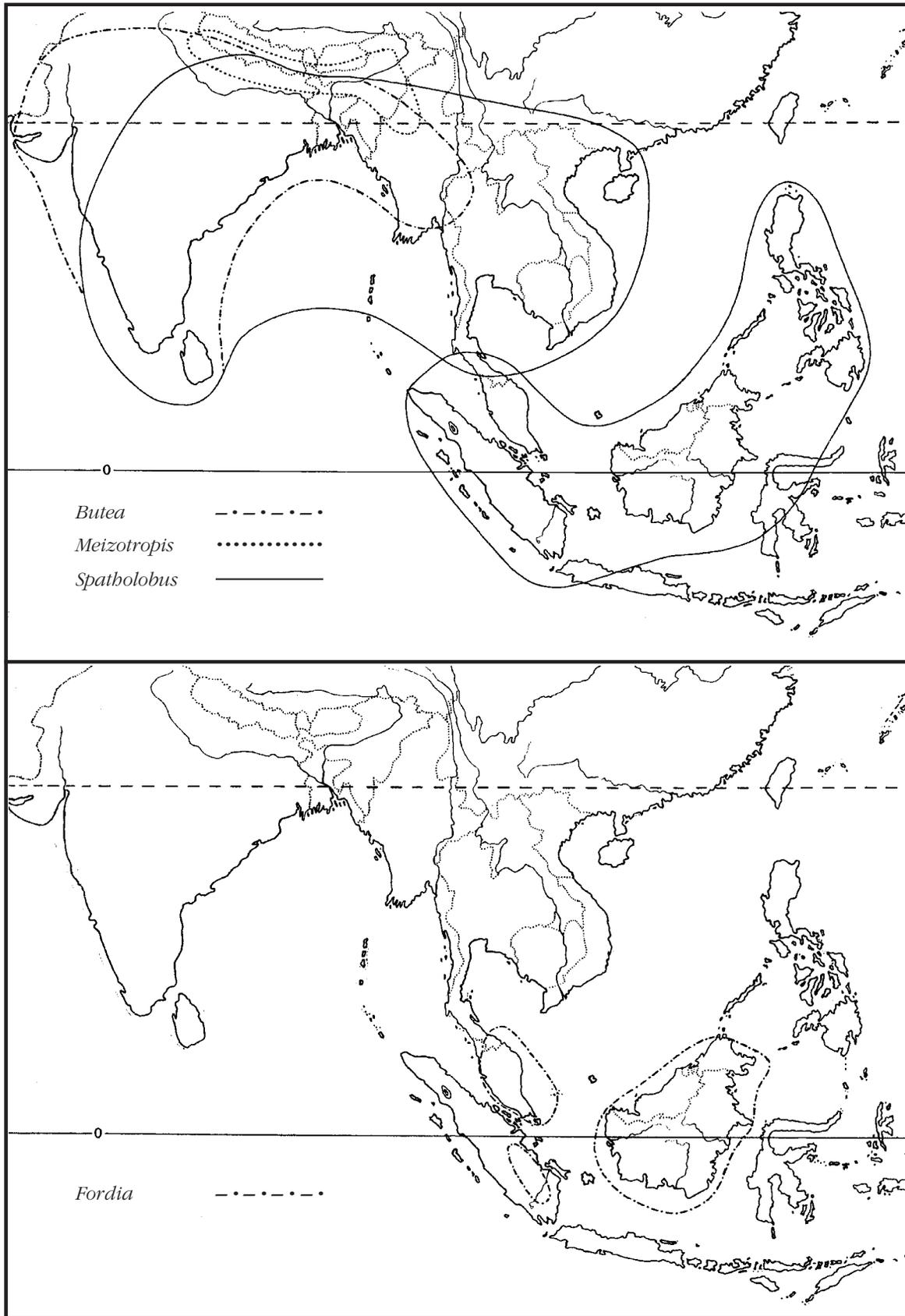


Fig. 3. Distribution of the genera *Butea*, *Meizotropis*, *Spatholobus* and *Fordia*.

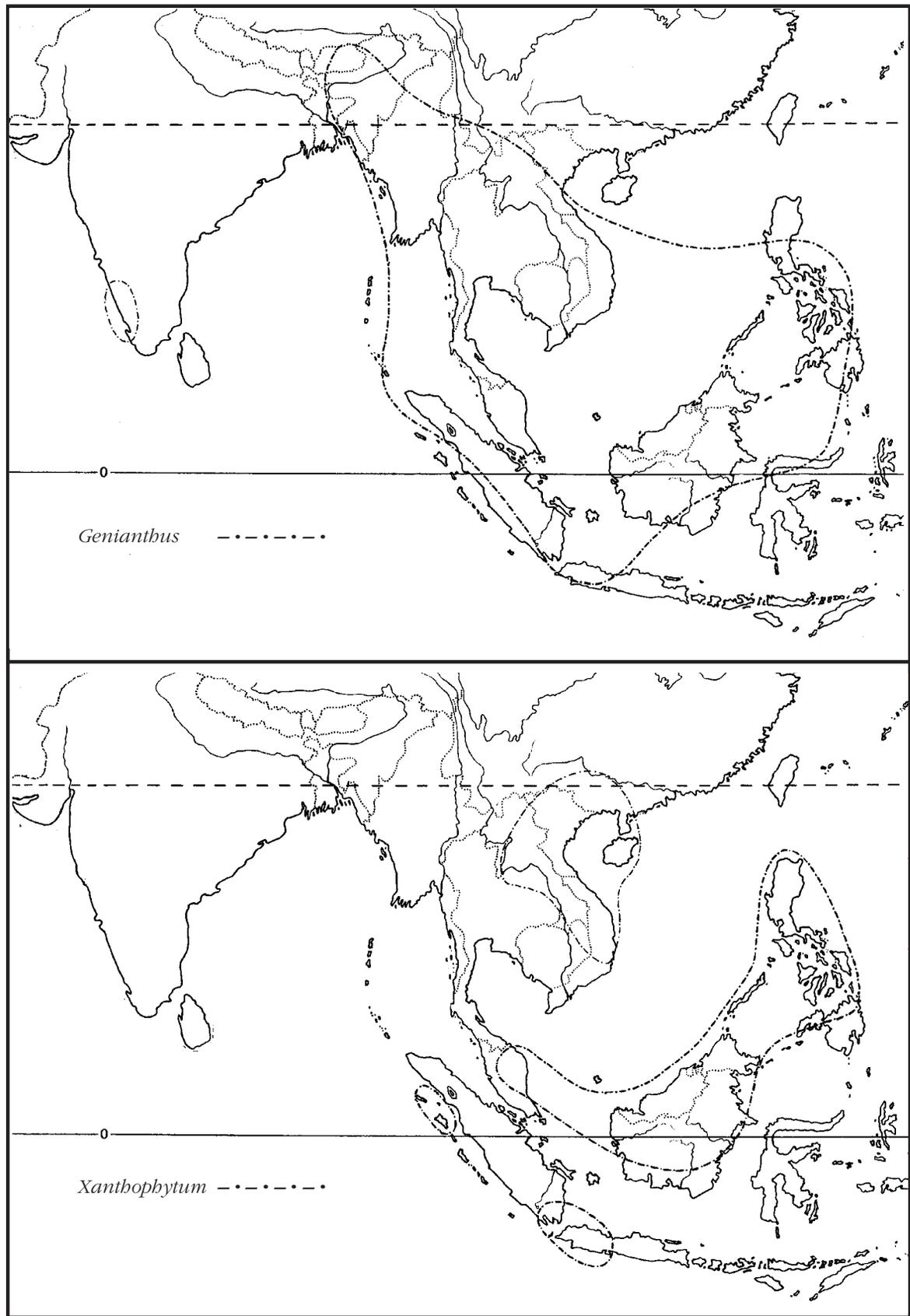


Fig.4. Distribution of the genera *Geniantbus* and *Xanthophytum*.

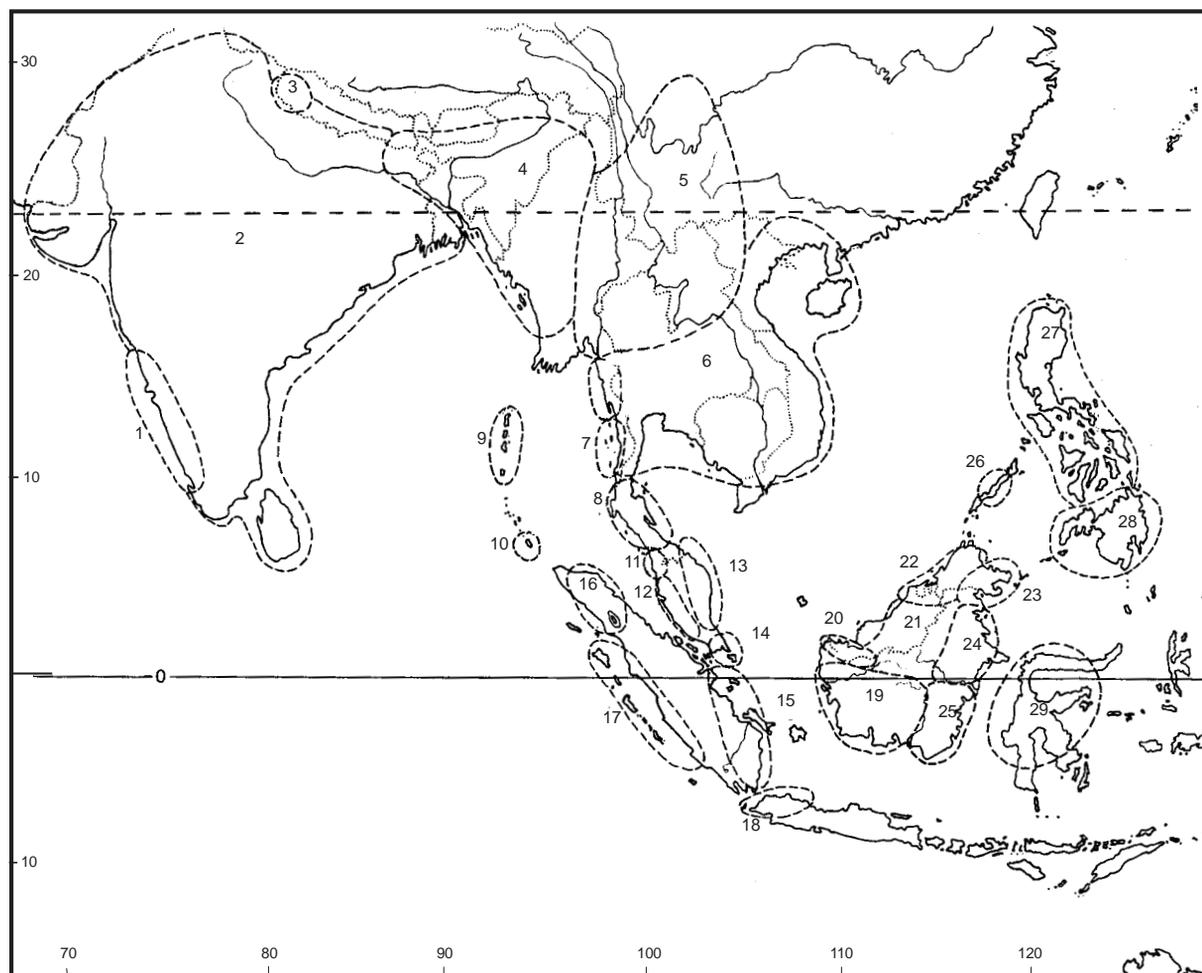


Fig. 5. Principal areas of distribution. 1: Kerala; 2: India; 3: Kumaon and W Nepal; 4: Bangladesh and eastern India up to Burma; 5: E Burma, northern Thailand and northern Laos, Yunnan; 6: Indochina, Hainan, S Guangxi, central Thailand and part of Burma; 7: Mergui Archipelago/Tenasserim; 8: S Thailand; 9: Andaman Islands; 10: Nicobar Islands; 11: Penang and Kedah; 12: W Malay peninsula; 13: E Malay peninsula; 14: Singapore; 15: SE Sumatra; 16: N Sumatra; 17: Sumatra coast and islands; 18: W Java; 19: SW Borneo; 20: Semitau; 21: Sarawak and central mountain range of Borneo; 22: NW Borneo; 23: NE Borneo; 24: Central E Borneo; 25: Meratus; 26: Palawan; 27: Northern Philippines; 28: Southern Philippines; 29: Sulawesi.

3.1.1 (Swofford, 1993), both under assumptions 0 and 1 for missing areas. It is important to check for clades solely based on the absence of taxa, as mentioned above. For the analysis with CAFCA (Zandee, 1995) no outgroup was needed. The four matrices (for each group its own matrix) were analysed under both assumptions 0 and 1.

#### *The areas*

The distribution areas shown in Fig. 5 are based only on the distribution of the species. A large part of these areas coincide with the tectonic

terranes of Fig. 6. In the text below, geological (and other historical) information on each of the separate areas is summarised. Abbreviations of area names (as used in the computer analyses) are given in parentheses. These abbreviations (instead of full geographical names) are also used further on in the text of the present chapter. In addition to the historical information of the areas, the presence of endemic species is given.

*Kerala* (1) is part of the Indian continent. This part of India has retained tropical rain forest during all of the last 18,000 years. In other parts of India, there have been extensive grasslands during dry periods, but this seems to have been

one of the rain forest refuges. There are four species, one endemic (*S. purpureus*).

*India* (2) is the continental part of the Indian plate that separated as a large fragment from Australia in the Jurassic (c.160 Ma). It started colliding with Eurasia in the Early Eocene (c.50 Ma), causing the Himalayas to uplift. There are six species, no endemics.

*W Nepal* (3). West Nepal and Kumaon are part of the Himalayan region, which was uplifted after the Late Eocene. This area changed significantly after the uplift and provided a geographical barrier to the north. There are four species, no endemics.

*W Burma/E India* (4). Bangladesh and eastern India up to Burma almost entirely overlaps with the W Burma plate, which was uplifted in the Early Eocene by the subducting Indian plate, and during the Cenozoic moved northwards to its present position. This area is composed of several parts, because Bangladesh forms part of the Indian plate. There are nine species, no endemics.

*Yunnan/N Thailand* (5). East Burma, northern Thailand, northern Laos and Yunnan amalgamated from different continental fragments. East Burma and the north of Thailand (west part) are part of Sibumasu; N Laos and the northeast of Thailand are part of Indochina; Yunnan is the southwest part of S China. S China and Indochina rifted away from Gondwanaland in the Palaeozoic, and sutured along the Song Ma line in the Early Carboniferous. Sibumasu rifted off the Gondwana margin, during the Early to Middle Permian. Indochina and Sibumasu collided in the Late Permian/Early Triassic, and since that time have behaved as a single geological entity. There are thirteen species, five endemics (*F. leptobotrys*, *G. bicoronatus*, *G. hastatus*, *S. pulcher*, *S. suberectus*).

*Indochina* (6). Indochina, Hainan, South Guangxi, Central Thailand and part of Burma are parts of Indochina, South China, and Sibumasu respectively. This composite area has a history comparable to area 5. There are eleven species, four endemic (*F. cauliflora*, *G. siamicus*, *X. balansae*, *X. polyanthum*).

*Mergui/Tenasserim* (7). The Mergui archipelago and Tenasserim are part of Sibumasu. Tenasserim is part of the continent itself. The Mergui archipelago, however, consists largely of much younger material which did not exist before c.30-25 Ma. There are two species, one endemic (*S. merguensis*). Due to incomplete material, the other species (*S. bracteolatus*) was excluded from the analysis.

*S Thailand* (8). South Thailand is the narrow part of Thailand, near the Isthmus of Kra. It mainly represents the transition between the more seasonal and ever-wet climates during the present. This part has been inundated extensively in the past, during periods of high sea level. Tropical rain forest became established here at least 18,000 years ago. At that time sea level was low and a savannah corridor from Indochina to Java was present, bordered by monsoon forest (Adams, 1995; Steenis, 1961). Only the largest parts of Sumatra and Malaya, extending up to the Isthmus of Kra, were carrying rain forest. Other tropical rain forest refugia were present in Borneo, the Philippines and Sulawesi. There are six species, no endemics.

*Andaman Islands and Nicobar Islands* (9 and 10) represent an outer arc ridge, produced during subduction of the Indian plate. The Andaman Sea began to open in the Middle Miocene (13 Ma). The Andaman Islands have one species. On the Nicobar Islands there is one endemic (*G. nicobarensis*).

*Penang/Kedah, W Malaya and N Sumatra* (11, 12, 16). Penang and Kedah, the West Malay peninsula and North Sumatra are part of Sibumasu (see also area 5). For Penang/Kedah there are seven species, no endemics. *Spatholobus auritus* is possibly endemic here. For W Malaya there are sixteen species, three endemics (*F. lanceolata*, *F. ophirensis*, *F. unifoliolata*). For N Sumatra there are two species, no endemics.

*E Malaya, Singapore, and SE Sumatra* (13, 14, 15). The East Malay peninsula, Singapore, and SE Sumatra are part of the same fragment as Indochina. The Bentong-Raub line is the suture between East Malaya and West Malaya (Late Triassic). E Malaya has seven species, one endemic (*F. ngii*). Singapore has seven species, three endemic (*F. incredibilis*, *F. joborensis*, *F. spec. A*). SE Sumatra has eight species, two endemic (*F. nivea*, *F. stipularis*).

*Sumatra coast* (17) The west coast of Sumatra and its islands are largely the same as the Woyla terranes of Metcalfe (1996). These terranes rifted from the Gondwana margin and were accreted to the Sundaic margin in the Cretaceous. All islands are forearc material and emerged for the first time in the Miocene (R. Hall, pers.comm., 1995). There are two species, no endemics.

*W Java* (18). West Java is underlain by Cenozoic volcanic rocks formed by subduction of the Indian plate resting on pre-Tertiary continental crust. There are six species, one endemic (*Genianthus macrophyllus*).

*SW Borneo* (19) is the oldest part of Borneo,

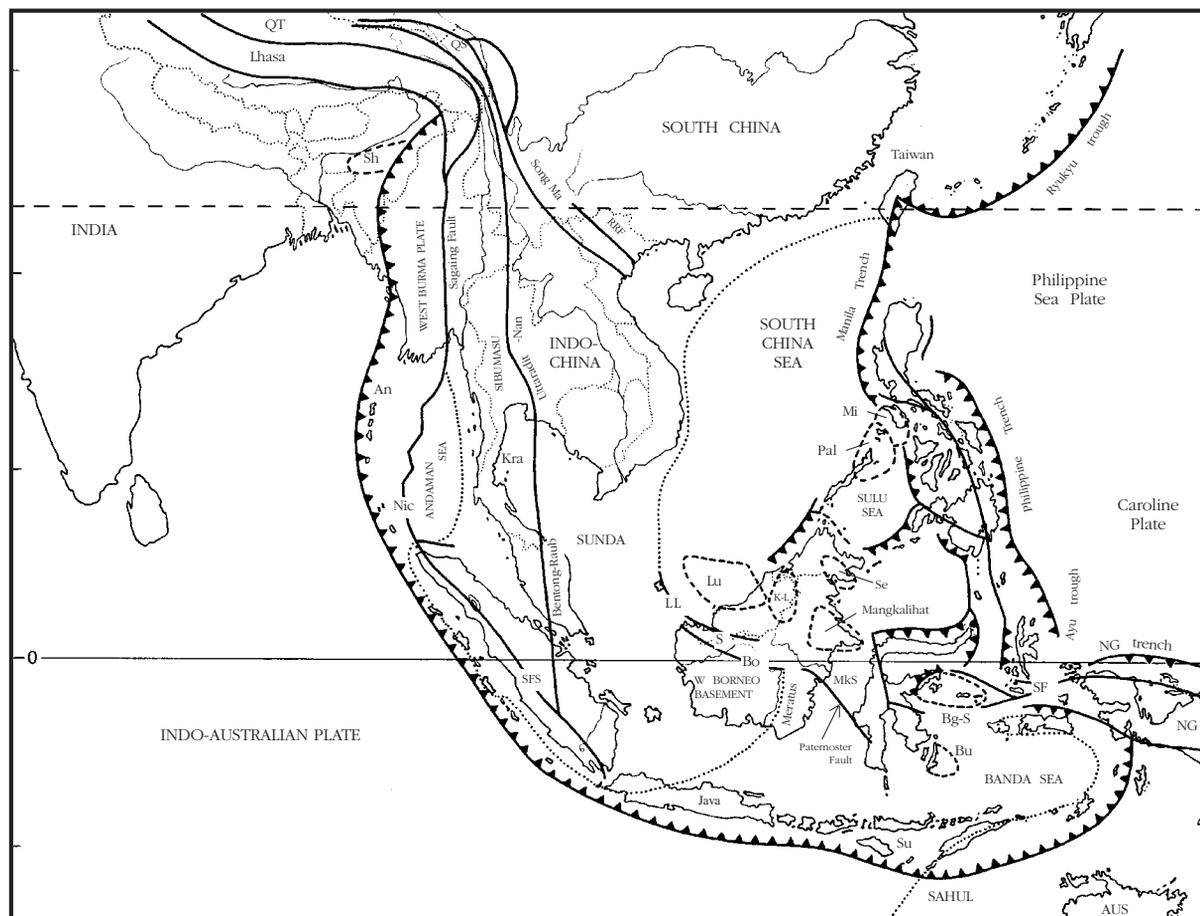


Fig. 6. Principal geological features of SE Asia. Heavy lines represent fault systems, indented lines show plate margins with the indentation on the overriding plate, and dotted (bold) lines represent the border of Sahul and Sunda platform. An: Andaman Islands, AUS: Australia, Bg-S: Banggai-Sula, K-L: Kelabit-Longbowan, Kra: Isthmus of Kra, LL: Lupar Line, Lu: Luconia, Mg: Mangkalahat, Mi: Mindoro, Mks: Makassar Strait, NG: New Guinea, Nic: Nicobar Islands, Pal: Palawan, QS: Qamdo Simao terrane, QT: Qiangtang terrane, RRF: Red River Fault, S: Semitau, Se: Segama, SF: Sorong Fault, SFS: Sumatra Fault System, Sh: Shillong Plateau, Su: Sumba.

parts of which may have been emergent since the late Mesozoic. There are thirteen species, one endemic (*X. johannis-winkleri*).

*Semitau* (20), including the region around Kuching, includes Mesozoic and Lower Tertiary rocks and has been an area close to sea level or emergent since the early Tertiary. There are fifteen species, three endemics (*X. involucreatum*, *X. sessile*, *X. setosum*).

*Sarawak/C Borneo and NW Borneo* (21 and 22). Sarawak, the central mountain range of Borneo, and NW Borneo are part of the Rajang-Crocker accretionary complex that was uplifted in the Early Miocene. Parts of the central mountain range have probably been emergent since the Paleocene. There are nineteen species in both areas; in addition, six in Sarawak/C Borneo, of

which four are endemics (*X. alopecurum*, *X. glomeratum*, *X. grandifolium*, *X. minus*). No endemics in NW Borneo.

*NE Borneo* (23) is underlain by Mesozoic and early Tertiary accretionary complexes, and younger Tertiary sediments. Parts of central NE Borneo probably became emergent in the Late Miocene-Pliocene. There are ten species, one endemic (*X. longipediculatum*).

*CE Borneo* (24). Central East Borneo includes the Mangkalahat peninsula, and the Kutei and Tarakan basins. The Makassar Strait opened in the early Tertiary. The Tarakan and Kutei deltas began to fill the deep basins from the early Miocene. There are seventeen species, two endemics (*G. valvatus* and *X. foliaceum*).

*Meratus* (25). The Meratus mountains were up-

lifted rather late, probably in the Late Miocene, before which most of SE Borneo was a shallow marine area. There are six species, no endemics. *Palawan* (26) is part of the South China margin that rifted away after the opening of the South China Sea in the mid-Oligocene (32 Ma). Part of the Philippines (Mindoro) has the same origin. Rifting stopped at 17 Ma. There are two species, no endemics.

*N Philippines and S Philippines* (27, 28). The northern and southern Philippines are part of a geologically complex and active region. Most of the southern part formed before the Miocene as an arc at the southern edge of the Philippine Sea plate, whereas Luzon formed part of an arc at the north side of the Celebes Sea-West Philippine Sea basin in the same plate. The N Philippines has five species. The S Philippines has five species. There are no endemics.

*Sulawesi* (29) is geologically very complex. The groups studied are not well represented in this area and, consequently, no subdivision of Sulawesi can be made using my data. There are two species, no endemics.

### Results

The results of the analysis with PAUP under assumption 0 (the most restricted option: information taken as it is) are: 19 equally most parsimonious area cladograms with a length of 366 steps and a consistency index of 0.45 (homoplasy index (HI) = 0.55, retention index (RI) = 0.66, rescaled consistency index (RC) = 0.3). The strict consensus tree and the 50% majority rule consensus tree of the 19 most parsimonious area cladograms are presented in Fig.7. The consensus trees are shown to give an indication of the support to particular groups in the 19 most parsimonious cladograms. The percentages of the trees that support a particular branch are indicated in the 50% majority rule cladogram. Differences within the 19 trees are caused by the changing position of the following areas, more or less within their clade: 1) India/W Burma, 2) Mergui/Tenasserim (and Andaman Islands), 3) the clade of Sumatra coast and Palawan, and N Sumatra. The summary results (for details on all analyses see Ridder-Numan, 1996) show that in the area cladograms obtained there are parts with similar topologies: a continental SE Asia group, a Borneo group, an Isthmus of Kra group and a Malay peninsula-SE Sumatra group.

The areas Sulawesi, N Sumatra, Sumatra coast, and Palawan are not very informative due to a

lack of species occurrences and endemics, and appear low at the base of the cladogram. On the Nicobar Islands an endemic is present. This one species, however, is outnumbered in its clade to define a node in the area cladogram by the other six species with a distribution around the Sundaland plateau, and the area is placed basal in the area cladogram. West Nepal is probably at this basal position because the species present in this area (*Butea monosperma*, *Meizotropis buteiformis*, *M. pellita*, and *Spatholobus parviflorus*) are all basal in the fundamental cladogram. As working hypothesis the summarized area-cladogram in Fig.7A is used in the rest of this study, because it best shows the four groups of areas mentioned above.

### Comparison with the geological information

In the case of splitting areas (vicariance events), it is possible to construct a geological 'cladogram' in which branches represent geographical entities. The splitting up in the case of SE Asia, however, took place at the Gondwanaland margin, and the continental fragments accumulated in different areas in SE Asia. This geological information dominated by accretion makes it difficult to construct a cladogram-like structure (even when reticulations are taken into consideration). Instead, these events are summarised below according to the information found in the literature mentioned before; the different continental fragments and sutures are shown in Fig.6.

Before the Eocene no reliable fossils are known for Leguminosae (Raven and Polhill, 1981; Herendeen *et al.* 1982), and one cannot expect to see geographical vicariance events before that time reflected in the distribution of the group. Only Miocene and younger fossils can be attributed to specific genera within the Leguminosae. This is probably the reason why the areas of distribution on the continent and Indochina (*e.g.*, areas 4, 5, and 6 in Fig.5) are less similar to the geological entities than those in, *e.g.*, Borneo, because they had already welded in the Triassic and formed one area at the time the Leguminosae evolved.

Before the Eocene the Tethys Ocean was subducting beneath the Asian margin forming a volcanic arc from Lhasa, through W Burma, Sumatra and part of Java to W Sulawesi. In the Early Eocene India started to collide with Asia. Between the Oligocene to the mid-Miocene the South China Sea opened, and areas such as Palawan-Mindoro moved southwards, separat-

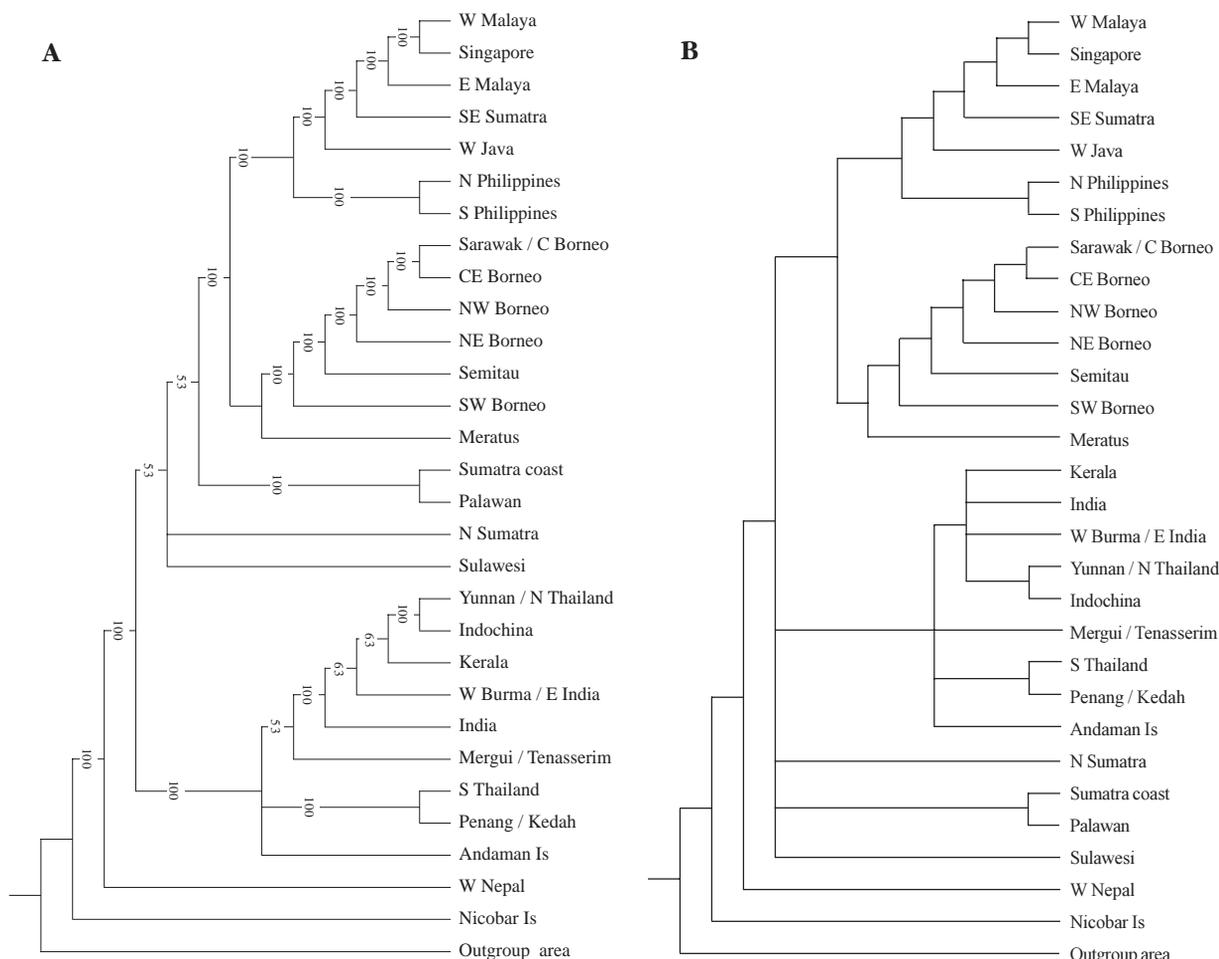


Fig. 7. A. 50% majority rule consensus tree of the nineteen equally most parsimonious area cladograms obtained by analysis with PAUP of the area-taxon matrix of *Spatholobus*, *Butea*, *Meizotropis*, *Fordia*, *Genianthus*, and *Xanthophyllum*, under assumption 0 (missing areas coded as 0). Values on the branches indicate the percentage of trees supporting a specific clade. B. Strict consensus tree. Differences between the 19 MPT's are mainly caused by the changing position of the following areas, more or less within their clade: 1) India/W Burma, 2) Mergui/Tenasserim (and Andaman Islands), 3) the clade of Sumatra coast and Palawan, and N Sumatra.

ing from the Chinese continental margin. In the Palaeocene large parts of Borneo were not yet uplifted, but there was land south of what is now Sarawak and Sabah. Sarawak and Sabah were part of the Rajang-Crocker accretionary complex receiving sediment from the uplifted parts of Borneo as well as from the Indochinese part of the Sunda shelf. The Makassar Strait opened in the Late Eocene/Oligocene resulting in the separation of W Sulawesi. The Meratus mountains were uplifted rapidly in the Late Miocene-Pliocene. In the Miocene the Philippines were formed. The Andaman Sea began to open at the end of the Middle Miocene.

In the Late Oligocene, the sea level was as

low as 250 m below the present level, thus the Sunda platform was for the largest part above sea level (Hutchison, 1989a). The climate at that time was probably tropical monsoon, and before that, in the Oligocene, there was a wet tropical monsoon or a tropical rain forest climate. In the mid-Miocene the sea level changed again in three stages up to 220 m above present sea level, after which there was a lowering again of up to 220 m below the present sea level in the Upper Miocene. At that time the Leguminosae became dominant among the phanerogams in India. According to Awasthi (1992) this was after migration from Africa and SE Asia to India. In the Pliocene the sea level rose up to 140 m

above the present level. After the Pliocene there were many glacial periods and interglacials which coincided with lower and higher sea levels, although by then the spectacular sea-level rises and falls were over (Hutchison, 1992). Hall (1998 this volume) indicates that the Sunda shelf remained above sea level during most of the Neogene, and that areas below sea level, e.g., the Malay basin and the S China Sea, did so for tectonic reasons and not because of global sea level change. If the groups studied were present in the region at the time these events took place and if they did react to these events, one may expect that this will be reflected in a general area cladogram.

The first major split in the general area cladogram is between the continental SE Asia group (including the Isthmus of Kra group and the Andaman Islands) and the Sundaland groups (Malay peninsula/Sumatra and the Borneo areas). This may be due to one of the high sea levels, which occurred between the mid-Eocene and the Pliocene as indicated above. The reconstructions of Rangin *et al.* (1990) show, that during high sea level there was a separation between the Malay peninsula and Indochina. It is impossible to indicate more exactly in what period this splitting off took place. If the place of the Andaman Islands is correct, *i.e.*, below the split between continental SE Asia and the Sundaland groups, it may be possible to date the split of the Andaman Islands to the time of the opening of the Andaman Sea (13 Ma). This is very speculative, however, because on the Andaman Islands only the widespread, but continental, species *Spatholobus acuminatus* is found. It would be better for future research to analyse taxa with more endemics on the Andaman Islands.

Nearly all area cladograms are resolved for the areas in Borneo. In the general area cladogram (Fig.7), the first area to split off is the Meratus. It is possible that this reflects the uplift of the Meratus mountains in the Late Miocene-Pliocene. The second area is SW Borneo, which is the oldest part of Borneo. The third area is the Semitau, which is in fact the extended part of the Semitau ridge, which was accreted to SW Borneo in the Cretaceous. According to Hutchison (1992), this part of Borneo is probably uplifted in the same period as the Meratus. The next area, NE Borneo, was, also part of the extensive landmass, and uplifted in the same period as the Meratus. This implies that the first four areas in the Borneo group were not yet uplifted prior to the Late Miocene-Pliocene, and

were probably submerged during some of the sea level rises. The first four splits may indicate these uplift events and the related changes in climatological/ecological factors. The other parts of Borneo in these times consisted of a large Rajang basin and the Crocker Range (Sarawak/C Borneo and NW Borneo). The last split in the Borneo group is formed by the central parts of Borneo: Sarawak/C Borneo and CE Borneo. The mountains of the Crocker Range form a natural delimitation between CE Borneo and the west central part of Borneo (Sarawak/C Borneo).

In the Malay peninsula group, W Malaya and E Malaya are in most cases placed as sister areas in the cladogram, together with Singapore. SE Sumatra is at the base. In the general area cladogram W Java is basal in the same clade, and the N and S Philippines are also connected to the base. The general area cladogram shows a sister relationship between the Singapore and the W Malaya part of the Sibumasu block; these two have a sister relation to the E Malaya part of the Indochina block. SE Sumatra belongs to the Sibumasu block. However, the connections between these blocks date back to the Triassic, long before the Leguminosae existed there. Although it is possible to recognise different distribution areas, more or less according to the delimitations of Sibumasu and E Malaya, it is not possible to distinguish in the area cladogram between these areas. The delimitation of the distribution areas may also be due to ecological or climatological factors: the areas around Singapore and SE Sumatra are both lowland areas. The E and W Malaya parts of the Malay peninsula consist mainly of a large, mountainous central area. If there is a relation between Malaya and Sumatra, one would expect, on account of distance, that there would be as many species occurring in W Malaya and mountains of NW Sumatra as there are species in the lowlands around Singapore and SE Sumatra. From the distribution of the species in this study the former is not evident. No species occurs exclusively in both W Malaya and N Sumatra. The relation between the Malay peninsula (West, East and Singapore), SE Sumatra and W Java may be understood in geological terms also as part of the border of Sundaland below which the Indian plate was subducting. Only after the rotation of the Malay peninsula, the northward movement of Burma and the opening of the Andaman Sea (13 Ma) were these parts slightly rearranged. The reconstructions of Rangin *et al.* (1990) indicate that during certain periods of high sea level, be-

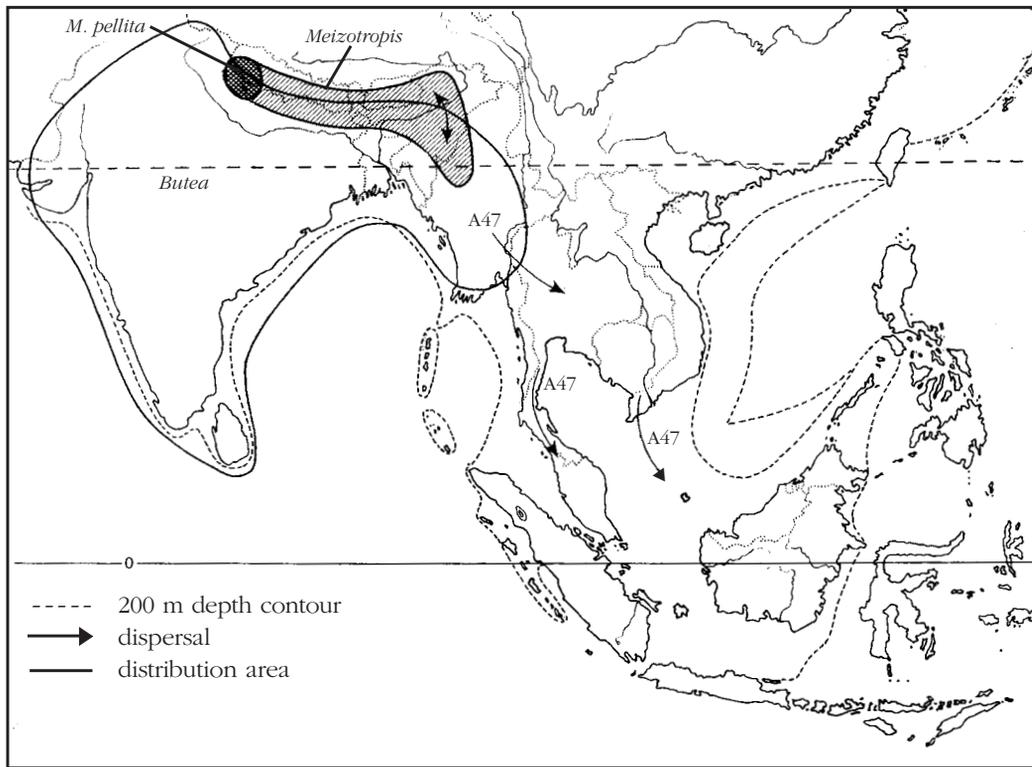


Fig.8. Hypothetical distributions of the ancestors of *Butea*, *Meizotropis* and *Spatholobus*. Dispersal of ancestor 47 (*Spatholobus*) into the Malay Archipelago.

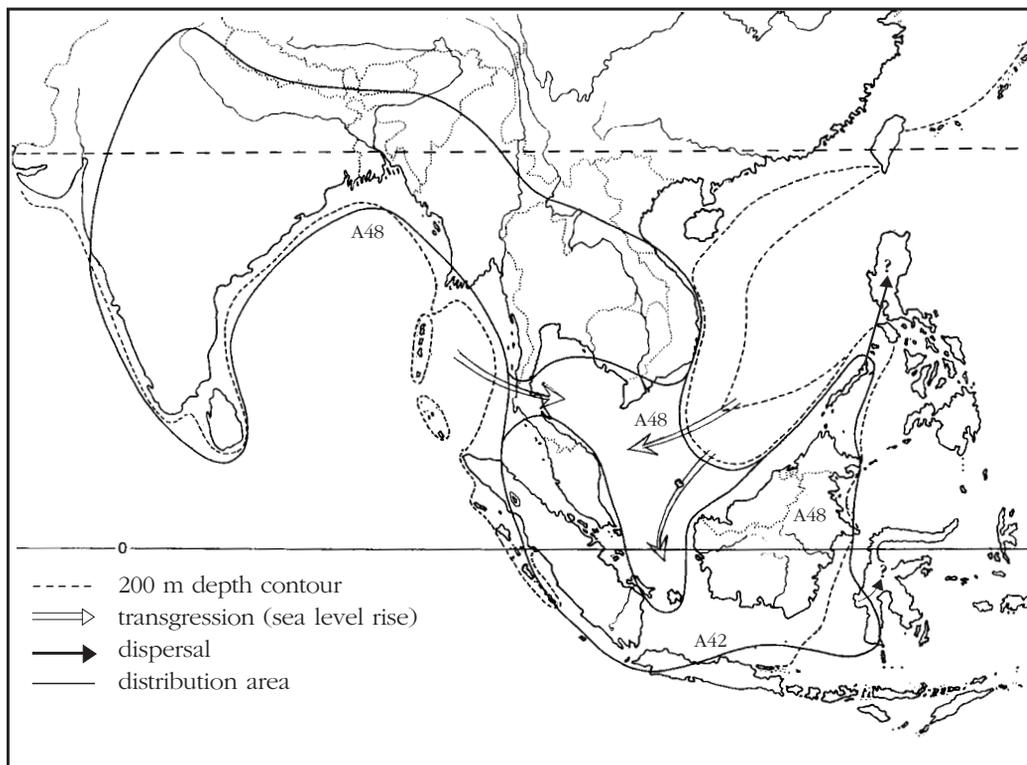


Fig.9. After a sea level rise part of the ancestor 48 became isolated and developed into the ancestor of the *Spatholobus ferrugineus* clade A42.

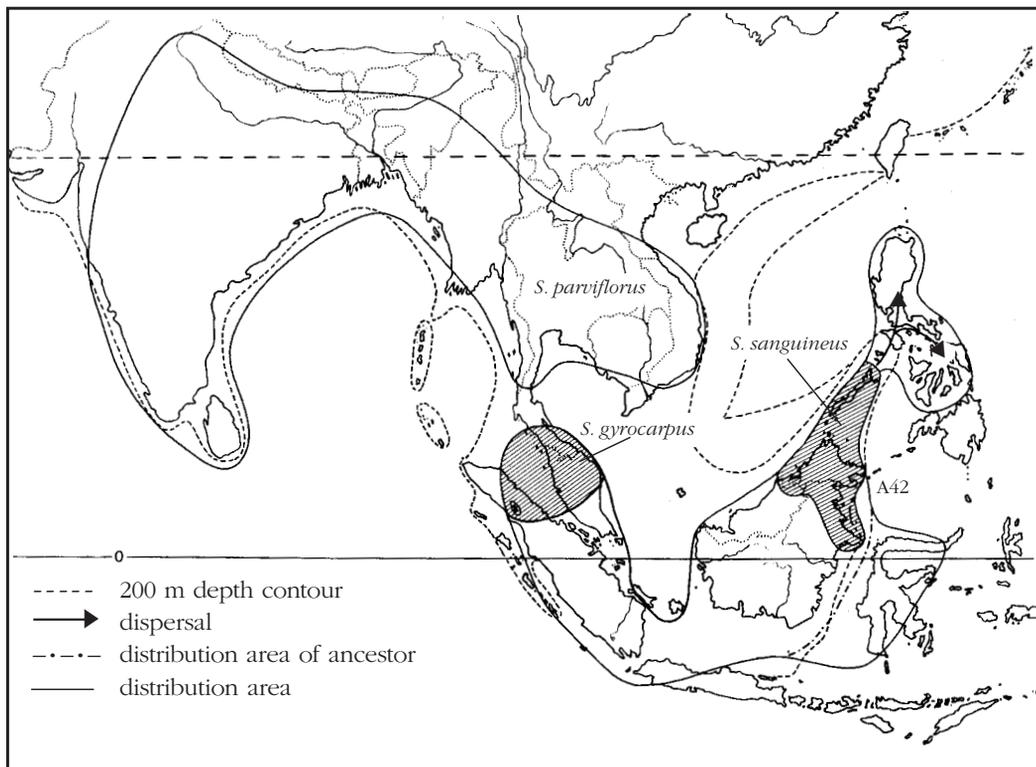


Fig. 10. In isolated parts of the area speciation occurred, *Spatholobus gyrocarpus* in the Malay peninsula, and *S. sanguineus* in northern Borneo.

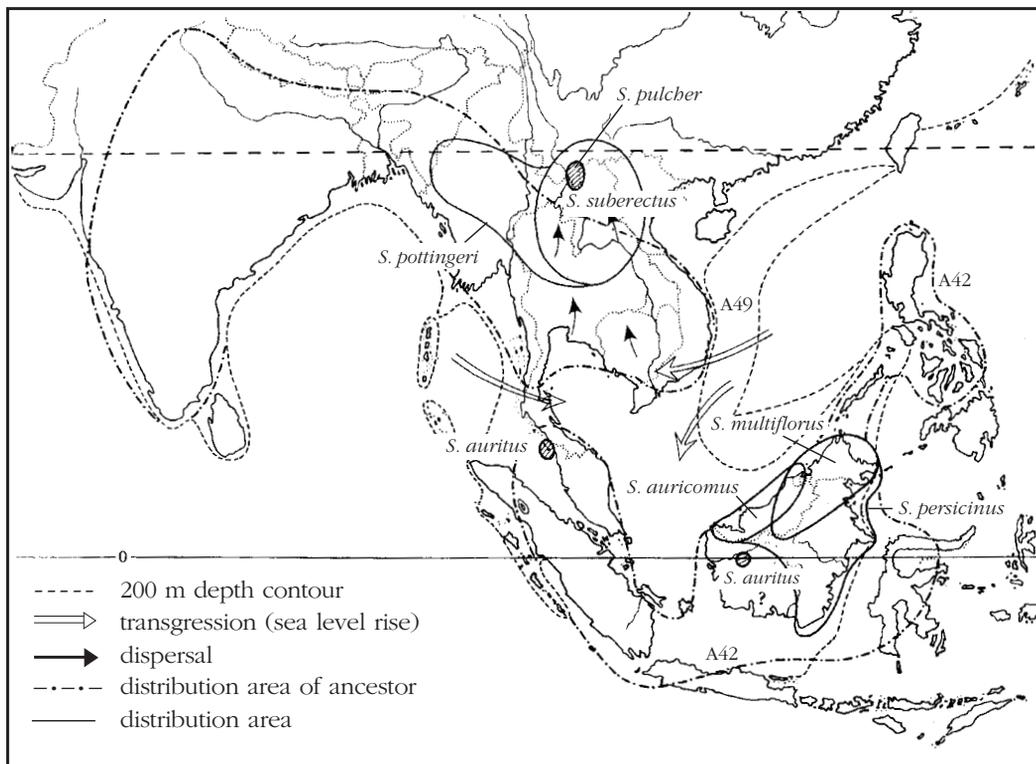


Fig. 11. Dispersal led to further speciation in the *Spatholobus ferrugineus* clade, and changing sea level and rise of mountains caused speciation throughout Sundaland.

tween the Middle Eocene and the Pliocene, there were emergent areas in Borneo, the Malay peninsula, large parts of Sumatra, and West Java. Other parts are shown as submerged, although based on continental crust, e.g., the areas of S Thailand and Penang/Kedah. The S Thailand and Penang/Kedah areas are placed very close to each other in all area cladograms. In the general area cladogram this clade is in polytomy to the continental SE Asian areas and the Andaman Islands. S Thailand and Penang/Kedah form the region around the Isthmus of Kra, which was easily inundated during periods of high sea level. Floristically this is the place where the distribution of the species from ever-wet and seasonal areas overlap. This small group of two areas does not contain any endemic species. It is possible that rain forest species do not have as much potential for dispersal than monsoon forest ones, and it is then probable that the invading species came mainly from the north and less from the south (with its rain forest climate).

#### *The history of Spatholobus*

Although historical biogeography is about areas, it is also possible to reconstruct the history of speciation within *Spatholobus* in the area. The speciation events indicated by the cladogram of *Spatholobus* and allies (Fig.1) were used to relate the general area cladogram (Fig.7) to the phylogenetic history of the genus as reconstructed in the *Spatholobus* cladogram (see for more details Ridder-Numan, 1996). It is assumed that the phylogenetic cladogram and the general area cladogram correctly reflect the history of speciation of the genus and the historical relation of the areas respectively.

It is rather speculative to superimpose geological events older than Pleistocene on the cladogram of *Spatholobus*. Although some events can be reconstructed, it is not possible to designate the time these events happened, especially because most events, e.g., changes in sea levels, have occurred several times during geological history. Later events, such as Pleistocene ice ages, could easily have disrupted part of the distribution area of some of the species and their ancestors, resulting in disjunct distribution patterns, which in their turn may have resulted in speciation events. As not all species respond with speciation, some disjunct patterns remain.

The ancestor of the genus *Spatholobus* probably originated on the SE Asian continent. The

genera *Butea* and *Meizotropis* developed in that part of the area where also the ancestral species of *Spatholobus* occurred; this species spread out over the whole area in a period when the sea level was low and the land emergent: during other periods these parts (the Sunda shelf) were below sea level (Fig.8). On the continent the ancestor of *S. parviflorus* had already developed.

For the *S. ferrugineus* clade, the first split in the cladogram after *S. parviflorus*, it can be concluded that its ancestor speciated in a period of isolation (high sea level) from the continent of SE Asia, spreading out over the whole area of the Malay peninsula, Sumatra, W Java and the oldest parts of Borneo (Fig.9). At the margins of its distribution area species developed, perhaps during a later period of isolation by high sea level that isolated Borneo from the Malay peninsula and Sumatra (Late Oligocene?): firstly *S. gyrocarpus* in the Malay peninsula and N Sumatra; secondly *S. sanguineus* more to the north, on all of the newly uplifted parts of northern Borneo (Fig.10). During later periods of lower sea level, the whole area was inhabited by the predecessor of *S. ferrugineus*, probably an adaptable species that was able to occupy larger regions at all latitudes, and frequently dispersed to parts outside the original range of its ancestor. In Borneo, at lower altitudes, *S. persicinus* developed, and at the same time or later on the island of Penang *S. auritus* (Fig.11). On Borneo, but only in the north, a small-flowered species evolved, later splitting into two species due to the separation by mountainous areas: *S. auricomus* and *S. multiflorus*. In the meantime speciation events occurred on the SE Asian continent as well (Fig.11). For the other species a similar history of invasion, isolation and speciation may be concluded from the results above (Ridder-Numan, 1996).

#### Conclusions

There have been many events that have led to isolation of parts of the Sundaland plateau from the Asian continent, as is also evident from the history of *Spatholobus*. The most obvious events are changes in sea level, which occurred during all periods. It would be useful if more was known about these sea level fluctuations in the SE Asian region. Studies like that of Kaars and Dam (1994), describing a rather recent but long period (135,000 years) on Java, are helpful.

*Spatholobus* probably originated on the conti-

ment of SE Asia, together with *Butea* and *Meizotropis*. After several invasions of *Spatholobus* into the West Malesian region, and after an equal number of isolation events, the present distribution pattern can be surmised. In this history, vicariance and dispersal events both played a role. The genera *Butea* and *Meizotropis*, and the first species of *Spatholobus*, *S. parviflorus*, remained on the continent. The ancestor of the rest of *Spatholobus* invaded the West Malesian archipelago, after which the history of invasion and isolation began.

A major problem is timing. In a large area it is possible that more than one species develops at the same time of the same widespread ancestor. For example, an ancestor occurring in the entire area from Indochina to Borneo, may split off species in each of the peripheral parts of the area: e.g., the north of Indochina and the northern part of Borneo. The species occupying the majority of the ancestral range after some time may have re-invaded the peripheral areas. This latter species may in turn again be split up into other species in the same peripheral areas. In this way it is evident that we recognise a split in the fundamental phylogenetic cladogram, but not in the general area cladogram, as an area can only appear in one position. It is possible that two species are placed as most related to each other because they are in fact the first splits from the ancestor; these two species are present in areas only related to each other by the ancestral distribution. In the N Borneo example this area is placed as sister to N Indochina, and these two together are placed as a sister group to the area in which the ancestor continued to exist.

For biogeographical analysis, it is not enough that an area contains one endemic species. The endemic should have relations with taxa in 'related' areas as well. It is best to use at least two groups with endemics in other areas (C. J. Humphries, pers. comm., 1997). If there are not enough relations, the endemic – with its distribution area – will stand on its own, e.g., in a basal position in the area cladogram, and will not be very informative. Similarly, it is unnecessary to use only distribution areas that are areas of endemism; areas containing overlapping widespread species can be informative as well. It depends on how informative the relatives are.

Similarly, some areas are not very informative due to a lack of species in the area. It would be worthwhile to expand this analysis with groups with a similar distribution pattern, but with more representatives in India, E India and W Burma, Sumatra, Sulawesi, Palawan and the Philippines.

The groups added should preferably be of about the same geological age – in this case not older than the Eocene – because more ancient groups may reflect a different pattern, and the results will be mixed and end up with an uninformative area cladogram.

On the other hand it would be worthwhile to extend the analysis also with biogeographical runs on larger basic areas, in that way avoiding too many 'absent areas'. In a way the outcome will be expected to be the same, but by different optimisations it is possible that different cladograms will turn out to be the most parsimonious ones.

Another interesting option is the possibility to use the geological entities as found in the geological literature instead of the areas of distribution. With these geological entities it may be possible to say something about the relationships of the areas of distribution if the phylogenetic relationships of the species are reflected in their distribution. If other factors are dominant in the distribution pattern and disturb the historical pattern it will not be possible to make sensible hypotheses on these relationships. In this case it will be even more difficult to score the presence/absence of a species, because the limitations are in this case independent from the distribution of the species. In some cases they may occur to some extent outside the chosen area. It may then be necessary to set a limit to the percentage of occurrences outside the scored area, in that way correcting for an occasional dispersal event.

I believe, however, that most will be gained by adding more genera to the analysis, thus probably giving a better supported generalised area cladogram and distribution areas that are better delimited.

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