Historical Biogeography of the Southeast Asian genus *Spatholobus* (Legum.-Papilionoideae) and its allies

Jeannette W. A. Ridder-Numan

CONTENTS

SUMMARY

The genera *Butea, Meizotropis* and *Spatholobus* (Leguminosae–Papilionoideae), oc-
curring in continental Southeast Asia and the West Malesian Archipelago, are treated
phylogenetically with *Kunstleria* as an outgroup. The genera *Spatholobus* (29 spe-
cies), *Butea* and *Meizotropis* (each 2 species) are usually placed in the tribe Phaseoleae
of the Papilionoideae, whereas *Kunstleria* belongs to the less advanced tribe Millet-
tieae. *Spatholobus* is probably basal in the Phaseoleae. An analysis with PAUP of the
datamatrix containing 80 macromorphological, 10 leaf anatomical and 7 pollen mor-
phological characters resulted in three most parsimonious trees (MPTs) with a length
of 589 steps. As for the method, it turned out that the option 'addition sequence ran-
dom' gave more MPTs than an 'addition sequence simple'. The standard option 'addi-
tion sequence simple' with taxon one as reference taxon resulted in trees a few steps
longer than the MPTs.

One of the three phylogenetic trees has been chosen to be used for the biogeographic
analysis. Other genera used for this analysis are *Fordia* (Leguminosae–Papilionoideae),
Genianthus (Asclepiadaceae), and *Xanthophytum* (Rubiaceae). Within Southeast Asia
29 areas of distribution were recognised. Although they are solely based on the distri-
bution pattern of the species, some areas coincide with geological entities, e.g., E Ma-
laya and SE Sumatra. The biogeographical analysis performed by PAUP (BPA) and
CAFCA (CCA) resulted for PAUP in 19 MPTs under assumption 0 with a length of 366
steps and 324 MPTs under assumption 1 with a length of 316 steps; for CAFCA the
analysis resulted in 1 MPT (450 steps) under assumption 0 and 1 MPT (417 steps)
under assumption 1. In all results more or less the same larger groups of areas were
present: the areas recognised on Borneo, those on the Malay Peninsula together with
SE Sumatra and W Java, and the areas on the continent of Southeast Asia. Some areas
with only one species were found basal to the other nodes, and were considered not
informative. After comparing the 19 MPTs, the 50% Majority-rule consensus tree was
used to discuss the possible link with the geology. The geology of the region is very
complex as there are four major tectonic plates in collision with each other: the Eur-
asian Plate, the Indo-Australian Plate, the Pacific Plate, and the Philippines Sea Plate.

A summary of the geology of Southeast Asia is given. It is probable that the general
area-cladogram reflects the split (during high sea level) between continental Southeast
Asia and Peninsular Malaysia and the Malay Archipelago. Furthermore it is remark-
able that the areas in Borneo are splitting off in the order of age, where the youngest
areas are at the top and the oldest at the base of the tree. The history of the genus *Spa-
tholobus* is hypothesised by backtracking the phylogenetic relationships on the
general area-cladogram. Probably the history of *Spatholobus* was influenced by the
differences in sea level. During low sea levels the Sundaland Plateau was dry and it
was possible to migrate into the Malesian Archipelago, but high sea levels resulted in
isolation and speciation. It is impossible to say more about timing than that it could
have started at the earliest in the Early Eocene. In the last case the ancestor of the
genus was present in an area without the northern parts of Borneo, and with the south
arm of Sulawesi still connected to Borneo.

Chapter 1

INTRODUCTION

The aim of this study is to reconstruct the phylogeny of the genus *Spatholobus* (and allies) and to use this phylogeny in a historical biogeographical analysis. This project is part of an ongoing research programme on the historical biogeography of the Malesian region at the Rijksherbarium / Hortus Botanicus Leiden. Other groups already studied are the sapindaceous genera *Cupaniopsis* (Adema, 1991), *Guioa* (Van Welzen, 1989), *Arytera* and *Mischarytera* (Turner, 1995), and sections from the orchid genus *Bulbophyllum* (Vermeulen, 1993). These studies focus on the East Malesian region, whereas this study will go into more detail on the West Malesian region including the Southeast Asian continent.

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 & McLennan, 1991; Cracraft, 1983, 1988; Forey et al., 1993; Nelson & Platnick, 1981; Page, 1988, 1990; Wiley, 1981, 1987; Zandee & Roos, 1987). Several computer programs are available for use with morphological or molecular data, e.g., PAUP (Swofford, 1991, 1993) Hennig 86 (Farris, 1988), and CAFCA (Zandee, 1995).

For a phylogenetic treatment it is necessary to assume the monophyly of the group under study. In addition it is necessary to include an outgroup, to polarise the character states used in the phylogenetic analysis. The computer program CAFCA can run without the use of an outgroup.

The legume genus *Spatholobus* consists of 29 species of lianas in Southeast Asia (Ridder-Numan & Wiriadinata, 1985; Ridder-Numan, 1992). The closely allied genera *Butea* and *Meizotropis* occur only on the mainland of Southeast Asia. Both comprise two species (Sanjappa, 1987). The two species of *Butea* have large red or yellow flowers, and are probably bird-pollinated. One species, *B. monosperma*, is a tree, the other is a liana. The genus *Meizotropis* occurs in the Himalayan region and is a shrub. All three genera are usually placed in the tribe Phaseoleae (Lackey, 1981). On account of the resemblance in mainly pod and leaflets, however, these three genera have also been treated as one genus, *Butea* [e.g., Blatter (1929), and in several regional Floras]. The pod is one-seeded and samaroid; the leaves are trifoliolate and asymmetric, as in most Phaseoleae (Lackey, 1981). Not all species of *Spatholobus* closely resemble *Butea*, since in *Spatholobus* there are, e.g., two types of leaflets: strongly asymmetrical leaflets (Fig. 2.8 and 2.10), as is usual in the tribe Phaseoleae, and more or less symmetrical leaflets (Fig. 2.2), as is usual in the Millettieae. This last tribe is considered to be less derived than the Phaseoleae (Geesink, 1981, 1984). A basal position in the tribe Phaseoleae is indicated also by a phylogenetic analysis that is based on molecular data (Bruneau et al., 1995). Here *Spatholobus* has a position low in the tribe Phaseoleae as sister taxon to *Butea*.

Kunstleria (Fig. 2.2 and 2.20b) has been chosen as an outgroup. This genus with eight species in the tribe Millettieae bears a great resemblance to *Spatholobus*. The flowers are of the same size and appearance, and have the same number of ovules (two). The leaflets of *Kunstleria* are more or less symmetrical. Some species have uni- or trifoliolate leaves, others have more than three leaflets. *Kunstleria* differs from *Spatholobus* mainly in the

vexillary stamen, which is adnate to the claw of the standard in *Kunstleria* (versus free in *Spatholobus*), the extraordinary long and often curled dorsal auricle on the wing petals, and the flat strap-like pod with the seed(s) placed centrally (Ridder-Numan & Kornet, 1994; Fig. 2.20b). Unfortunately no molecular data on this rare liana genus are available. *Kunstleria* has been mentioned in molecular treatments, but this appeared to be *K. blackii*, which is synonymous with *Austrosteenisia blackii. Austrosteenisia* is a genus probably related to the less derived genera in the Millettieae, i.e. *Callerya* and *Ostryocarpus*, and it occurs in Australia and New Guinea (Geesink, 1984).

The phylogenetic treatment of *Spatholobus* is given in **Chapter 2**. The characters used for the phylogenetic analysis are discussed in this chapter in the section on morphology. They include macromorphological characters as well as some from leaf anatomy and pollen morphology. The pollen morphological characters were selected after an extensive review of the pollen morphology of *Spatholobus, Butea, Meizotropis* and *Kunstleria*, which will be published separately (Ridder-Numan, in press; in the thesis added as **Chapter 5**). The result of the phylogenetic analysis has been used in the biogeographical analyses.

The historical biogeographical analysis serves two purposes: to construct a generalised area cladogram providing information on the biogeographic history of Southeast Asia, and to explain the developments of the genus *Spatholobus* in space and time in the area as a special case. Of course without any knowledge of the geology of the region it is impossible to interpret a generalised area cladogram other than as a sequence of areas. Combining this area sequence with the geological background may give an indication of geological events causing cladogenesis. It is difficult to establish the order of these events unless there are either well-dated events recognisable in the area cladogram, or there is a complete fossil record of the group. As for fossils, there are none available as far as I know from the group under study. It can only be assumed that the vicariance events which caused speciation in this group occurred after the existence of the (sub)family in the area. **Chapter 3** gives an overview of the geological knowledge on the Southeast Asian region. The general informa-tion available on fossils of Leguminosae in the region is presented.

Chapter 4 deals with the historical biogeographical analyses. The basis of these analyses are the phylogenies of the genera *Spatholobus* and allies (*Chapter 2*), *Fordia* (Schot, 1991), *Genianthus* (Klackenberg, 1995), and *Xanthophytum* (Axelius, 1990). Phylogenies of these genera, which are distributed in more or less the same region as *Spatholobus*, were avail-able at the time of this study. With their combined phylogenies and distributions a general-ised area cladogram has been established, after analysis with CAFCA and PAUP, computer programs appropriate for use in cladistic biogeographic analysis. The result of these analy-ses, the generalised area cladogram, is compared with the geological information. The genus *Spatholobus* is optimised on the area cladogram, and its possible history is given.

Acknowledgements

Chapter 2

PHYLOGENETIC ANALYSIS

INTRODUCTION

The legume genus *Spatholobus* (Ridder-Numan & Wiriadinata, 1985; Ridder-Numan, 1992), and the closely allied genera *Butea* and *Meizotropis* (Sanjappa, 1987) are used as an ingroup for the phylogenetic analysis. *Spatholobus* and its allies are basal in the tribe Phaseoleae (Bruneau et al., 1995). The genus *Kunstleria*, which resembles *Spatholobus*, is chosen as an outgroup. This latter genus belongs to the tribe Millettieae (Geesink, 1981, 1984). The Millettieae are a complex paraphyletic group, and the last to be revised for Flora Malesiana. The genera are chosen to study the historical biogeography of the West Malesian area, and – in addition – the choice of these genera may add to a better understanding of the Millettieae.

MATERIAL AND METHODS

Introduction

A data matrix with 97 characters, 7 of which relate to pollen morphology, 10 to leaf anatomy, and 80 to macromorphological characters, is presented for all species of *Spatholobus*, *Butea* and *Meizotropis* (Table 2.1). The characters and their states are described in the section on Morphology, and the quantitative characters are given in Table 2.2. The outgroup *Kunstleria* was considered a single taxon by coding the combined information on the species as is otherwise done for specimens in describing a species. Autapomorphic character states occurring in only one species were ignored, and the state occurring in the rest of the genus was taken as representative for the genus.

Data for the matrix were taken from herbarium specimens. Where possible, samples of pollen or leaves were taken, preferably from 10 samples per species. A list of specimens used for the pollen morphological samples can be found in Ridder-Numan (in press). Specimens used for leaf anatomical sections are listed in the Appendix to the present chapter.

Method of analysis

The data matrix was analysed using the computer program PAUP (Swofford, 1993) under the heuristic search option with a stepwise addition sequence either simple or random, and the branch-swapping method tree-bisection-reconnection (TBR). All characters were analysed unordered; uninformative characters, e.g., autapomorphies, were ignored and characters with multiple states were treated as polymorphisms. The possibility of using multistate characters that are treated as polymorphisms was one of the

reasons for using PAUP. It must be noted, however, that PAUP counts steps differently from other programs, especially when polymorphisms are involved. Polymorphic characters contain enough phylogenetic information to be included in a phylogenetic analysis (Wiens, 1995). In one stage or another characters must have been polymorphic during species development. To avoid too much homoplasy due to the increased variability by polymorphy, it is perhaps best to keep the number of states for one character as low as possible. I did this by re-evaluating the character states using the program MacClade (Maddison & Maddison, 1992), and recoding the characters where possible. Polymorphic species were coded as such, i.e. taxa coded as having multiple states for a particular character were not treated as uncertain (= '?') for that character, as is often necessary in other computer programs. In theory polymorphic species should be coded following the locally plesiomorphic state. This state, however, is not known in advance, and should be derived from outgroup comparison if possible. For a detailed discussion on coding of polymorphic species see Turner (1995).

A search with a random addition sequence was performed to find more solutions than with the simple addition sequence. As described in more detail below, it became evident that with a simple addition sequence not all islands of trees were found. This may be caused by the different trees created initially when different taxa are chosen as reference taxa (a simple addition sequence needs a reference taxon). After tree bisection and reconnection (TBR) these different initial trees may lead eventually to different islands of trees (Swofford, 1991). By creating more starting trees, a random addition sequence is more successful in finding more islands of trees (and in that way more parsimonious trees).

The default option for running a TBR search is a simple addition sequence and has as reference taxon 1, which will be in most cases the outgroup. By assigning each time a different member of the taxa in the analysis as reference taxon and performing a new TBR search different trees appeared, which were in some cases shorter. Using different taxa as reference taxon in a TBR search thus led to different results. To explore more possible solutions (by creating more different starting points and thus possibly different islands of trees) an analysis with addition sequence random (1000 repetitions) was performed. This analysis resulted in one additional most parsimonious tree. The first two most parsimonious trees (MPT) were found during the first replicate, the additional one during the fifteenth. During the other 85 replications no additional trees were found.

Finally the most parsimonious trees that resulted from the search with PAUP were analysed using MacClade (Maddison & Maddison, 1992) with several options such as Trace Character, Trace All Changes, Compare Two Trees.

MORPHOLOGY

The characters used for the phylogenetic analysis were taken from various parts of the plant. Although revisions of the genera were available (Ridder-Numan & Wiriadinata, 1985; Sanjappa, 1987; Ridder-Numan, 1992; Ridder-Numan & Kornet, 1994), all characters were checked against material available. Due to the fact that more material was

available than at the time of the revision and that the revisions were not written with the intention of a phylogenetic treatment, it turned out that not all data presented in these revisions were detailed enough, and, moreover, that not all characters I wanted to use for the analysis could be found in the descriptions. In addition to macromorphological characters I checked pollen morphology as well as leaf anatomy for characters useful for a phylogenetic analysis. Due to the limitations of the herbarium material the characters selected are restricted to those parts which are generally collected from lianas (or trees), i.e. the terminal parts of the plants where the inflorescences may be found. Features of the older stems and leaves are not discussed as they are not available for most of the species. For some species material is very scarce, and consequently the data for these species is based on a small number of specimens only. A description of the characters and states used for the phylogenetic analysis is presented below. An overview of the characters and the states recognised is given in Table 2.1. The numbers between square brackets in the descriptions below refer to the numbers of the characters in this table. For quantitative characters Table 2.2 gives more details. In case of absence of a plant part, a question mark is used for the characters that relate to this part and cannot be scored. Thus, all flower characters are designated as a '?' for species of which no flowers were available. The lack of material was considerable for some species, making it impossible to avoid question marks. Poorly known species can be best omitted. One species, *Spatholobus bracteolatus*, was excluded from the phylogenetic analyses because the data that could be collected were too incomplete.

Table 2.1. Characters and character states used in the phylogenetic analysis.

a. List of characters and character states

Stem

1. Stem hollow
   1 = yes
   2 = no
2. Indumentum
   1 = sparse / not pubescent
   2 = pubescent / puberulous / sericeous
   3 = hirsute / strigose / pilose
3. Lenticels
   1 = not conspicuous / small
   2 = wart-like
   3 = elongated
4. Exudate
   1 = present
   2 = absent
5. Bark
   1 = smooth
   2 = with ridges / wrinkles

Leaves

6. Ultrajugal part of the rachis
   1 = less than 1/10 of the rachis / no ultrajugal part
   2 = ultrajugal part more than 1/10
7. Stipules
   1 = recurving
   2 = not recurving

8. Stipules
   1 = (early) caducous
   2 = more or less persistent
9. Stipules symmetrical
   1 = yes
   2 = no (asymmetrical)
10. Stipules nerves
    1 = nerves visible
    2 = no visible nerves
11. Stipules indumentum
    1 = glabrous / glabrescent
    2 = hairy
12. Stipule length
    1 = as long as wide
    2 = 2 or 3 times as long as wide
    3 = 4 or more times as long as wide
13. Pulvinus colour
    1 = black / darker than rachis
    2 = same colour as rachis
14. Pulvinus indumentum
    1 = glabrous / glabrescent / sparsely hairy
    2 = pubescent / hirsute
    3 = densely pubescent / strigose
15. Stipellae caducous
    1 = (early) caducous
    2 = more or less persistent

(Leaves continued)

16. Stipellae length
    1 = up to the length of the petiolule
    2 = conspicuously longer than the petiolule
17. Upper surface colour
    1 = green / brownish (dried colour)
    2 = greyish blue (glaucous)
18. Lower surface colour
    1 = green / brownish (dried colour)
    2 = always brown
19. Upper surface indumentum
    1 = glabrous to sparsely pubescent
    2 = pubescent (dense)
    3 = sericeous
    4 = hirsute / strigose
20. Lower surface indumentum
    1 = glabrous to sparsely pubscent
    2 = pubescent (dense)
    3 = sericeous
    4 = hirsute / strigose
21. Shape of top leaflet
    1 = only elliptic
    2 = ovate to elliptic
    3 = obovate to elliptic
22. Apex leaflet
    1 = acute
    2 = acuminate / cuspidate
    3 = emarginate / rounded
    4 = abruptly acuminate
23. Base leaflet
    1 = acute / obtuse / subcordate
    2 = decurrent
24. Lateral leaflet symmetrical
    1 = more or less symmetrical
    2 = strongly asymmetrical
25. Main nerve
    1 = sunken or flat
    2 = raised
26. Secondary nerves at upper surface
    1 = flat
    2 = raised
27. Nerves at lower surface
    1 = only midrib prominent
    2 = midrib and secondary nerves prominent
    3 = venation also prominent
28. Venation
    1 = reticulate
    2 = reticulate-scalariform
    3 = scalariform
29. Angle secondary nerves with midrib (average)
    1 = up to 45°
    2 = more than 45°
30. Secondary nerves terminate
    1 = diffusely
    2 = in the margin
    3 = forming marginal arches
31. Pairs of secondary nerves (average)
    1 = 5–8
    2 = more than 8

Inflorescence

32. Place of inflorescence
    1 = axillary / terminally
    2 = terminally

(Inflorescence continued)

33. Indumentum of inflorescence
    1 = puberulous / pubescent
    2 = hirsute / strigose / tomentose
    3 = (nearly) glabrous
34. Number of branches
    1 = main axis with (secondary) side branches / fascicles
    2 = main axis with secondary and tertiary branches / fascicles
    3 = main axis with secondary, tertiary and quaternary branches / fascicles
35. Brachyblasts
    1 = present
    2 = absent, flowers solitary
36. Number of bracts of the first order (= secondary) side branch
    1 = one bract
    2 = two bracts
37. Shape of the bracts
    1 = linear
    2 = triangular
    3 = broadly ovate
    4 = elliptic, surrounding the bud
38. Number of bracts of the tertiary branch / flower
    1 = one bract
    2 = two bracts

Flower

39. Length of the pedicel
    1 = very short, up to 1 mm; flower nearly sessile
    2 = pedicel > 1 mm; flower not nearly sessile
40. Place of the bracteoles
    1 = immediately below the calyx
    2 = on the upper half of the pedicel
    3 = on the lower half of the pedicel
41. Indumentum of the calyx
    1 = sparsely pubescent / nearly glabrous
    2 = pubescent / sericeous
    3 = hirsute
42. Top of the vexillary lobe
    1 = emarginate
    2 = not emarginate
43. Length of the vexillary lobe
    1 = as long as the cup
    2 = about half the length of the cup
    3 = less than half the length of the cup
44. Shape of the other calyx lobes
    1 = triangular
    2 = truncate / somewhat rounded
    3 = more or less rhomboïd
    4 = with a rounded apex
45. Indumentum on the standard
    1 = present
    2 = absent
46. Apex of the standard
    1 = emarginate
    2 = not emarginate
47. Standard with auricles
    1 = present
    2 = absent
48. Base of the standard blade
    1 = decurrent into the claw
    2 = truncate

(Flower continued)

49. Dorsal auricle on the wing
    1 = present
    2 = absent
50. Ventral auricle on the wing
    1 = present
    2 = absent
51. Wing with lateral pocket
    1 = present
    2 = absent
52. Wing with indumentum outside
    1 = present
    2 = absent
53. Wing with indumentum inside
    1 = present
    2 = absent
54. Wing with indumentum on dorsal auricle / margin
    1 = present
    2 = absent
55. Wing with indumentum on ventral auricle / margin
    1 = present
    2 = absent
56. Keel with a dorsal auricle
    1 = present
    2 = absent
57. Keel with a ventral auricle
    1 = present
    2 = absent
58. Keel with a lateral pocket
    1 = present
    2 = absent
59. Keel with indumentum outside
    1 = present
    2 = absent
60. Keel with indumentum inside
    1 = present
    2 = absent
61. Keel with indumentum on dorsal auricle / margin
    1 = present
    2 = absent
62. Keel with indumentum on ventral auricle / margin
    1 = present
    2 = absent
63. Keel petals
    1 = connate
    2 = free
    3 = overlap
64. Vexillary filament
    1 = free
    2 = connate to the claw of the standard
65. Filaments connate for
    1 = less than half of their length
    2 = more than 3/4 of their length
    3 = more than half, but less than 3/4 of their length
66. Indumentum on filament sheath
    1 = absent
    2 = present
67. Size of the anthers
    1 = less than 0.5 mm
    2 = more than 0.5, but less than 1 mm
    3 = more than 1, but less than 2 mm
    4 = more than 2 mm

(Flower continued)

68. Anthers
    1 = fertile and equal
    2 = all fertile and alternately larger and smaller
    3 = alternately fertile and sterile
69. Nectary glands
    1 = 10
    2 = 5, all equal
    3 = connate, no separate lobes
    4 = 10 thickened filament bases
70. Nectary with indumentum
    1 = absent
    2 = present
71. Indumentum of the ovary
    1 = pubescent / sericeous
    2 = very densely pubescent / woolly
    3 = sparsely hairy
72. Indumentum on the style
    1 = up to halfway
    2 = at the base
    3 = up to at least 3/4
73. Number of ovules
    1 = 2
    2 = 2–4
    3 = more than 4
74. Place of the ovules
    1 = basal
    2 = in the middle / apical
75. Stipe of the ovary present
    1 = no
    2 = yes
76. Stigma
    1 = flat
    2 = capitate
    3 = elongated

Pod

77. Stipe of pod exceeding calyx
    1 = yes
    2 = no
78. Top of the pod
    1 = with the style remnant pointing to the dorsal side
    2 = with the style remnant pointing forward
    3 = with the style remnant bent downwards
79. Shape of the wing
    1 = straight, as narrow as the seed-bearing part
    2 = wider than the seed-bearing part
80. Indumentum of pod
    1 = puberulous or nearly glabrous
    2 = densely pubescent

Leaf anatomy

81. Hair base
    1 = basal cell not in palisade layer
    2 = basal cell in palisade layer
82. Bulbous septate hair base
    1 = absent
    2 = present
83. Glandular hair
    1 = stalk 1–2, head 2–6 cells
    2 = stalk 2–5, head 4–8 cells
    3 = head cup-shaped

(Leaf anatomy continued)

84. Epidermis lower surface
    1 = straight
    2 = curved cell walls
    3 = undulate
    4 = strongly undulate
85. Hypodermis
    1 = absent
    2 = only near larger veins
    3 = present throughout leaves
86. Stomata adaxial
    1 = absent
    2 = present
87. Vascular bundle in midrib
    1 = open
    2 = closed / semi-closed
88. Veins transcurrent (larger veins)
    1 = absent (smaller palisade layer continuous)
    2 = present
89. Tannin (?) containing cell layer between phloem and
       xylem
    1 = present
    2 = absent
    3 = in xylem itself
90. Tannin in bundle sheath
    1 = present
    2 = absent

Pollen

91. Ornamentation pollen
    1 = closed ornamentation (rugulate, psilate-perfo-
       rate, fossulate)
    2 = microreticulate / coarse perforate
    3 = verrucate
92. Fused colpi
    1 = absent
    2 = yes, sometimes
    3 = often
93. Foot layer / endexine ratio
    1 = more than 0.6
    2 = less than 0.6 and more than 0.1
    3 = less than 0.1
94. Colpus ends
    1 = acute
    2 = obtuse
95. Mesocolpial pouches
    1 = present
    2 = absent
96. Infratectal layer
    1 = well-spaced columellae
    2 = irregular (short) columellae
    3 = granules
    4 = indistinct / dense
97. A/E
    1 = mean < 0.28, max 0.31
    2 = mean 0.28, but < 0.4
    3 = mean > 0.4

b. Data matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
S. acuminatus	2	1/2	2	1	2	2	2	1	1	3	2	3	2	2	1	1	1	1	1	1
S. albus	2	1	2	1	1	1/2	1	1	1	3	2	1	2	1	1	1	2	2	1	1
S. apoensis	2	1	1	2	1	2	2	1	1	3	1	2	1	1	1	1	2	2	1	1
S. auricomus	2	2	1	2	1	2	2	1	1	?	?	?	2	3	1	2	1	2	1	3
S. auritus	1	2	1	1/2	2	2	2	1	1	2	2	2	2	1	2	1	1	1	1	2
S. bracteolatus	1	3	1	2	1	2	2	1	1	3	2	2	1/2	3	1	1	1	1	1	1
S. crassifolius	2	1	1	1	1	2	?	1	?	?	?	?	2	1	1	1	1	1	1	1
S. dubius	2	1	3	1	1	2	2	1	1	2	2	2	2	2	1	2	2	2	1	2
S. ferrugineus	1/2	2	1	1	1	2	1	1	1	3	2	1	2	3	1	1	1	1	1	2/3/4
S. gyrocarpus	2	2	1	1	1	2	?	1	?	?	?	?	2	3	1	1	1	1	1	2
S. harmandii	2	1	1	2	1	2	2	1	1	1	2	2	2	3	2	1	2	2	1	1
S. hirsutus	1	1	1	2	1	2	2	2	1	1	1	3	1	2	1	1/2	1	1	1	1
S. latibractea	2	2	3	2	1	2	2	1	1	1	2	2	2	2	1	1	2	2	1	2
S. latistipulus	2	1	1	1	1	2	2	2	2	1	1	1	1	1	2	1	2	2	1	1
S. littoralis	2	1	3	1/2	1/2	2	2	1	1	3	1	2	2	1	1	1	1	1	1	1
S. macropterus	1/2	1	1	2	2	2	2	1	1	1	1	3	1	1	1	1	1	1	1	1
S. maingayi	2	1	1	2	1	2	2	1	1	1	1	2	1	1	1	1	1	1	1	1
S. merguensis	2	1	1	2	1	1	2	1	1	1	2	2	2	1	1	1	1/2	1	1	1
S. multiflorus	2	2	1	1	1	1	2	2	1	3	2	2	2	3	2	2	2	2	1	3
S. oblongifolius	1	1	1	2	2	1	?	1	?	?	?	?	1	1	1	1	1	1	1	1
S. parviflorus	2	2	1	1	2	2	1	1	1	3	2	1	2	3	1	1	1	1	1	1/2/3
S. persicinus	2	2	1	1	1	2	2	1	1	3	2	2	2	2	1	1	1	2	1	2
S. pottingeri	1	3	1	1/2	2	2	1/2	1	1	3	2	2	1/2	1	2	1/2	1	1	1	1/4
S. pulcher	2	1/3	3	2	1	2	?	1	?	?	?	?	2	2	1	1	1	1	1	4
S. purpureus	2	1	1	2	2	2	?	1	?	?	?	?	2	2	1	1	1/2	1	1	1
S. ridleyi	2	1	1	2	2	2	1	1	1	1	1	2	1	1	2	1	1	1	1	1
S. sanguineus	2	2	1	1	1	2	1	1	1	3	2	2	2	3	1	2	1	1	1	2
S. suberectus	2	1	2	1	2	2	2	1	1	3	2	2	2	1	1	1	1	1	1	1
S. viridis	2	2	2	2	1	2	2	1	1	2	2	2	2	2	1	1	1	1	1	2
B. monosperma	1	2	1	1	2	2	1	1	1	3	2	2	2	2	1	1	1	1	1/3	3
B. superba	1	2	1	1	2	2	1	1	1	3	2	2	2	2	1	1	1	1	2/3	2
M. buteiformis	2	2	1	1	2	2	2	1	1	1	2	1	2	2	1	1	1	1	2	2
M. pellita	1	3	1	1	2	2	2	1	1	3	2	1	2	3	1	1	1	1	4	4
Kunstleria	1	2	2	2	2	2	2	1	1	3	2	2	2	2	?	?	1	1	1	2

(Table 2.1 contd)	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
S. acuminatus	1	1	1	1	1	1	1	1	2	1	1	1	1	1	2	2	2	1	2	3
S. albus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	2	1	2	1
S. apoensis	1	4	1	1	1	1	2	1	2	1	1	1	1	2	2	2	2	1	2	2
S. auricomus	1	2	1	1	1/2	1	2	1	1	1	1	1	1	2	1/2	1	3	1	2	1
S. auritus	1	2	1	1	1	1	3	2	1	3	2	1	1	2	1	2	1	1	2	1
S. bracteolatus	1	2	1	2	2	1	3	2	1	1	2	1	2	1	2	1	2	1	?	1
S. crassifolius	1	2	1	1	2	1	1	1	2	1	2	1	2	2	2	2	2	2	2	2
S. dubius	1	1	1	1	2	1	2	1	1	1	1	1	1	2	1	1	1	1	2	2
S. ferrugineus	2/3	1/3	1/3	2	2	2	3	2	2	2	1	1	1	2/3	1	2	2	1	2	2
S. gyrocarpus	2/3	4	1	2	2	1	3	2	1	1	2	1	1	2	1	2	1	1	1	1
S. harmandii	1	2	1	1	1	1	1	1	2	1	1	1	1	1	2	2	2	1	2	2
S. hirsutus	1	2	1	1	1	1	3	2	1	1	1	1	1	2	1	2	4	1	2	1
S. latibractea	1	4	1	1	2	1	2/3	1/2	2	3	2	1	1	2	1	1	2/3	1	2	3
S. latistipulus	1	4	1	1	1/2	1	2	1	2	1	2	1	1	2	1	2	1	1	2	2
S. littoralis	2	1	1	1	2	1	2	1	1	1	1	1	1	2	1	2	2	1	2	2
S. macropterus	2	1	1	1	1/2	1	2	1	1	1	1	1	1/3	2	1	2	1	1	2	1/2
S. maingayi	1	1	1	1	2	1	2	1	1	1	1	1	3	2	1	2	2	1	2	1/2
S. merguensis	1	1/3	1	1	2	1	1	1	2	1	2	?	1	2	2	2	?	1	2	1
S. multiflorus	1	2	1	1	2	1	2	1	2	3	2	1	1	2	1/2	2	1	1	2	1
S. oblongifolius	3	1	3	2	2	1	2	1	1	1	2	1	2	1/2	2	1	2	1	2	2
S. parviflorus	2	1/3	1	2	2	2	3	2	1	1	2	1	1	3	1	2	1	2	2	1
S. persicinus	1	4	1	1	2	1	3	2	2	3	2	1	1/2	2	1	2	2	1	2	1
S. pottingeri	3	1/3/4	1	2	2	2	3	2	1	1	2	1	1/2	2	2	2	2	2	2	1
S. pulcher	3	3	1	2	2	1	3	1	1	1	1	1	2	2	2	2	2	2	2	1
S. purpureus	1	2	1	1	2	1	2	1	2	1	2	1	1	2	1	2	2	1	2	1
S. ridleyi	1	1	1	1	1	1	1	1	1	1	2	1	2	1	2	2	1	1	2	1
S. sanguineus	2	2	1	2	2	1	3	2	1	1	2	1	1	2	2	2	1	1	1/2	1
S. suberectus	1	4	1	2	2	1	3	3	1	1	1	1	2	2	1	2	1	1	2	2
S. viridis	1	4	1	1	1	1	2	1/2	2	3	2	?	1	2	1	1	?	1	2	2
B. monosperma	3	3	3	2	2	2	3	3	1	2	1	1	1	1	1/2	2	2	1	2	1
B. superba	3	3	1/3	2	2	2	3	3	1	2	1	1	1	1	1/2	2	2	1	2	1/2
M. buteiformis	2	1	1/3	2	2	2	3	3	1	2	1	2	1	1	1	1	?	1	2	1
M. pellita	2	1	1/3	2	2	1	3	3	1	2	1	2	1	1	1	1	2	1	2	1
Kunstleria	1	2	1	1	1	1	2	1/2	1	1	1	1	1	1	2	2	2	2	1	1	1

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
S. acuminatus	2	1	1	4	2	1	2	1/2	1	2	1	2	2	2	2	2	2	1	2	2
S. albus	1	1	3	1	2	1	2	2	1	1	2	2	2	2	2	1	2	1	2	2
S. apoensis	1	2	3	1	2	1	2	1	1	2	2	2	2	2	2	1/2	2	2	2	2
S. auricomus	2	1	2	1	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2
S. auritus	2	1	3	2	2	1	2	2	1	2	1	2	2	2	2	1	2	1	2	2
S. bracteolatus	2	1	1	1	2	1	2	2	?	?	?	?	?	?	?	?	?	?	?	?
S. crassifolius	2	1	1	1	2	1	2	2	1	2	1	2	2	2	2	2	2	1	2	2
S. dubius	2	1	2	1	2	1	2	2	1	2	1	2	2	2	2	1	2	2	2	2
S. ferrugineus	2	1/2	2	1	2	1	2	1	1	1	1	2	2	2	1/2	1	2	1	2	2
S. gyrocarpus	2	1	2	1	2	1	2	1	2	2	1	2	2	2	2	2	1	1	2	2
S. harmandii	2	1	2	3	2	1	2	2	1	2	1	2	2	2	2	2	1	2	2	2
S. hirsutus	2	1	3	1	2	1	2	1	1	2	1	1	2	2	1	1	2	1	2	2
S. latibractea	2	1	2	1	2	1	2	2	2	2	1	1	2	1	1	2	2	1	1/2	2
S. latistipulus	1	2	3	2	2	1	2	2	1	2	1	2	2	2	2	1/2	2	2	2	2
S. littoralis	2	2	3	1	2	1	2	1	1	2	1	2	2	2	2	2	2	2	2	2
S. macropterus	2	1/2	2	1	2	1	2	1	1	2	1	1	2	1	1	1/2	2	1	2	2
S. maingayi	1	2	3	2	2	1	2	1	1	2	2	2	2	2	2	1	2	2	2	2
S. merguensis	2	1	1	3	2	1	2	2	2	2	1	2	2	2	2	2	1	1	2	2
S. multiflorus	2	1	2	1	2	1	2	1/2	1	1	1	2	2	2	2	1/2	2	1	2	2
S. oblongifolius	2	1	2	3	2	1	2	1/2	2	2	1	2	2	2	2	1/2	1	2	2	2
S. parviflorus	2	2	1	1	2	2	1/2	2	1	2	1	2	2	2	2	1	2	1	2	2
S. persicinus	2	2	3	2	2	1	2	2	1	2	2	2	2	2	2	1	2	2	2	2
S. pottingeri	2	1	2	3	2	1	2	1	1	2	1	2	2	1	1	1	2	1	2	2
S. pulcher	3	2	1/2	1	2	1	2	1	1	1	1	2	2	2	2	1	2	1	2	2
S. purpureus	2	1	1	1	2	1	2	1	2	2	1	2	2	2	1	2	2	1	2	2
S. ridleyi	2	2	·2	4	2	1	1/2	1	2	2	1	2	2	2	1	2	2	1	2	2
S. sanguineus	2	1	2	1	2	1	2	2	1	2	1	2	2	2	2	1	2	1	2	2
S. suberectus	2	1/2	2	3	2	1	2	1/2	1	2	1	2	2	2	2	2	1	2	2	2
S. viridis	2	2	2	1	2	1	2	1	1/2	1	1	1/2	2	2	1/2	2	1	1	2	2
B. monosperma	2	1/2	2	1	1	2	2	1	1	2	1	1	1	1	1	1	2	1	1	2
B. superba	2	1/2	2/3	1	1	2	2	1	1	2	1	1	1	1	1	2	2	1	1	1
M. buteiformis	2	1	3	1	1	2	1	2	1	2	1	1	2	1	2	2	1	1	1	1
M. pellita	3	2	2	3	1	2	1	2	1	2	1	1	2	2	1	2	2	1	1	2
Kunstleria	2	1/2	2	3	2	2	2	2	1	2	1	1	2	1	1	1	2	1	1	2

(Table 2.1 contd)	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
S. acuminatus	2	2	1	1	3	1/2	1	1	1	1/2	1	2	1	2	1	1/2	2	1	1	1
S. albus	2	2	1	1	3	1	1	1	1	1	2	3	1	2	1	2	2	1	2	1
S. apoensis	2	2	1	1	1	1	2	1	1	1	2	3	1	2	1	1	?	?	?	?
S. auricomus	2	2	1	1	1	1	1	3	1	1	3	2	1	2	1	2	?	?	?	?
S. auritus	2	2	1	1	3	1	2	1	1	1	1	2	1	2	2	1	?	?	?	?
S. bracteolatus	?	?	?	1	?	1	1	3	4	1	2	1	1	2	1	3	?	?	?	?
S. crassifolius	2	2	1	1	1	1	1	1	4	2	1	2	1	2	2	2	?	?	?	?
S. dubius	2	2	1	1	3	1	1	1	1	1	1	2	1	2	2	1	1	3	2	1
S. ferrugineus	2	2	1	1	1	1	1	3	1	1	1	1	1	2	2	1	2	2	2	2
S. gyrocarpus	2	2	1	1	1	1	1	1	1	1	3	2	1	2	1	1	2	2	2	2
S. harmandii	2	2	1	1	1	1	1	1	1	1	2	2	1	2	2	1	1	2	2	2
S. hirsutus	2	2	1	1	2/3	1	1	1	1	1/2	1	1	1	1	2	1/2	1/2	2	2	1
S. latibractea	1	2	1	1	3	1	2	1	1	1	1/2	1	1	2	1	1	?	?	?	?
S. latistipulus	2	2	1	1	1	1	2	1	1	1	2	3	1	2	2	2	2	3	1	1
S. littoralis	2	2	1	1	1	1	2	1	1	1	2	1	1	2	2	2	2	2	1	1
S. macropterus	2	2	1	1	2/3	1	1	1	1	2	2	1	1	1/2	2	2/3	1/2	1	2	1
S. maingayi	2	2	1	1	1	1	2	1	1	1	1	1	1	2	2	2	2	3	1	1
S. merguensis	2	2	1	1	1	1	1	1	4	1	1	1	1	2	2	2	?	?	?	?
S. multiflorus	2	2	1	1	1	1	1	1	1	1	1	2	1	2	1	2	2	3	2	2
S. oblongifolius	2	2	1	1	3	1	1	1	1	1	1	2	1	1	1	2	2	3	2	1
S. parviflorus	2	2	1	1	3	1	1	1	1	1	1	2	1	1	2	1	1	2	2	2
S. persicinus	2	2	1	1	1	1	2	1	1	1	2	3	1	1	1	2	?	?	?	?
S. pottingeri	2	2	1	1	3	1	1	3	4	1	1	1	1	2	1	2	2	2	2	2
S. pulcher	2	2	1	1	3	1	1	1	2	2	2	2	2	2	2	2	2	3	2	2
S. purpureus	2	2	1	1	2	1	1	1	2	2	1	2	1	2	2	1	2	3	1	1
S. ridleyi	2	2	1	1	3	1	1	1	1	2	1	1	1	1	2	1	2	2	2	1
S. sanguineus	2	2	1	1	1	1	1	3	1	1	3	2	1	2	1	2	2	3	2	2
S. suberectus	2	2	1	1	3	1	1	1	3	1	3	2	1	1	2	1	1	2	2	2
S. viridis	2	2	1	1	3	1	1	1	1	1	2	1	1	2	2	2	?	?	?	?
B. monosperma	1	1	1	1	2	2	3	1	4	1	2	2	3	2	2	3	1	2	2	2
B. superba	1	1	1	1	2	2	4	1	4	1	2	2	3	2	2	3	1	2	2	2
M. buteiformis	2	1	1	1	3	2	3	1	4	1	1	3	1	2	1	3	2	2	1	1
M. pellita	2	1	1	1	3	2	3	1	4	1	2	3	1	2	1	3	2	2	1	2
Kunstleria	1	1	1	2	3	1	1	2	4	1	2	2	1	1	2	2	2	2	1	2

	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97
S. acuminatus	1/2	2	1	3	1	2	2	1	2	2	1	2	1	1	1	2	1
S. albus	2	2	1	3	1	1/2	2	1	2	2	1	2	2	1	1	2/3	1
S. apoensis	2	2	1	3	1	1/2	2	1/2	2	2	2	1	1	1/2	1	2/3	2
S. auricomus	1/2	2	1	2/3	1	2	2	1	1	2	1	1	?	1	?	2/3	2
S. auritus	?	?	?	?	?	?	?	?	?	?	1	1	?	2	?	4	2
S. bracteolatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
S. crassifolius	1/2	2	1	3	1	1	2	1/2	2	1	1	2	?	1	?	3	1
S. dubius	1/2	2	1	3	1	1	2	1	1	2	1	2	?	1	?	3	2
S. ferrugineus	1/2	2	1	2/3	2	1/2	1/2	2	3	1	1	1	2	1	1	1	1
S. gyrocarpus	2	2	1	3	1/2	1	1/2	2	2	2	1	1	?	1	1	?	3
S. harmandii	2	2	1	4	1	2	1/2	1/2	2/3	2	1	3	?	1	1	2/3	1
S. hirsutus	2	2	1	3	1	2	2	1/2	3	1	1	1	2	1	1	1/2	2
S. latibractea	1/2	2	1	3/4	1	2	2	1	3	2	1/2	2	1	1	1	2/4	1
S. latistipulus	2	2	1	3/4	1	1/2	2	1	3	2	1/2	1	?	1/2	?	3	2
S. littoralis	2	2	1	3	1	2	2	1	3	2	1/2	2	2	1/2	1	2/3	1
S. macropterus	2	2	1	3	1	2	2	1/2	2	2	1	1	2	1	1	1/2	2
S. maingayi	2	2	1	3	1	2	2	1/2	2	2	1/2/3	2	1	1/2	1	3	2
S. merguensis	?	?	?	?	?	?	?	?	?	?	1	2	?	1	1	3/4	2
S. multiflorus	1/2	2	1	1/4	1	1	2	1	1	2	1	1	2	1	1	1/2/4	2
S. oblongifolius	1/2	2	1	3	1	2	2	1	1/3	1	1	2	2	1	1	2/3	1
S. parviflorus	1	1	3	3	3	1	2	2	1	2	1	1	3	1	2	2/3	2
S. persicinus	1/2	2	1	3	1	2	2	2	2	2	1/2	3	1	1	1	2/3	1
S. pottingeri	1/2	2	1	3	1/2	1	2	1	3	2	1	1	?	1	1	2/3/4	2
S. pulcher	1	1	1	2	1	1	2	2	?	2	1	1	?	1	2	?	3
S. purpureus	2	?	1	3	1/2	1	2	2	2	1	1	2	2	1	1	2/3	1
S. ridleyi	1/2	2	1	3	1	2	2	2	2	2	1	1	?	1	1	?	2
S. sanguineus	1/2	2	1	3	1	2	1/2	2	2	2	1	1	1	1	1	1/2	3
S. suberectus	?	?	1	3	1	1	2	2	3	2	1	1	2	1	1	2/3/4	2
S. viridis	1/2	2	1	4	1	2	2	1	3	2	1	3	2	1	1	2/3	1
B. monosperma	1	1	1	2	1/2	1	2	2	1	1	1/2	1	2	2	2	1/2	2
B. superba	1	1	1	?	1	1	2	1/2	1	1	1/2	1	?	2	2	1/2	2
M. buteiformis	1	1	1	2	1	1	2	2	1	2	1/2/3	1	3	2	2	2/3	3
M. pellita	?	?	?	?	?	?	?	?	?	?	2/3	1	3	2	2	2/3	3
Kunstleria	1	1/2	2	3	1/2	1	1	1/2	1	2	1	1	1	1	1	1/2	3

Table 2.2. Quantitative characters used for the phylogenetic analysis.

Characters: / Species:	stipule length by width [12]	angle of nerves [29]	pairs of nerves [31]	pedicel length in mm [39]	connate filaments [65]	anther size in mm [67]	A/E [97]		foot layer in µm	endexine in µm
S. acuminatus	6-7×1-1.5	(45-)50-60	6-9	2-5	>2/3	0.2-0.5	0.22 (0.26)	0.30	0.18-0.32	0.13-0.23
S. albus	2×1	35-50	3-11	1-1.5	2/3	ca.0.5	0.15 (0.27)	0.31	0.046-0.13	0.27-0.32
S. apoensis	7×3	40-55	7	2-3	1/2	0.5-1	0.23 (0.28)	0.38	0.2-0.4	0.2-0.4
S. auricomus	?×4	less than 40	5-7	1-2	1/2	0.3	0.23 (0.27)	0.41	?	?
S. aurinus	7×2-3	45	12-16	1-2	2/3	0.5	0.25 (0.33)	0.45	?	?
S. bracteolatus	?	35-40	8-10	?	?	?	?		?	?
S. crassifolius	5-8×2	50	7-10	3	1/2	0.3	0.16 (0.21)	0.29	?	?
S. dubius	8×2	32-38	4-7	1.5-2.5	2/3	0.3	0.22 (0.31)	0.36	?	?
S. ferrugineus	3-6×2-6	45-60	4-8	1-4	<1/2	0.2	0.17 (0.22)	0.26	?	?
S. gyrocarpus	?	40	7-11	1	1/2	0.2	0.4 (0.44)	0.49	0.6-0.13	0.3-0.4
S. harmandii	1.5-2×0.5-1.5	50	5-10	2-6	1/2	0.3	0.18 (0.2)	0.24	?	?
S. hirsutus	7-17×2-4	15-30(-40)	5-7(-11)	1-1.5	3/4	0.2-0.3	0.31 (0.37)	0.43	?	?
S. latibractea	13-18×5-8	50-65	9-11	1-2	1/2-2/3	0.3-0.75	0.13 (0.18)	0.23	0.18-0.27	0.5-0.69
S. latisiipulus	11-12×7-12	45-55	7-12	1-2(-4)	1/4-1/2	0.75	0.2 (0.3)	0.4	0.32-0.6	0.55-0.69
S. littoralis	4-8×1.5-4	20-45	5-8	1.5-3	<1/2	0.5	0.2 (0.24)	0.29	?	?
S. macropterus	7×1.5	35-40(-50)	4-8	1-1.5	>3/4	0.3	0.24 (0.36)	0.39	0.27	0.18-0.4
S. maingayi	3-5(-10)×2-3	35-45	5-8	1-2	1/3-1/2	0.5-0.75	0.27 (0.31)	0.36	0.06-0.13	0.33-0.46
S. merguensis	5-6×1-2	55	10	1	1/2	0.3	0.27 (0.38)	0.44	0.2-0.3	0.2-0.4
S. multiflorus	10-16×3-5	50	9-14	1-2	up to 1/2	0.2-0.3	0.3 (0.33)	0.37	?	?
S. oblongifolius	?	20-40	8-10	1	2/3	0.2	0.16 (0.21)	0.25	0.23-0.32	0.37-0.69
S. parviflorus	4-6×5-7	40	7-9	2-4	2/3	0.3	0.27 (0.3)	0.33	0.093	0.37-0.5
S. persicinus	7-12×3-5	50-60	7-16	1-2	1/2	0.5-0.75	0.24 (0.26)	0.3	0.055(-0.11)	0.55-0.8
S. pottingeri	8-14×2-5 or 4×6	40-45	7-12	1-3	1/2-2/3	0.2-0.5	0.25 (0.34)	0.41	0.2-0.4	0.26-0.4
S. pulcher	?	40-50	4-7	2	2/3	0.3	0.5 (0.58)	0.65	?	?
S. purpureus	?	60-80	6-11	2	3/4	0.3	0.12		?	?
S. ridleyi	?	40-45	7-9	1.5-2	up to 3/4	0.2	0.38		?	?
S. sanguineus	7-12×4-7	30-45	6-11	0.25-1.5	<1/2	0.2	0.43 (0.44)	0.47	0.093-0.13	0.27-0.37
S. suberectus	7-10×2-4	40-50	6-8	1-2	2/3	0.2-0.3	0.29 (0.33)	0.37	?	?
S. viridis	11-13×4-5	50-55	9-12	1-2	1/2-3/4	0.3-0.5	0.2 (0.25)	0.31	0.18-0.27	0.23-0.37
B. monosperma	5-7×1.5-4	35	5-9	1.5-4	>5/6	1-2	0.30 (0.36)	0.44	0.093-0.18	0.5-0.64
B. superba	5-7×1.5-6	30-45	6-8	2-4.5	nearly all	2.5-4.5	0.36 (0.43)	0.51	0.13-0.26	0.33-0.66
M. buteiformis	8-18×5-14	35-50	5-9	5-15	2/3	1.5	0.43 (0.5)	0.57	?	?
M. pellita	15-30×10-16	25-40	5-8	7-10	>2/3	1-1.5	0.53 (0.62)	0.67	0.06-0.13	0.26-0.53
Kunstleria	6×2.5-5	25-55	4-8(-12)	up to 1	1/2-3/4	0.3-0.5	0.35 (0.39)	0.45	0.03-0.24	0.1-0.7

Stem

Most species in this analysis are lianas, only *Butea monosperma* is a tree, and the two species of *Meizotropis* are shrubs. The stem characters are all taken from branches with a diameter of 1 cm or less.

In some species of *Spatholobus* the stem is hollow [1]. Small ants, of the genus *Cladomyrma*, may inhabit the stem as is often observed in *S. oblongifolius* (Moog & Maschwitz, 1994). The ants enter the stem by small holes. Hollow branches occur also in *S. auritus, S. bracteolatus, S. hirsutus*, and *S. pottingeri. Spatholobus ferrugineus* and *S. macropterus* show both states. Moog found ants as well in specimens of most probably *S. bracteolatus*. The other species of *Spatholobus* do not have hollow branches, or, if so, only in part.

Stems are often glabrescent, the indumentum [2] being usually present on the younger branches only. Most species in *Spatholobus* have either nearly glabrous stems, or a pubescent/puberulous or sericeous indumentum. In contrast to these *S. bracteolatus, S. pottingeri*, and *S. pulcher* are hirsute or strigose. The genera *Butea* and *Meizotropis* are usually densely pubescent, except *M. pellita*, which is covered by a dense pilose type of indumentum. *Kunstleria* is pubescent as well, except for one species, *K. forbesii*, which has a woolly indumentum on the branches. This character state is unique within *Kunstleria* and very rare in the tribe Millettieae. Therefore it is not included in the data set for the genus as a whole.

Lenticels [3] are small and rounded in most species of *Spatholobus* as well as in those of the genera *Butea* and *Meizotropis*. In *Kunstleria* and some species of *Spatholobus* (*S. acuminatus, S. albus, S. suberectus, S. viridis*) the lenticels are wart-like. Elongated lenticels (Fig. 2.1a) are found in *S. dubius, S. latibractea, S. littoralis*, and *S. pulcher*. The two last types of lenticels are more conspicuous than the first.

The exudate [4] is a specific feature and visible as a dark stained residue on the branches where they are cut off. Also on some of the field labels this feature is mentioned. The species of *Butea* and *Meizotropis* all have exudate. Although the branches of the species of *Kunstleria* also contain a dark substance, they do not show the dark stains of an exudate. The only species that is different in this character is *K. forbesii*, which most probably produces exudate. Within *Spatholobus* there are species with and without exudate. The only polymorphic species are *S. littoralis* and *S. pottingeri*.

The bark of the branches [5] may be either smooth or with ridges or wrinkles. Most species of *Spatholobus* have a smooth bark. The other species of *Spatholobus* and the other genera in this study usually have small ridges or wrinkles on the bark (Fig. 2.1b). Two species, *S. auritus* and *S. littoralis*, show a polymorphism here.
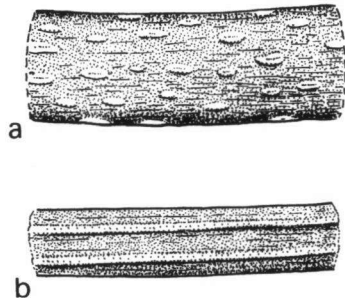
Figure 2.1. a. Part of the stem of *Spatholobus latibractea* showing lenticels. b. Part of the stem of *S. latistipulus* showing small ridges on the stem. — After a drawing by J. Wessendorp in Ridder-Numan (1992).
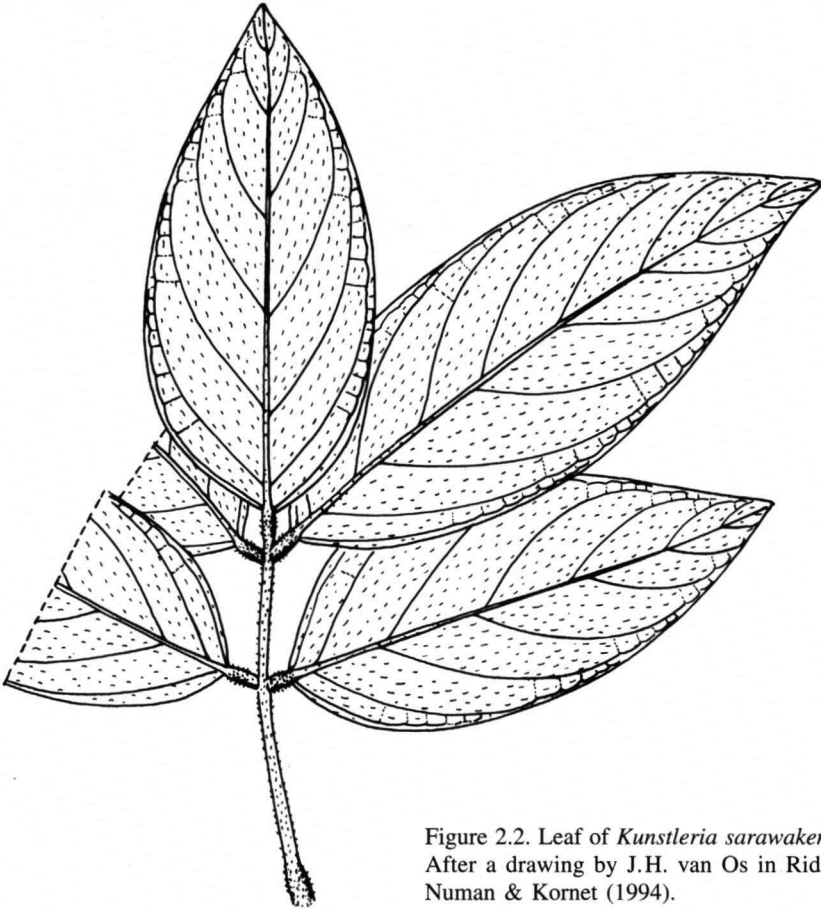
Figure 2.2. Leaf of *Kunstleria sarawakensis*. After a drawing by J.H. van Os in Ridder-Numan & Kornet (1994).

Leaves

The genera *Butea, Meizotropis*, and *Spatholobus* have trifoliolate leaves (Fig. 2.3, 2.4, 2.7, 2.8, 2.10). This is a common feature in the tribe Phaseoleae. The lateral leaflets in this tribe usually have an enlarged basiscopic side (Geesink, 1984). All leaves have stipules and stipellae, although these may be early caducous. The absence of stipules in the available material is responsible for the question marks in the data matrix for stipule characters [7–12]. The genus *Kunstleria* has species with uni- and trifoliolate leaves, but most of the species have more than five leaflets (Fig. 2.2). Here the leaflets are (almost) symmetrical. The leaves of *Kunstleria* have stipules, but are exstipellate.

The ultrajugal part of the rachis [6] is very short or absent in some species of *Spatholobus*. The absence of the last part of the rachis in combination with the narrowly obovate shape of the leaflets is very characteristic for *S. oblongifolius*(Fig. 2.4). Sometimes, perhaps due to the absence of the ultrajugal part, there are four or five leaflets per leaf in contrast to the usual three. Other species with short or nearly absent ultrajugal parts are *S. merguensis* and *S. multiflorus*. One species, *S. albus*, has an ultrajugal
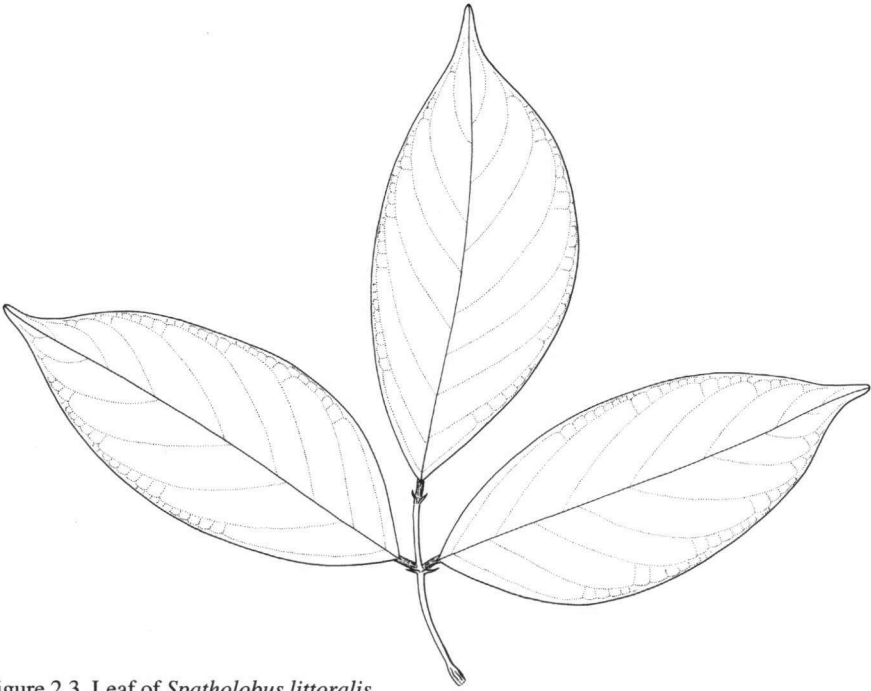
Figure 2.3. Leaf of *Spatholobus littoralis*.
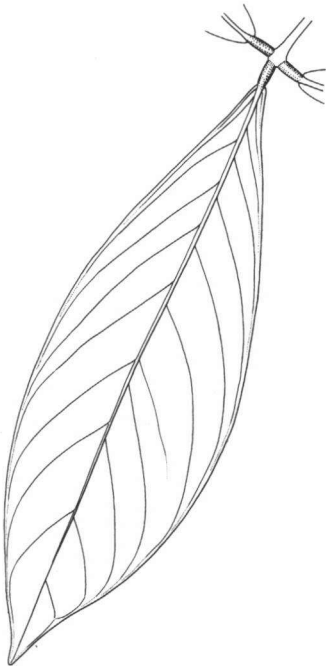
part varying from nearly 0 up to 1/3 of the total length of the rachis, and is thus coded polymorphic for this character.

In most species the stipules [7] are straight (Fig. 2.5a). In some, however, the stipules curl back (Fig. 2.5b). These stipules seem to be thicker than the stipules that are straight. Recurving stipules are present in the genus *Butea* and some of the species of *Spatholobus*: *S. albus*, *S. ferrugineus*, *S. parviflorus* and *S. sanguineus*. It was not possible to code this character for all species, because in some species all stipules were caducous.

Stipules [8] are easily caducous in most species, as already mentioned above; in others they are more persistent, e. g., in *Spatholobus auritus*, *S. hirsutus*, *S. latibractea*, *S. latistipulus*, and *S. multiflorus*.

Figure 2.4. Leaf of *Spatholobus oblongifolius*. Shown are the top leaflet and the rachis. Note the absence of the ultrajugal part of the rachis.
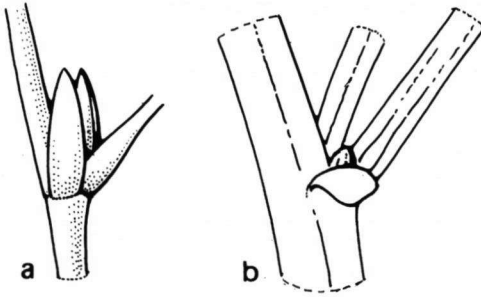
Figure 2.5. a. Straight stipules (*S. auritus*), b. curled stipules (*S. ferrugineus*).

Stipules [9] are either more or less symmetrical or not. Most species, as far as is known, have more or less symmetrical stipules. Only those of *Spatholobus latistipulus*, which are relatively wide, are asymmetric.

Sometimes the veins [10] of the stipules are prominent, in other cases the veins are not raised (and not visible). Two species have only 1–3 veins: *Spatholobus harmandii* and *S. maingayi*; others have many parallel veins.

Most species have an indumentum [11] on the stipules. Some species of the genus *Spatholobus*, however, are glabrous or glabrescent: *S. apoensis, S. hirsutus, S. latistipulus, S. littoralis, S. macropterus, S. maingayi* and *S. ridleyi*.

The length [12] of the stipules is usually two to three times the width. Some species have shorter stipules (about as long as they are wide): *Spatholobus albus, S. ferrugineus, S. latistipulus, S. parviflorus* and the two species of the genus *Meizotropis*. Others, *S. acuminatus, S. hirsutus* and *S. macropterus* have relatively long stipules that may be more than four times as long as they are wide. In Figure 2.6 the relative length of the stipules is given, calculated from the averages of the values of length and width of the stipules.

The colour [13] of the pulvinus of the leaflets can be darker than the rachis itself (Fig. 2.3). In most cases the colour is the same, but in some species of *Spatholobus* the pulvinus is nearly black in dried material. These species are: *S. apoensis, S. bracteolatus, S. hirsutus, S. latistipulus, S. macropterus, S. maingayi, S. oblongifolius* and *S. ridleyi*. The only species polymorphic for this character are *S. bracteolatus* and *S. pottingeri*. The material of the first species, however, is very scarce, and it may be possible that one of the sterile specimens studied is misidentified.

The pulvinus can be either glabrous (or sparsely hairy) or with an indumentum [14], which is either pubescent to hirsute or with longer hairs and more densely pubescent. The latter state is found in *Meizotropis pellita* and in several species of *Spatholobus*.

The stipellae of the leaflets are in most cases caducous [15], and are in most species only present in juvenile leaves. In other species they are more or less persistent and may even be present when the leaflets have dropped. The persistence of the stipules is not associated with this feature of the stipellae. In *Spatholobus latibractea, S. latistipulus* and *S. multiflorus* both stipules and stipellae are more or less persistent (Fig. 2.7), while in *S. auritus* and *S. hirsutus* the stipules stay longer on the leaves than the stipellae.
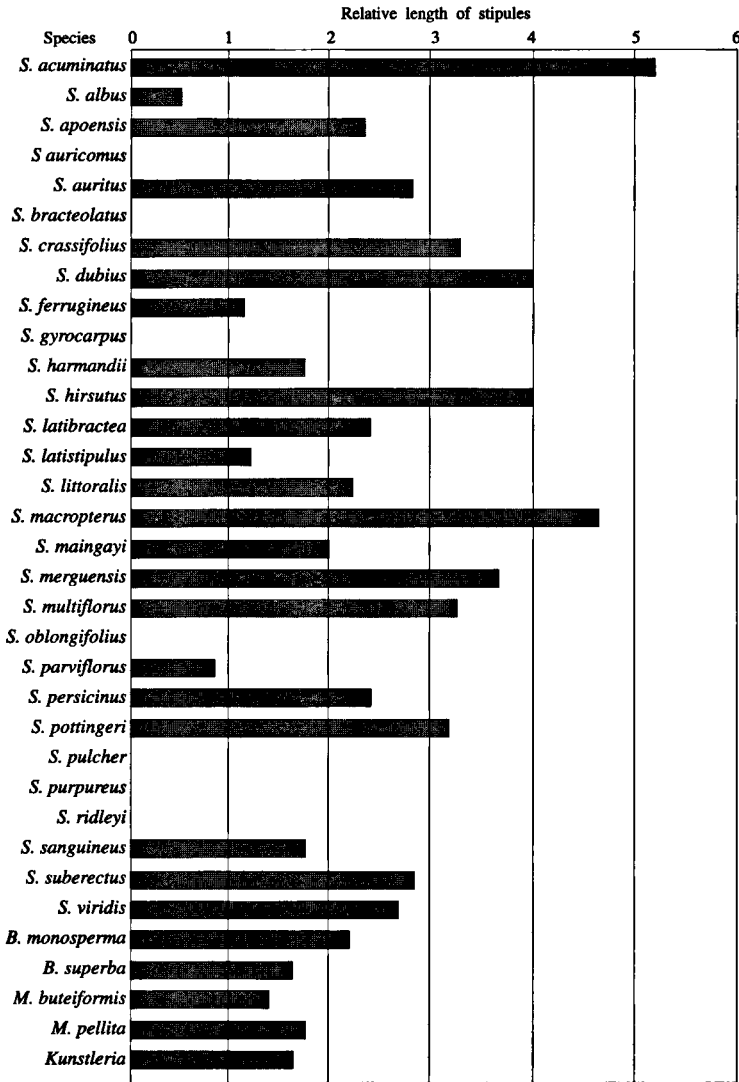
Figure 2.6. Relative length of the stipule.
Species of which the stipules were not seen are not represented by a bar.

Spatholobus dubius, S. harmandii, S . pottingeri and *S. ridleyi*, however, have persist-
ent stipellae, but early caducous stipules. In the genus *Kunstleria* no stipellae are present,
and a question mark is entered for the two characters concerning stipellae [15 & 16].

The second character of the stipellae that I used in the analysis is the length [16].
Stipellae are usually not longer than the petiolule (Fig. 2.3). In some species of *Spa-
tholobus*, however, the stipellae are conspicuously longer than the petiolule. It was not
always easy to score this character, because some of the more persistent and long sti-
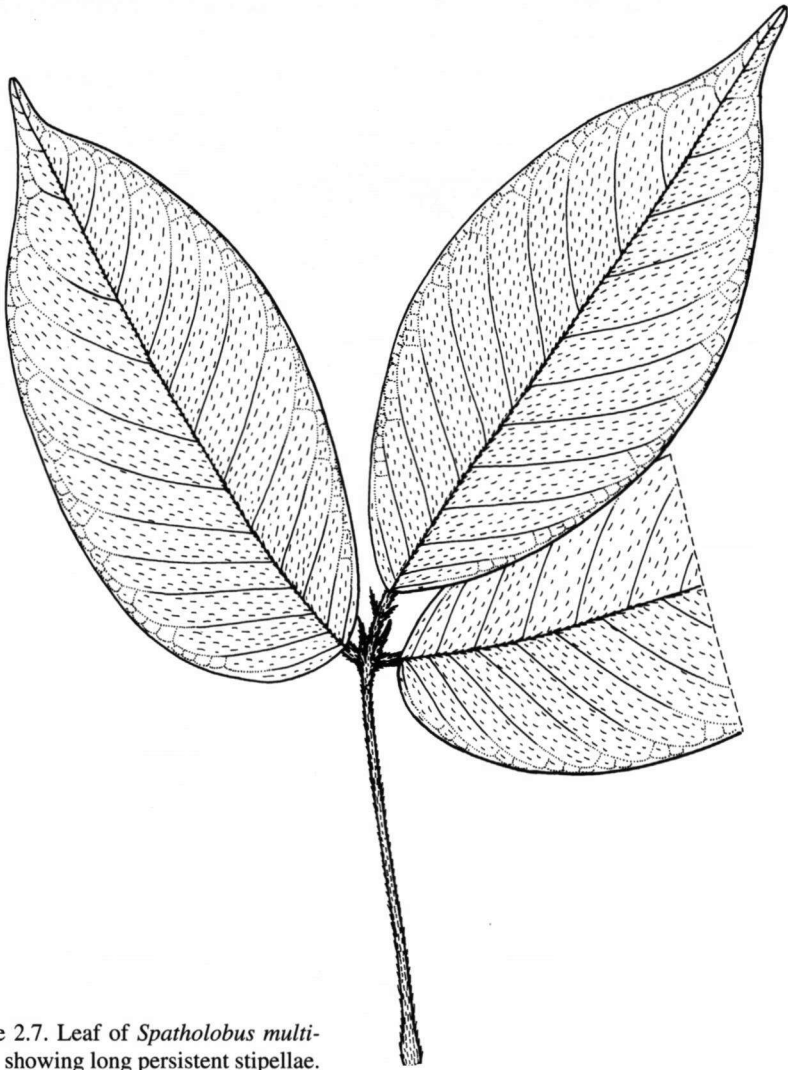
Figure 2.7. Leaf of *Spatholobus multi-florus* showing long persistent stipellae.

pellae had a tendency to break off at the tip. There are only two species with such long stipellae that are persistent, *S. multiflorus* (Fig. 2.7) and *S. pottingeri*. In all other cases the stipellae are caducous.

The upper surface [17] of the leaflets in some species of *Spatholobus* deviated from the usual green/brownish (dried) colour. In these species the upper surface is glaucous.

The lower surface [18] may be dull brown versus the usual green/brownish colour of dried material. The character is not in all cases associated with a glaucous upper surface.

All species of *Spatholobus* and *Kunstleria* have leaves with a glabrous upper surface [19]. In the genera *Butea* and *Meizotropis* the leaves are hairy above. *Meizotropis pellita* is the most densely hairy species, having a hirsute to strigose indumentum on the upper surface of the leaflets. When the leaves are very young they are covered with a thick layer of hairs on both sides. Also other species, e.g. *Spatholobus ferrugineus*, have an indumentum on the upper surface of the very young leaves, but this disappears as soon as the leaves expand. In microscopical sections of the leaf surface the bases of the hairs are often still visible.

The lower surface indumentum [20] is more variable, and although many species of *Spatholobus* are glabrous (glabrescent) on the lower leaf surface, about half of the species show one or more types of pubescence. Three species of *Spatholobus* are polymorphic for the indumentum on the lower surface. In two of these species infraspecific taxa have been recognised mainly on account of this character. In the revision of *Spatholobus* (Ridder-Numan & Wiriadinata, 1985) infraspecific taxa are only recognised in *S. ferrugineus*. Apart from the indumentum, the shape of the leaflets is also aberrant in these taxa. Baker (1867) also recognised a separate variety based on the glabrous leaflets in *S. parviflorus* (i.e., var. *denudatus*).

To represent the shape of the leaflets the terminal leaflet [21] is taken to avoid confusion between asymmetric and symmetric leaflets. Most species of *Spatholobus* and *Kunstleria* (except *K. forbesii*) have only elliptic leaflets (Fig. 2.2, 2.3), but some species have obovate (Fig. 2.4) or ovate (Fig. 2.7) leaflets as well. *Spatholobus ferrugineus* and *S. gyrocarpus* are polymorphic for this character: their leaflets can be elliptic, ovate, or obovate, but never are only elliptic. The state 'elliptic' was scored if only elliptic leaflets were present (i.e. obovate or ovate leaflets absent). When the outgroup *Kunstleria* is considered as possessing the plesiomorphic state, the state 'elliptic' is plesiomorphic. The coding for this character is in fact favouring the apomorphic situation in polymorphic species. I chose this way of coding to avoid too many polymorphic situations.

The apex of the terminal leaflet [22] is in most cases acute or acuminate to cuspidate (Fig. 2.3, 2.4). In *Butea* the leaflets are usually emarginate at the apex (Fig. 2.8). In some species of *Spatholobus* emarginate apices are present, usually in obovate leaflets; sometimes in combination with leaflets which have acute or abruptly acuminate apices. An apex that is abruptly acuminate (Fig. 2.7) is found in all types of leaf shapes.

The base of the leaflet [23] is usually acute to obtuse or more rounded (Fig. 2.3) to subcordate. In some species the base of the leaflet can be decurrent (Fig. 2.4 and 2.8) in the species of, e.g., *Butea* and *Meizotropis, Spatholobus oblongifolius* and sometimes in *S. ferrugineus*. The latter species has a rather variable leaf shape.

Symmetrical lateral leaflets [24] are present in the species of *Kunstleria* and in more than half of the species of *Spatholobus* (Fig. 2.2, 2.3). It is obvious that one of the characteristic features for the tribe Phaseoleae, strongly asymmetrical lateral leaflets, does not hold for *Spatholobus*. In the genera *Butea* and *Meizotropis*, and the rest of *Spatholobus* asymmetric leaflets occur as may be expected in Phaseoleae (Fig. 2.8, 2.10).
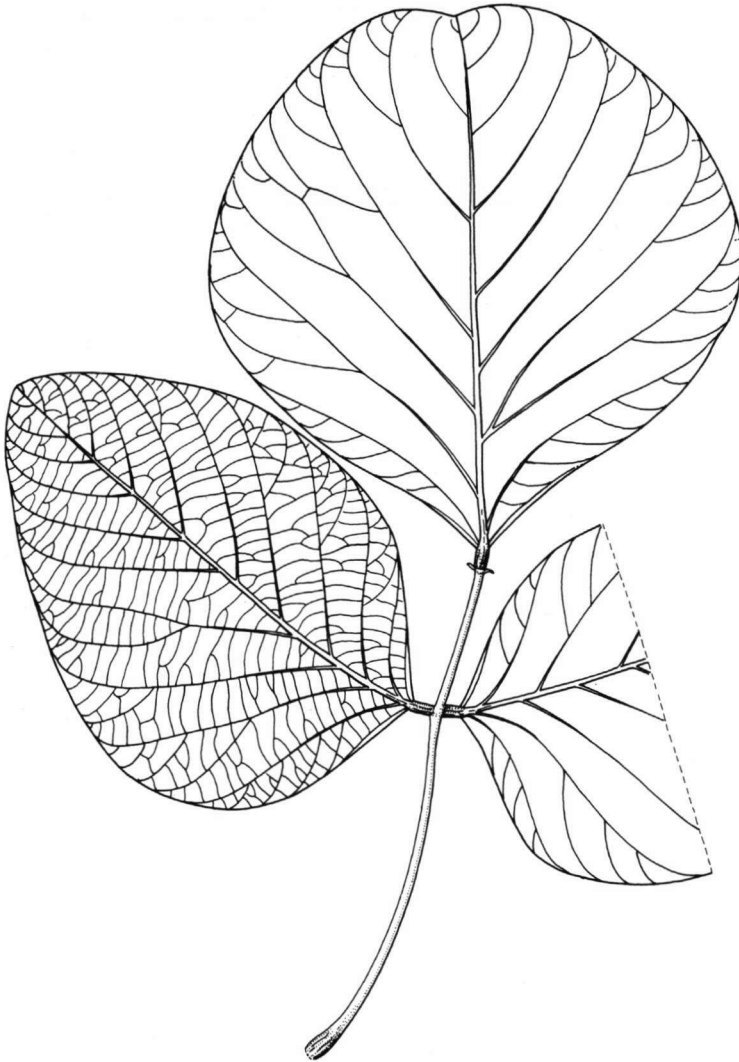
Figure 2.8. Leaf of *Butea monosperma*. Note the emarginate apex, the decurrent base, and the strongly asymmetric lateral leaflets.

The main nerve [25] can be either flat, raised, raised in a furrow, or sunken. Some species never have the main nerve sunken, others have the main nerve usually sunken, e.g. *Kunstleria*. This character was checked with leaf anatomical sections. The main nerve is never sunken in species with strongly asymmetrical leaves.

In contrast with the main nerve, the secondary nerves [26] are usually not raised on the upper surface. Only in some species with relatively large leaves, i.e. the species of *Butea, Meizotropis buteiformis, Spatholobus ferrugineus, S. parviflorus* and *S. pottingeri,*
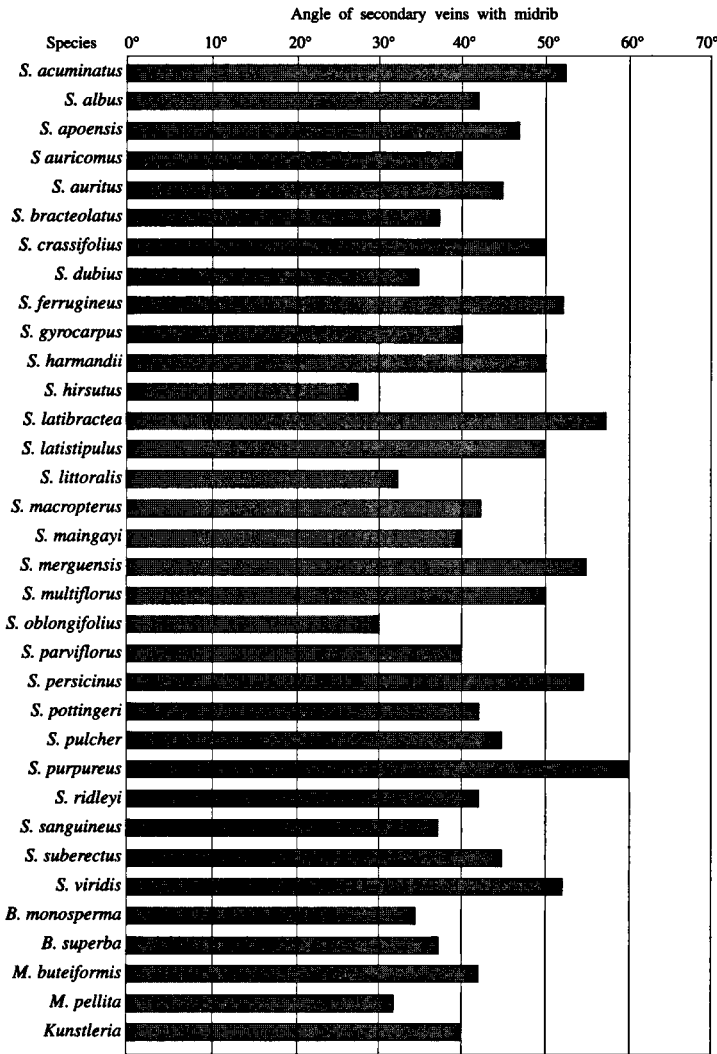
Figure 2.9. The average values of the angles between midrib and secondary veins.

both main and secondary nerves are raised. However, not in all species with large leaves both main and secondary nerves are raised at the upper surface.

On the lower surface [27] the veins may be prominent or not. In some species of *Spatholobus* (*S. acuminatus*, *S. albus*, *S. crassifolius*, *S. harmandii*, *S. merguensis*, *S. ridleyi*) only the midrib is prominent. In other species of *Spatholobus* and all species of *Kunstleria* both the main nerve and first order veins are prominent (Fig. 2.2, 2.3). The species with larger leaflets, *Butea*, *Meizotropis* and some species of *Spatholobus*, also have a prominent venation. *Spatholobus latibractea* may have leaflets with the venation prominent or not.
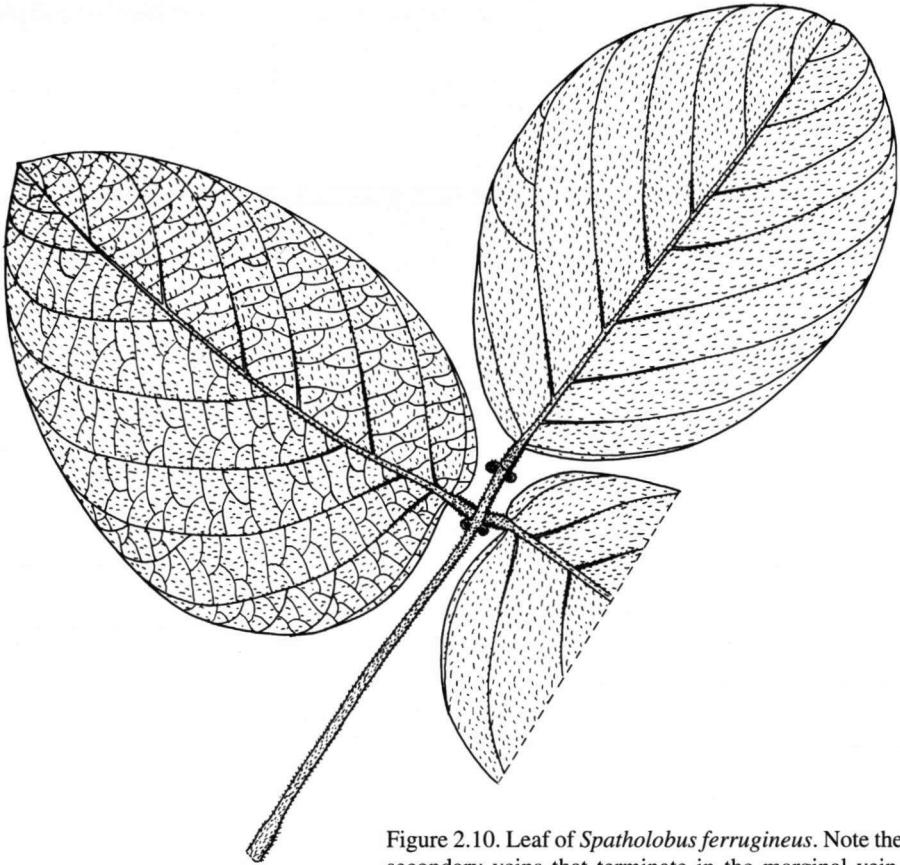
Figure 2.10. Leaf of *Spatholobus ferrugineus*. Note the secondary veins that terminate in the marginal vein.

The venation [28] is usually reticulate (Fig. 2.10) or reticulate-scalariform. In *Spatholobus latibractea*, *S. viridis* and *Kunstleria* the venation can have both states. A scalariform venation is present in the genera *Butea* (Fig. 2.8) and *Meizotropis*, and in *S. suberectus*.

The secondary veins are curved towards the top. The angle of the secondary nerves [29] with the midrib is taken at the place of the secondary vein in the middle of the lamina. In this way there is no difference between the course of a geniculate and a curved type of secondary veins. Most species have a low or moderately angled course. Some *Spatholobus* species, however, have high angles (more than 50°), others have low angles with the midrib (less than 40°). The other species have values in between, but the average of these values can be divided into two groups: one more than 45°, the other less than 45° (Fig. 2.9).

Secondary nerves [30] in most species of *Spatholobus* and *Kunstleria* terminate diffusely towards the margin, and do not form marginal arches (Fig. 2.3, 2.4). In *S. ferrugineus* and in the species of *Butea* and *Meizotropis* the nerves terminate in the margin (Fig. 2.8, 2.10). In *S. auritus*, *S. latibractea*, *S. multiflorus*, *S. persicinus*, and
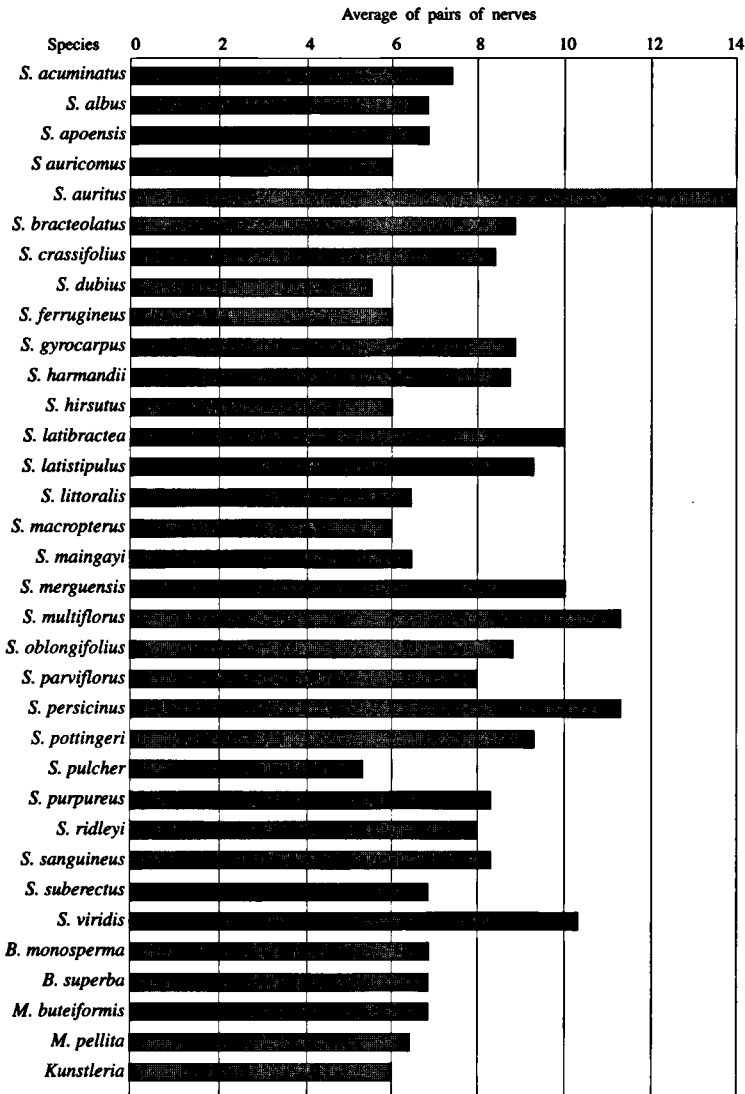
Figure 2.11. Average of the number of pairs of secondary nerves.

S. viridis the secondary veins do not end in the margin but in the vein above and form marginal arches (Fig. 2.7).

The number of pairs of secondary nerves [31] in most species of *Spatholobus* and in all species of the other genera studied is five to eight. Some species have more than eight pairs of secondary veins, and *S. auritus* and *S. multiflorus* always have more than 10 pairs of veins. The average of the number of pairs of nerves was taken to code this character (Fig. 2.11).
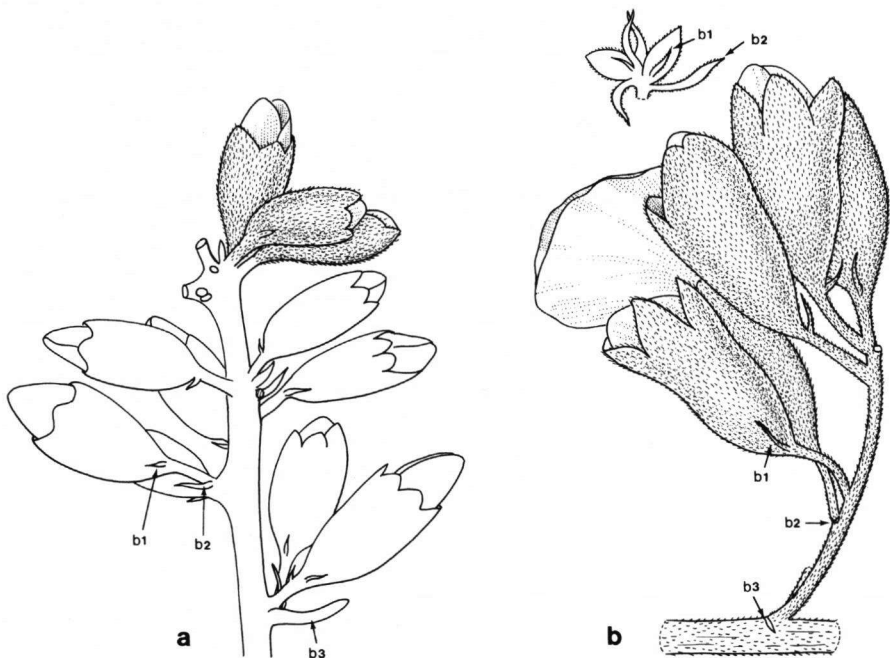
Figure 2.12. a. Part of the inflorescence of *Spatholobus suberectus* showing brachyblasts. b. Part of the inflorescence of *S. pottingeri*; b1 = bracteole, b2 = bract of the flower, b3 = bract of the side branch. Not all bracts are visible. After Ridder-Numan & Wiriadinata (1985).

Inflorescence

The inflorescence is variable among the species. Mostly there is a main axis with secondary branches bearing the (single) flowers directly or on an extra order of side branches (tertiary branches). Each flower is subtended by two bracteoles on the pedicel and a bract. Instead of bearing a single flower it is also possible that the side branch is reduced to a brachyblast (Fig. 2.12a). These brachyblasts are in some cases stalked. The tertiary branches again can bear either solitary flowers or (shortened) branches with more than one flower (Fig. 2.12b). Side branches are usually subtended by one bract. In some species, however, two bracts instead of one are present at the base of the flowering axis. To define a character state I only considered the middle part of the inflorescence. The lowest side branches can act as if they were a main axis themselves, and also the dormant bud of the second bract can have developed. Towards the top of the inflorescence reductions are usually present. The inflorescence types are schematically represented in Figure 2.13.

In some groups of the Leguminosae the position of the inflorescence [32] is an important diagnostic feature. At first glance this seems also the case in *Spatholobus*. However, in all groups studied both axillary and terminal inflorescences were observed. In the shrubs of *Meizotropis* inflorescences are strictly terminal.
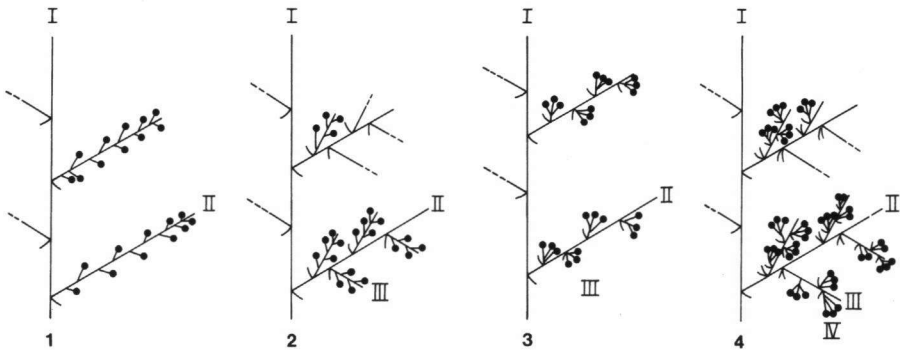
Figure 2.13. Schematic representation of the types of inflorescence. Roman numbers indicate the side branch order. The first diagrams (1, 2) with the flowers solitary on the side branches, the other (3, 4) with the flowers in brachyblasts (modified after Ridder-Numan & Wiriadinata, 1985).

In most species the indumentum of the branches of the inflorescence [33] is puberulous or pubescent. Some species have an indumentum with longer hairs, others (*S. maingayi* and in part *S. macropterus*) have more or less glabrous branches.

Species may have more than one order of side branches of the inflorescence (Fig. 2.13). The number of orders of side branches is indicated in feature [34]. The brachyblast, which can be considered a shortened side branch, represents an extra level of side branches, and is coded as 'side branch' (and not as 'flower'). This character does not indicate the presence of brachyblasts; this latter feature is coded in character 35. *Butea* and *Meizotropis* have one order of side branches. In *Butea* the side branches are shortened, but not always as short as a brachyblast. In *Meizotropis* the flowers are arranged in brachyblasts. In the species of *Spatholobus* with only one order of side branches the flowers are placed singly on branches which are never shortened (*S. acuminatus*, *S. albus*, *S. bracteolatus*, *S. harmandii*, *S. ridleyi*, and sometimes *S. multiflorus*). In *Kunstleria* there are secondary and tertiary side branches. The tertiary branches bear solitary flowers. This is also found in *S. crassifolius*, *S. merguensis*, *S. oblongifolius*, *S. pottingeri*, *S. pulcher*, and *S. sanguineus* (Fig. 2.12b). The other species of *Spatholobus* have secondary branches bearing brachyblasts (or nearly so) (Fig. 2.12a). Of these *S. littoralis* has the brachyblasts stalked. Tertiary branching with brachyblasts is found in *S. ferrugineus* and *S.parviflorus*. Inflorescences in *S. ferrugineus* can have the brachyblasts either placed on secondary or on tertiary branches.

The presence of brachyblasts [35] is a diagnostic character. One of the reasons to resurrect the species *S. sanguineus* from synonymy in *S. gyrocarpus* was the presence of brachyblasts in the former and their absence in the latter. Brachyblasts can be considered as reduced side branches. The outgroup *Kunstleria* never has the flowers placed in brachyblasts. This is in agreement with the view of Geesink (1984), who indicated a true panicle (without brachyblasts) as the less derived condition. In one species the brachyblasts are clearly stalked (*S. littoralis*), in others the brachyblasts are sessile or shortly stalked. For the analysis only the absence or presence of the brachyblasts has been coded.

The number of bracts under the first order side (= secondary) branch [36] can be either one or two. The presence of two bracts may be an indication of the reduction of a side branching (Ridder-Numan & Wiriadinata, 1985) or may be interpreted as the two stipules of a reduced leaf. This second bract is sometimes holding a dormant bud, and it is possible that a second side branch may sprout from this bud. Usually an inflorescence axis develops from the axil of one leaf or bract. In several specimens I noticed that the main axis had the side branches developing from small leaves instead of bracts. In these cases I considered the main axis in these parts to be purely vegetative, considering the side branches as axillary inflorescences, and the rest of the inflorescence as a terminal inflorescence.

The shape of the bracts of the side branches [37] is in most species either linear or triangular. Only in a few species the bracts are broadly ovate (*S. auricomus* and *S. latibractea* in part) or elliptic (*S. hirsutus*). In the latter the bracts are even surrounding the buds, whereas in other species the bud scales are the only surrounding features.

The number of bracts supporting the tertiary branch [38] is in most cases one. In case there is no tertiary branch the number of bracts to the flower is considered. Only in *S. crassifolius*, *S. parviflorus*, *S. pottingeri* and *S. pulcher* two bracts are present.

Flower

The differences in size and shape of the flower are large between the genera, and are possibly correlated with differences in pollination. The flowers of both *Spatholobus* and *Kunstleria* are small and not brightly coloured; they have a dark red or purple to whitish colour. The pollination mechanism is not known. The flowers of *Butea*, however, are large and orange-red or yellow. It is quite possible that these large flowers are pollinated by birds. The flowers of the genus *Meizotropis* are intermediate in size relative to the other genera. The colour is red, but nothing is known of the pollinator. It is possible, however, that birds or hawkmoths are involved (see references in Ridder-Numan, 1995; in press).

Most species have a pedicel longer than 1 mm [39]. In some species, however, the flowers are nearly sessile. This is the case in most species of *Kunstleria*, in *Spatholobus gyrocarpus*, and in most specimens of *S. sanguineus*.

The bracteoles [40] are mostly placed immediately below the calyx, but sometimes they have a position lower on the pedicel. Their position is usually on the upper half of the pedicel, but in *S. acuminatus* and *S. latibractea* the bracteoles are inserted on the lower half of the pedicel. In *Kunstleria*, and usually in *Butea* and *Meizotropis* as well, the bracteoles are placed immediately below the calyx.

The indumentum of the calyx [41] is in nearly all species pubescent or sericeous (rather short-hairy, sometimes more adpressed). A few species of *Spatholobus* have a nearly glabrous calyx. A hirsute indumentum (longer hairs) is found in the species *S. pulcher* and *Meizotropis pellita*, which are more hairy over the whole plant than the other species.

The tip of the vexillary lobe [42], which comprises the two fused dorsal lobes of the five-lobed calyx, may be bidentate (Fig. 2.16e) or entire. In the latter case the tip can be rounded (or more acute) or reduced to truncate. Species with a truncate vexillary
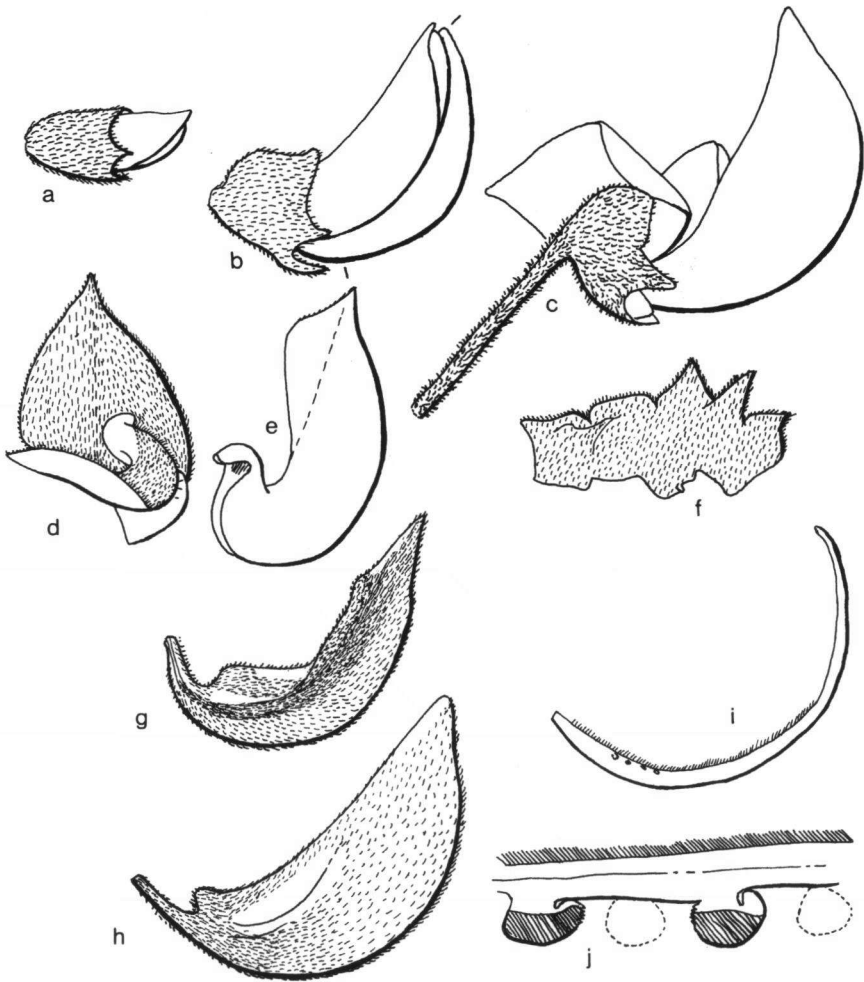
Figure 2.14. *Butea monosperma*. a–c. Flower in different stages of development; d–e. standard; f. calyx; g. wing; h. keel; i. pistil; j. ovules on one side of the ovary.

lobe are *S. apoensis*, *S. latistipulus*, *S. persicinus*, *S. ridleyi*, and sometimes *B. superba*. Some species are polymorphic, showing both bidentate or entire vexillary lobes.

The length of the vexillary lobe of the calyx [43] is another floral character varying between the species. In most species the vexillary lobe is about half the length of the calyx tube. In a number of species the vexillary lobe is much shorter (*S. albus*, *S. apoensis*, *S. auritus*, *S. hirsutus*, *S. latistipulus*, *S. littoralis*, *S. maingayi*, *S. persicinus*, and *Meizotropis buteiformis*). However, other species of *Spatholobus*, i.e. *S. acuminatus*, *S. bracteolatus*, *S. crassifolius*, *S. merguensis*, *S. multiflorus*, *S. parviflorus*, *S. purpureus* and often *S. pulcher*, have a conspicuously longer vexillary lobe. *Spatholobus pulcher* and *Butea superba* are polymorphic for this character.

The shape of the calyx lobes [44] other than the vexillary one varies between triangular and more or less rhomboid, both with acute apices, to a more or less triangular calyx lobe with a rounded apex. The short calyx lobes are often truncate or rounded.

The surface of the standard of both *Butea* and *Meizotropis* is nearly completely covered with an indumentum. Indumentum on the standard [45] is not found in *Kunstleria* or *Spatholobus*. Only one species of the outgroup, *K. kingii*, has a few hairs on the standard. I considered this last feature to be an autapomorphy for this specific species, and therefore it has been coded as absent for the genus itself.

The apex of the standard [46] is emarginate (Fig. 2.16f) in all species of *Spatholobus*, except *S. parviflorus*. The other genera have standards with an acute apex (Fig. 2.14, 2.15).

Usually the standard has no auricles or other appendages. In *Meizotropis* the standard has auricles at the lower margin of the blade, which are sometimes inflexed (Fig. 2.15d). Occasionally, the standard has auricles [47] in *S. parviflorus* and *S. ridleyi*.
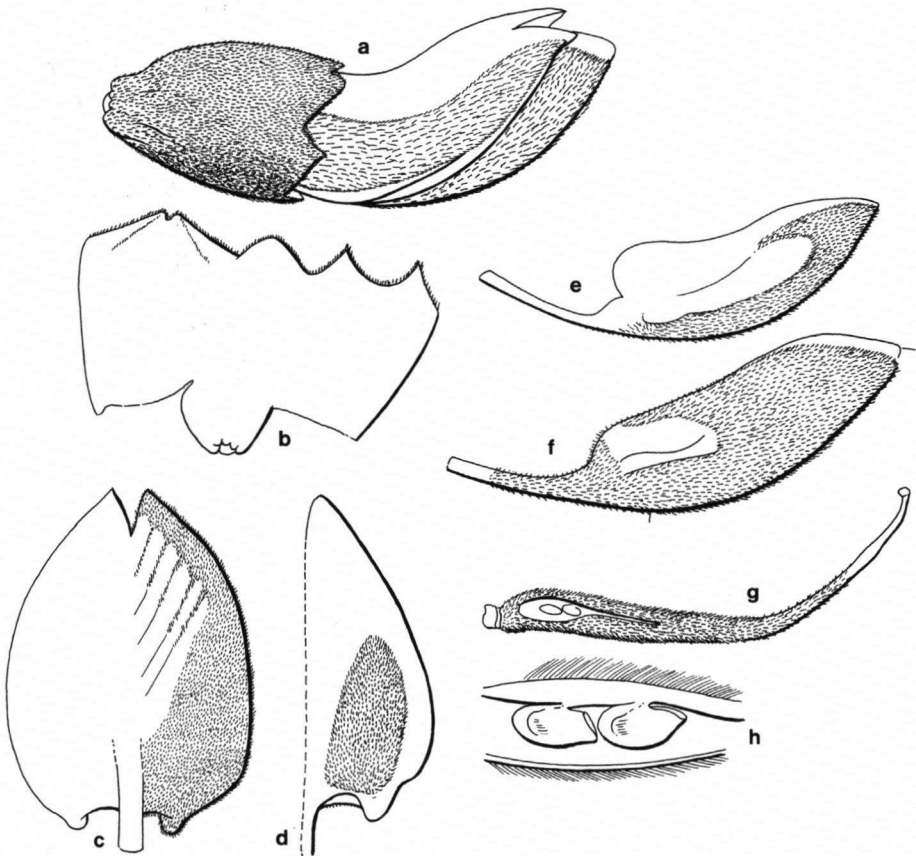

Figure 2.15. *Meizotropis buteiformis*. a. Flower; b. calyx; c. outside of the standard; d. inside of the standard; note the inflexed auricles; e. wing, f. keel; g. pistil; h. ovules in the ovary.
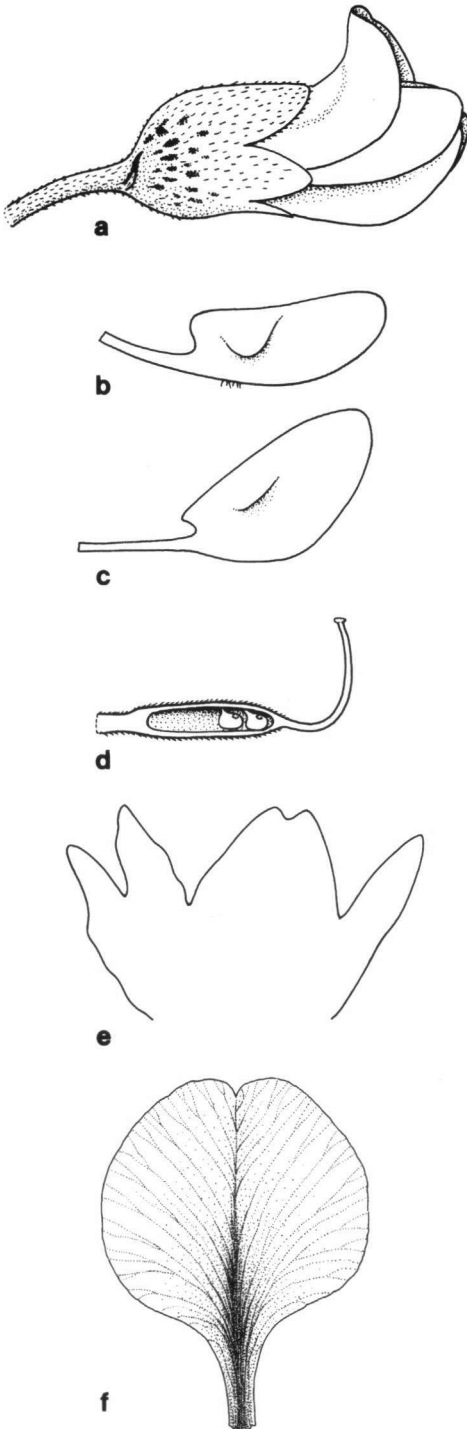
The base of the blade of the standard [48] may taper in two different ways to the claw: decurrent or truncate. In *Kunstleria* and *Meizotropis* the base is never decurrent into the claw (Fig. 2.15, 2.17), but in *Butea* and half of the species of *Spatholobus* a decurrent base is normal (Fig. 2.14d & e, 2.16f). Young petals, however, do not have a full-grown claw and are still truncate.

The shape of the blades of wing and keel petals depends on the presence of auricles on ventral and dorsal margins near the claw of the petals. The auricles of the species of *Spatholobus* are usually rather small (Fig. 2.16, 2.18), in *Kunstleria* they may be very conspicuous (Fig. 2.17c).

The dorsal auricle on the wing [49] is always present in *Butea*, *Meizotropis* and *Kunstleria*. In some species of *Kunstleria* the dorsal auricle on the wing petal may even be curled towards the claw (Fig. 2.17c). Not all species of *Spatholobus*, however, have a dorsal auricle. In *Kunstleria* and many species of *Spatholobus* the keel also has a dorsal auricle [56]. *Butea* and *Meizotropis* (Fig. 2.15) do not have a dorsal auricle on the keel petals, except for a minute one in *B. monosperma*.

A ventral auricle on the wing [50], however, is much rarer in this group. There is no ventral auricle in *Butea*,

Figure 2.16. *Spatholobus purpureus*. a. Flower; b. wing; c. keel; d. pistil showing the apical position of the ovules; e. calyx with bidentate vexillary lobe. — *S. latistipulus*. f. Standard with an emarginate apex and decurrent base.
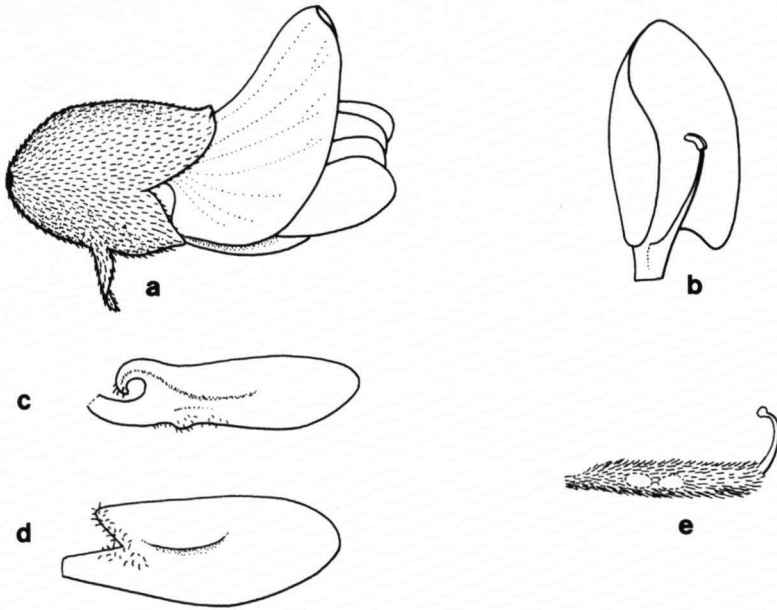
Figure 2.17. *Kunstleria sarawakensis*. a. Flower; b. standard with connate vexillary filament; c. wing with long, curled dorsal auricle; d. keel; e. pistil.
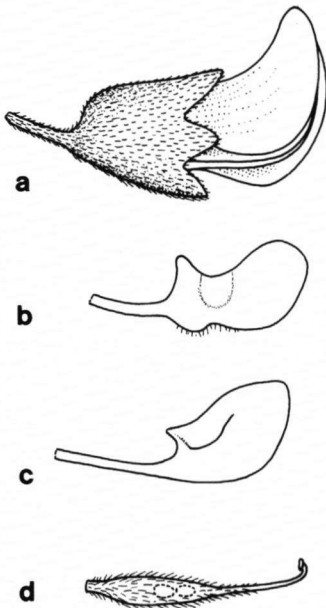
Figure 2.18. *Spatholobus ferrugineus*. a. Flower; b. wing; c. keel; d. pistil.

Meizotropis and *Kunstleria*, and it is present only in a few species of *Spatholobus*. These species, *S. albus*, *S. ferrugineus* (Fig. 2.18c), *S. multiflorus*, *S. pulcher*, and *S. viridis*, have both dorsal and ventral auricles on the wing blade. Only the last species, *S. viridis*, is sometimes without a dorsal auricle. On the keel ventral auricles are absent [57].

Lateral pockets [51] which connect the wing with the keel petals are not always present in all species of *Spatholobus*. The lateral pockets on the wing (Fig. 2.16), and on the keel [58] are always present in the other genera.

The indumentum on the petals is characteristic for several taxa. There is no indumentum on the inside of the wing petal [53] and of the keel petal [60] in *Kunstleria* and *Spatholobus*. The species of *Kunstleria* (Fig. 2.17c) usually have some pubescence on the outside of the blade of the wing petals [52].

In *Spatholobus* only a few species, i.e. *S. hirsutus*, *S. latibractea* , and *S. macropterus*, have some indumentum on the outside of the wings. In most species of *Kunstleria* the outside of the keel petal [59] has some indumentum, although this is usually restricted to the part of the blade below the auricle. In *S. latibractea* the outside of the keel petal sometimes has an indumentum. *Butea* and *Meizotropis* are rather hairy on both the inside and outside of the petals (Fig. 2.14, 2.15). *Meizotropis pellita* is glabrous on the inside of the blade of the keel and wing petals, and the inside of the keel is glabrous in *Butea monosperma*.

Cilia are present on the dorsal auricle or margin of the wing [54] and the keel [61] and on the ventral auricle or margin of the wing [55] and keel [62] in both *Kunstleria* and *Butea*, although they are much less dense in *Kunstleria* than in *Butea* (Fig. 2.14, 2.17). The two species of *Meizotropis*, however, are glabrous on the dorsal margins of both keel and wing petals (Fig. 2.15). In *Spatholobus*, only *S. latibractea*, *S. macropterus* and *S. pottingeri* have a few cilia on the dorsal and ventral margin of the wing petals. Occassionally, there are a few cilia on the ventral auricle of the wing petals in *S. ferrugineus* (Fig. 2.18b). The keel petals are glabrous in all species of *Spatholobus* except *S. latibractea*, which has a few cilia on the dorsal auricle of the keel.

The keel petals are always connate [63] to a greater or lesser extent along the lower margin to the top. In addition to being connate, the apical part of the keel petals of *Kunstleria* may slightly overlap as well. They are never free from each other.

The vexillary filament [64] is free from the other filaments, which are connate. In *Kunstleria*, however, the vexillary filament is connate at the base with the claw of the standard (Fig. 2.17b). This may be considered an autapomorphy for the outgroup; it does not occur in other genera in the Millettieae.

The surface along which the filaments are connate [65] is in most species of *Spatholobus* and *Kunstleria*, and in the genus *Meizotropis* more than half to 3/4 of the total length of the filaments. Filaments which are connate along more than 3/4 of the total filament length are present in *Butea* and in *S. hirsutus*, *S. macropterus*, *S. purpureus* and *S. ridleyi*. The other species of *Spatholobus* have their filaments connate over a much shorter length, less than half of the total filament length.

Usually there is no indumentum on the filament sheath [66], except in *Butea* and *Meizotropis*. In *Spatholobus* only one species, *S. acuminatus*, sometimes has a few hairs on the filaments.

The size of the anthers [67] is a diagnostic feature in *Butea* and *Spatholobus*. The anthers of *Meizotropis* and *B. superba* are between 1 and 2 mm long, while those of *B. monosperma* are longer than 2 mm. The anthers in the much smaller flowers of the genera *Kunstleria* and *Spatholobus*, however, are less than one millimetre in length (in most species the anther size is even less than half a millimetre). The size of the anthers was taken from mature anthers that were still carrying pollen, and in the case of alternately larger and smaller anthers the size of the larger anthers was used.

The filaments of the stamens are alternately longer and shorter. The anthers [68] are all equal in species of *Butea* and *Meizotropis* and in most species of *Spatholobus*. In *Kunstleria* the shorter filaments bear smaller anthers than the longer ones. These smaller anthers carry normal pollen grains. In some cases these pollen grains did not look
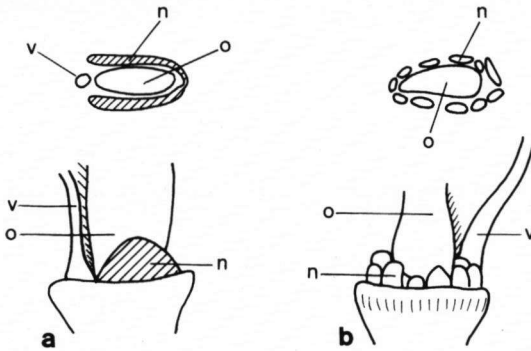
Figure 2.19. a. Ring-shaped nectary of *Spatholobus suberectus*; b. nectary consisting of 10 separate lobes (*S. ferrugineus*). n = nectary; o = ovary; v = vexillary filament.

maturewhen examined by scanning electron microscopy, but I did not test them to see whether they contained live material (Ridder-Numan, in press). Some species of *Spatholobus* – *S. auricomus*, *S. bracteolatus*, *S. ferrugineus*, *S. pottingeri* – also have smaller anthers, but here they are much smaller and did not contain pollen grains. This state is called sterile.

Nectary glands [69] are usually not very conspicuous. In most cases in *Spatholobus* there were ten small lobes inside the filament sheath, one at the base of each filament (Fig. 2.19b). In *S. suberectus* the nectariferous tissue is connate in a ring-like structure, and does not consist of separate lobes (Fig. 2.19a). *Spatholobus pulcher* and *S. purpureus* only have five lobes, which are situated at the base of the larger filaments. The other genera as well as some species of *Spatholobus* have no lobe-like structures, but the bases of the filaments are thickened.

The nectariferous tissue of the disk may have a short, sparse indumentum [70]. Most species, however, are glabrous.

The indumentum on the ovary [71] is pubescent or sericeous in most species, or, when denser, the appearance is more woolly. *Spatholobus latibractea* can have both a pubescent and a very densely pubescent ovary. In *S. auricomus*, *S. gyrocarpus*, *S. sanguineus* and *S. suberectus* the indumentum is sparse.

The indumentum on the ovary is continued on the style [72]. In *Butea* and some species of *Kunstleria* and *Spatholobus*, the indumentum does not reach further than the base of the style, with the rest of the style remaining glabrous. The species of *Meizotropis* and some other species of *Spatholobus* have an indumentum reaching up to at least 3/4 of the total length of the style. In the other species of *Spatholobus* and *Kunstleria* the indumentum extends halfway up the style.

The number of ovules [73] is usually two in *Kunstleria*, *Meizotropis*, and *Spatholobus*. The ovary in *S. pulcher*, however, may contain two to four ovules. In *Butea* there are usually more than four ovules.

The ovules are placed in the middle of the ovary or are more basal [74]. In *Butea* and *Meizotropis* they are found centrally in the ovary, while in *Kunstleria* the ovules are situated in the basal part of the ovary (Fig. 2.17e). In *Spatholobus* ovules may also be placed – apart from a median or basal situation – apically in the ovary (Fig. 2.18d). The ovary usually has a small stipe [75] in *Butea*, *Kunstleria* and about half the species of *Spatholobus* (Fig. 2.16, 2.17). In *Meizotropis* the ovary lacks a stipe.
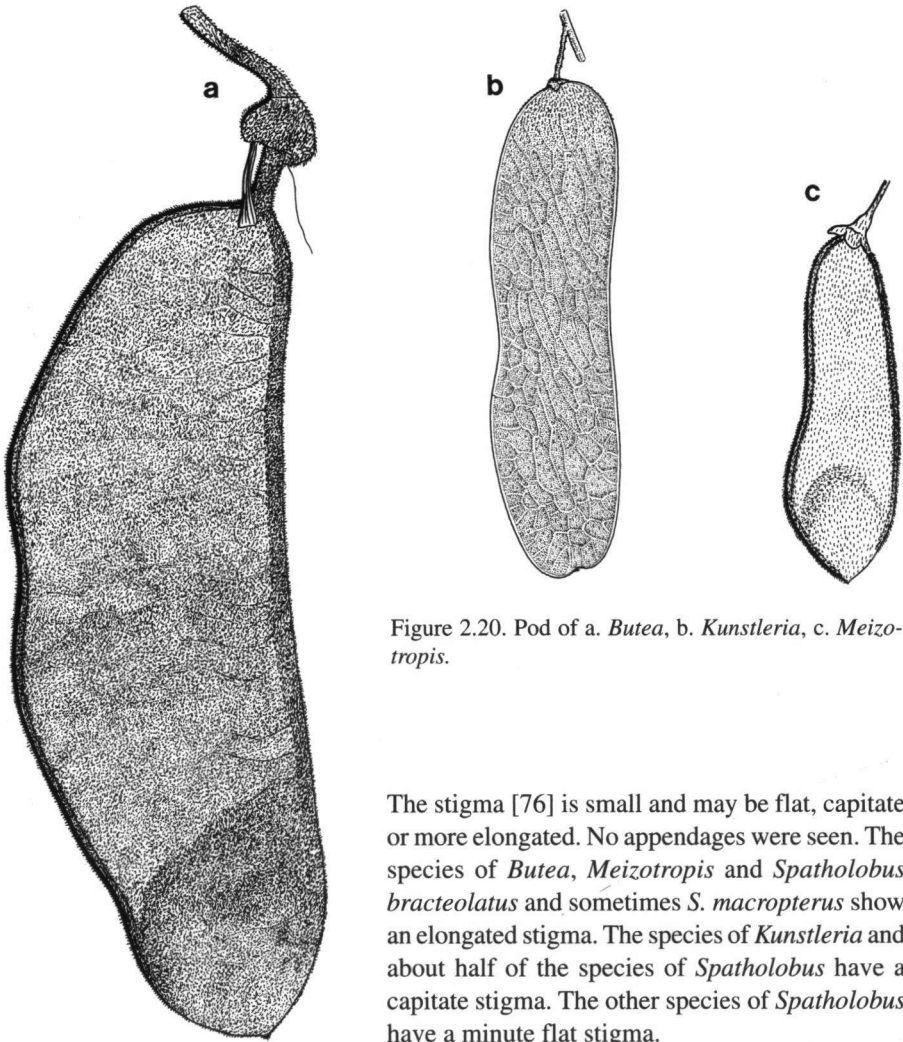
Figure 2.20. Pod of a. *Butea*, b. *Kunstleria*, c. *Meizotropis*.

The stigma [76] is small and may be flat, capitate or more elongated. No appendages were seen. The species of *Butea*, *Meizotropis* and *Spatholobus bracteolatus* and sometimes *S. macropterus* show an elongated stigma. The species of *Kunstleria* and about half of the species of *Spatholobus* have a capitate stigma. The other species of *Spatholobus* have a minute flat stigma.

Pod

The non-dehiscent pod of *Butea*, *Meizotropis*, and *Spatholobus* is samaroid with one apical seed (Fig. 2.20a & c; 2.21). The wing is the expanded part of the base of the ovary and may be as wide as or wider than the seed-bearing top. The wing is rather thin and the sutures on both sides are clearly visible. Only one of the ovules develops into a seed, which is connected to the dorsal suture. The style remnant is visible at the tip, sometimes pointing downwards due to the upper suture being slightly curved at the top. The pod of *Kunstleria* is strap-like and bears two very flat seeds in the middle (Fig. 2.20b).

The pod can have a stipe [77] which extends beyond the calyx. In some species there is a correlation between the presence of an ovary stipe with that of the stipe of the
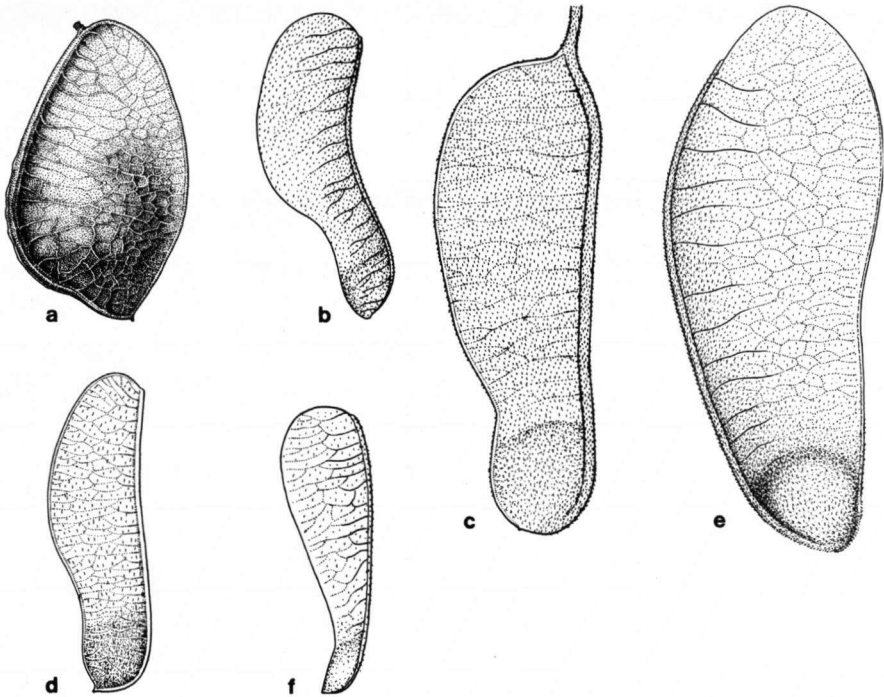
Figure 2.21. Pods of *Spatholobus*: a. *S. latistipulus*; b. *S. albus*; c. *S. parviflorus*; d. *S. oblongifolius*; e. *S. hirsutus*; f. *S. ferrugineus*. After Ridder-Numan & Wiriadinata (1985; b–f) and Ridder-Numan (1992; a).

pod, but in others there is no such correlation. The stipe of the pod does not always elongate very much when the pod expands and thus does not always exceed the calyx. The calyx is more or less persistent, and even other floral remnants may be found at the base of the pod. However, in *Butea* (Fig. 2.20a) and some species of *Spatholobus*, *S. dubius*, *S. harmandii*, *S. parviflorus* and *S. suberectus*, a conspicuous stipe is present (Fig. 2.21c). The other species of *Spatholobus*, and the genera *Kunstleria* and *Meizotropis*, have more or less sessile pods (Fig. 2.20b & c; 2.21a, b, d–f). *Spatholobus hirsutus* and *S. macropterus* show both features.

The apex of the pod [78] indicates the way the style remnant is connected to the seed-bearing top. The style can be pointing downwards or forward, or sometimes is pointing upwards. In the latter case the dorsal suture is curved downwards more than normally.

The shape of the wing [79] is one of the features of the pod. In *Spatholobus maingayi* the pod may be extremely curved with a narrow wing or straight with a wider curved wing. Usually the wing is wider than the tip and the dorsal suture is straight. Sometimes the wing is not wider than the seed-bearing top with the pod: *S. acuminatus*, *S. latistipulus* (Fig. 2.21a), *S. littoralis*, *S. maingayi*, *S. oblongifolius* (Fig. 2.21d) and *Kunstleria* (Fig. 2.20b).
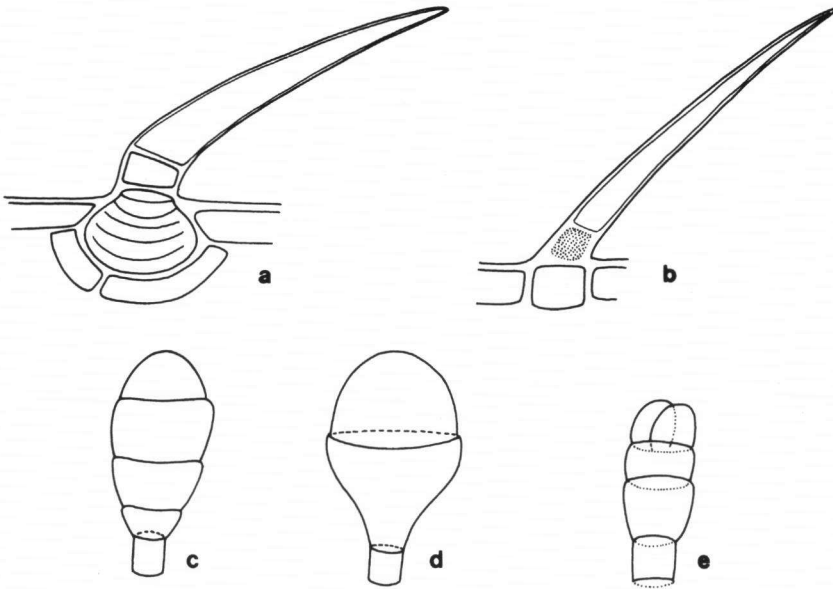
Figure 2.22. a. Non-glandular uniseriate hair of *Spatholobus*; b. non-glandular uniseriate hair of *Butea*; c. glandular hair of *Spatholobus*; d. glandular hair of *S. parviflorus*; e. glandular hair of *Butea*.

Leaf anatomy

The leaves are dorsiventral with one to three palisade layers on the dorsal side, a central layer and one to three layers of spongy parenchyma. Both glandular and non-glandular hairs are present.

The non-glandular hairs are uniseriate, with one long straight or slightly curved top cell and a few short basal cells (Fig. 2.22a & b). The hair base is often surrounded by epidermal cells in a rosette (Plate 2.1a). The base of the hair [81] is either sunken in the palisade layer (Fig. 2.22a, Plate 2.1b) or is situated in the epidermal layer and not sunken into the lower layers (Fig. 2.22b). In *Spatholobus* both types of hair bases are present, often in the same species. Of *Spatholobus* only *S. parviflorus* and *S. pulcher* do not have hairs with a base sunken in the palisade layer. In 13 species the character is polymorphic. *Butea*, *Kunstleria* and *Meizotropis* never have their hair bases sunken in the palisade layer.

The presence of a bulbous septate hair base [82] seems to be dependent on the presence of hairs with a base sunken below the epidermal layer (Fig. 2.22a, Plate 2.1b). Species that never have the hair base sunken in the palisade layer also never show a bulbous septate hair base. However, *Kunstleria*, which has no basal cells of the hairs sunken in the palisade layer, has both hairs with or without a bulbous septate base. Because this character turned out to be too much associated with the former character [81] and because of the relatively large number of species I decided to use only presence or absence of a bulbous septate hair base.
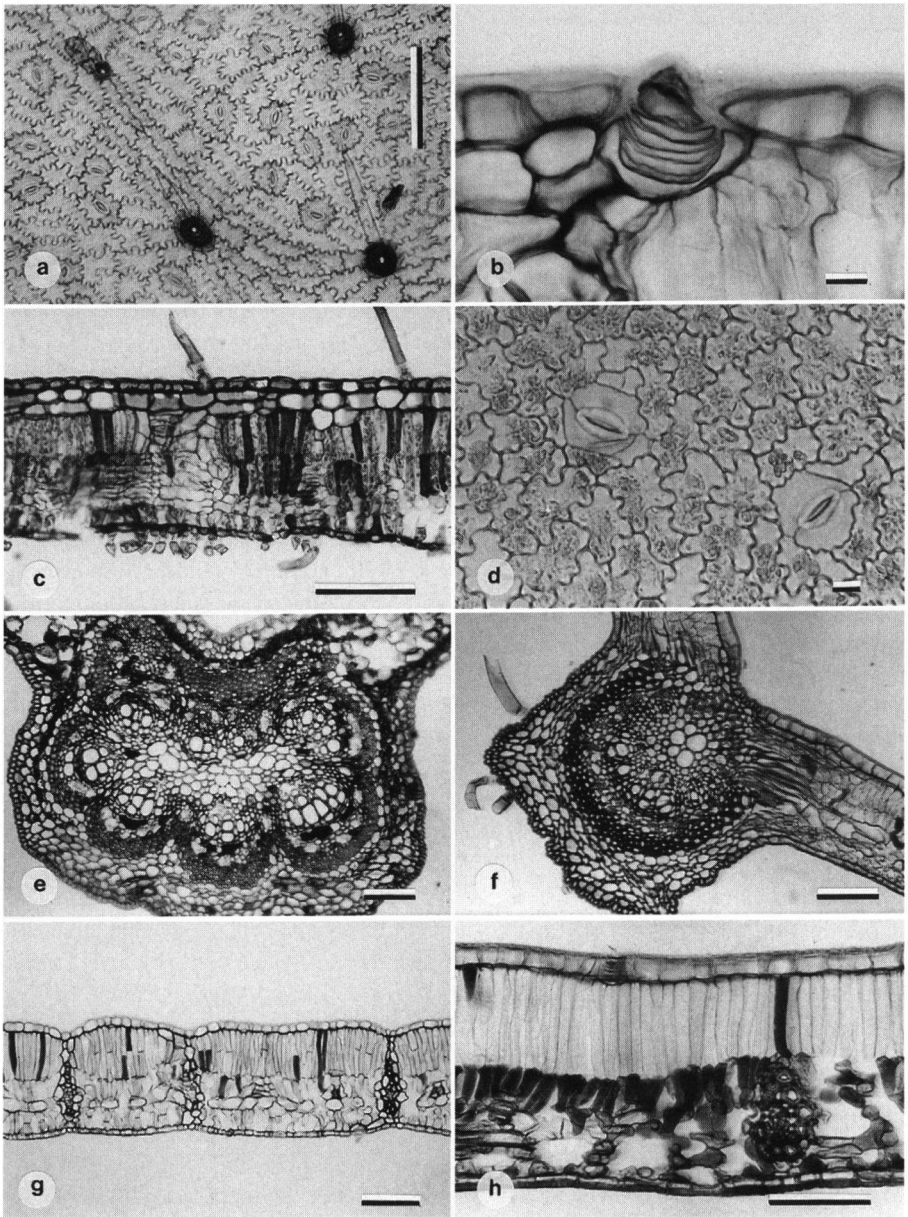
Plate 2.1. – a. Hairbase in surface view with epidermal cells in a rosette; note the undulating anti-clinal cell walls (*Spatholobus acuminatus*). – b. Bulbous septate hair base in cross section of a leaf of *S. littoralis*. – c. Cross section of a leaf of *S. parviflorus*; note the hypodermis. – d. Adaxial surface of a leaflet of *S. macropterus* showing stomata. – e. Midrib of a leaflet of *S. macropterus* showing the ring-like shape of the vascular bundle; note the dark substance, presumed to be tannin. – f. Midrib of *Kunstleria ridleyi* showing an arch-shaped vascular bundle. – g. Transcurrent veins in a cross section of a leaf of *Spatholobus pulcher*. – h. Continuous palisade layer in a cross section of a leaf of *Kunstleria kingii*. — Scale bars of a, c, f–h = 0.1 mm; of b, d, e = 0.01 mm.

Glandular hairs [83] are present in all species of *Spatholobus, Butea,* and *Meizotropis,* except in *S. crassifolius.* The glandular hairs are club-shaped and consist of a stalk and a head (Fig. 2.22c–e). The glands of *Kunstleria* have a longer stalk and head than those of *Butea, Meizotropis* and *Spatholobus*; *S. parviflorus* has a slightly aberrant glandular hair with the head divided into two parts; the lower half is holding – like an egg cup – the thinner walled upper half (Fig. 2.22d).

On both leaf surfaces the anticlinal walls of the epidermis show a specific shape. The walls can be straight, curved, or more or less strongly undulated (Plate 2.1c). The stronger undulations give the cells the impression of pieces in a jigsaw puzzle, and the strongest ones are those with undulations in the shape of an omega (Ω), where the tops of the undulation are (nearly) touching each other. The walls at the abaxial side [84] are usually more curved than the adaxial ones. For the analysis I used only the anticlinal cell walls at the abaxial side. This character may be influenced by the amount of light, and sun and shade leaves of the same plants may differ (shade leaves usually have more undulated cell walls). This is probably the reason why this character is polymorphic for five species of *Spatholobus.* A short discussion can be found in Metcalfe & Chalk (1979). A feature that makes it difficult to see the shape of the anticlinal wall clearly is the difference in undulation between inner and outer wall of the same cell.

In most species a real hypodermis [85] is absent. In some species there is sometimes a part near the larger veins where there is an extra layer between epidermis and palisade layer. *Spatholobus ferrugineus* always shows this feature near the larger veins; *S. parviflorus,* however, has a continuous layer of one or two translucent cells under the epidermis (Plate 2.1c). The presence of a continuous hypodermis in *S. parviflorus* seems to be an autapomorphy.

The stomata of all species are paracytic and usually not sunken. Adaxial stomata [86] are absent in *Butea, Meizotropis,* and *Kunstleria.* In *Spatholobus* the presence of adaxial stomata is not uncommon. They are absent in *S. crassifolius, S. dubius, S. gyrocarpus, S. multiflorus, S. parviflorus, S. pottingeri, S. pulcher , S. purpureus* and *S. suberectus* In some other species they are not always present. Adaxial stomata are very frequent in *S. hirsutus, S. latibractea, S. oblongifolius,* and *S. viridis,* and in some specimens of *S. albus, S. apoensis, S. latistipulus* and *S. macropterus* (Plate 2.1d).

In cross section the vascular system in the midrib [87] is usually a closed ring (Plate 2.1e). Only in *Kunstleria* the open arch-shaped type is found (Plate 2.1f). In some species of *Spatholobus* this feature is also present, however not in all specimens: i.e., *S. ferrugineus, S. gyrocarpus, S. harmandii,* and *S. sanguineus.*

Transcurrent veins [88] are present in several species. The veins can be transcurrent to the upper and lower epidermis by bundle sheath extensions or by the bundle sheath itself (Plate 2.1g). When the palisade layer is continuous above the larger veins, transcurrent veins were scored absent (Plate 2.1h).

Sometimes a cell layer with dark reddish brown contents, presumed to be tannins, occurs between phloem and xylem [89] in *Spatholobus* (*S. auricomus, S. dubius, S. multiflorus,* and *S. oblongifolius*) (Plate 2.1f). More often this layer was absent, or situated in the xylem itself. In *Butea, Meizotropis,* and *Kunstleria* the layer was always present between phloem and xylem.
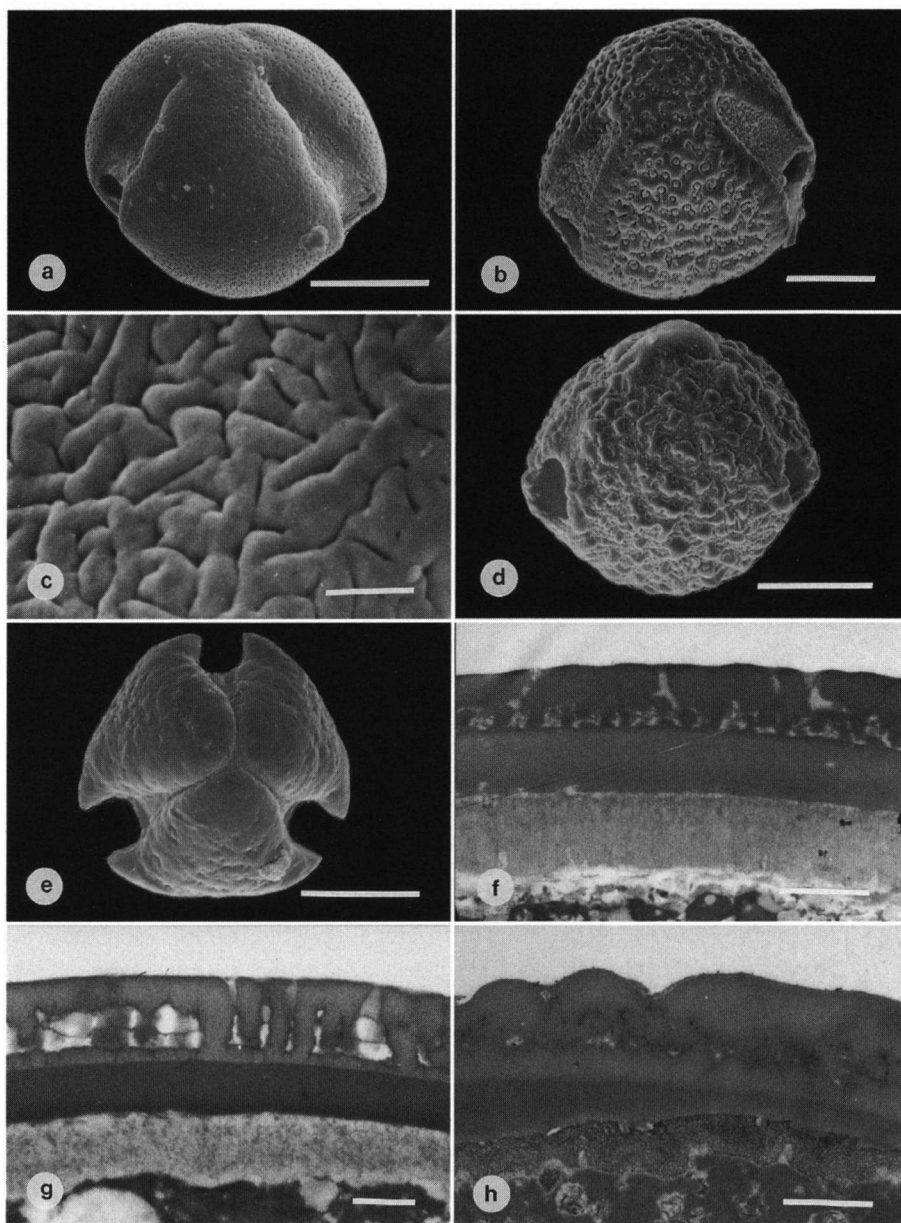
Plate 2.2. – a. Ornamentation psilate-perforate (*Spatholobus ferrugineus*); note the acute colpus ends. – b. Ornamentation microreticulate (*Butea monosperma*); note the obtuse colpus ends. – c. Rugulate ornamentation (*Kunstleria ridleyi*). – d. Verrucate ornamentation (*Meizotropis pellita*). – e. Fused colpi (*Spatholobus oblongifolius*). – f. TEM section of a pollen grain of *S. parviflorus* showing the very thin foot layer. – g. TEM section of a pollen grain of *S. ferrugineus* showing the relatively thick foot layer and the well-spaced columellae. – h. TEM section of pollen of *S. littoralis*. Note the thick foot layer and the granule-like infratectum. — Scale bars of a, b, d, e = 10 μm; of c, f–h = 1 μm.

Dark substances were also present in the bundle sheath cells [90] of some taxa. This was never the case in *Kunstleria* and *Meizotropis*, but always in *Butea* and some species of *Spatholobus*.

Pollen

The pollen grains are (sub)spheroidal and usually tricolporate, but (para)syncolporate pollen is found in several species of *Spatholobus*. For the analysis I used characters of the ornamentation, the ectoaperture morphology and the exine structure of the pollen. For a more extensive description of the pollen morphology see Ridder-Numan (in press).

The ornamentation of the pollen [91] is psilate-perforate to fossulate in most species of *Spatholobus* (Plate 2.2a). In some species the ornamentation is more open, showing elements of the infratectal layer. A more open ornamentation is present as well in *Butea* and *Meizotropis* (Plate 2.2b). Here the perforations may be a little wider, showing one or two, rarely up to seven free sexine elements (microreticulate). *Kunstleria* has a closed, usually rugulate ornamentation (Plate 2.2c). A verrucate ornamentation is present in *Meizotropis pellita*, and sometimes in *M. buteiformis* and *Spatholobus maingayi* (Plate 2.2d).

Fused colpi [92] are more or less frequent in some species of *Spatholobus*, *S. harmandii S. persicinus*, *S. viridis* (Plate 2.2e). However, (para)syncolpi never occurred in all grains of one sample. The apocolpium is in this case reduced by the fused colpi, or sometimes the colpi fuse in such a way that the apocolpium nearly becomes an island. In the other three genera no (para)syncolporate grains were observed.

Colpus ends [94] may be acute (Plate 2.2a) or obtuse (Plate 2.2c). Obtuse ends are present in *Butea* and *Meizotropis*. In some species of *Spatholobus* both acute and obtuse colpus ends were found. In the one sample of *S. auritus* I noticed only obtuse ends.

The A/E-index is a measure of the apocolpium size [97], in which A is the distance between two of the three colpi and E the width of the pollen grain in equatorial view. I took this measure from pollen grains that did not have fused colpi, which have an A/E-index of zero. When fused colpi were present in a sample, the A/E-index was low in most cases, as expected. In *Spatholobus ferrugineus*, however, the colpi were never fused and the A/E-index was low. If the A/E-index is high the colpi are relatively short. In *S. gyrocarpus*, *S. sanguineus*, and especially *S. pulcher* the colpi are short and the A/E-index is high. The other three genera also have relatively short colpi. The A/E-index values are given in Figure 2.23.

Of the exine stratification the relative size of the foot layer and the structure of the infratectal layer are the two characters chosen for the analysis. Unfortunately it was not possible to make TEM sections of all species; therefore several species had to be given a '?' for these characters.

The foot layer [93] is very thin (less than 1/10 of the endexine) in *Meizotropis* and *Spatholobus parviflorus* (Plate 2.2f). A thicker foot layer is present in *Butea* and most species of *Spatholobus* (Plate 2.2g). A relatively thick endexine associated with the reduction of the foot layer may be regarded as a morphologically advanced feature in the Papilionoideae (Ferguson & Skvarla, 1981; Ferguson, 1984). A foot layer thicker
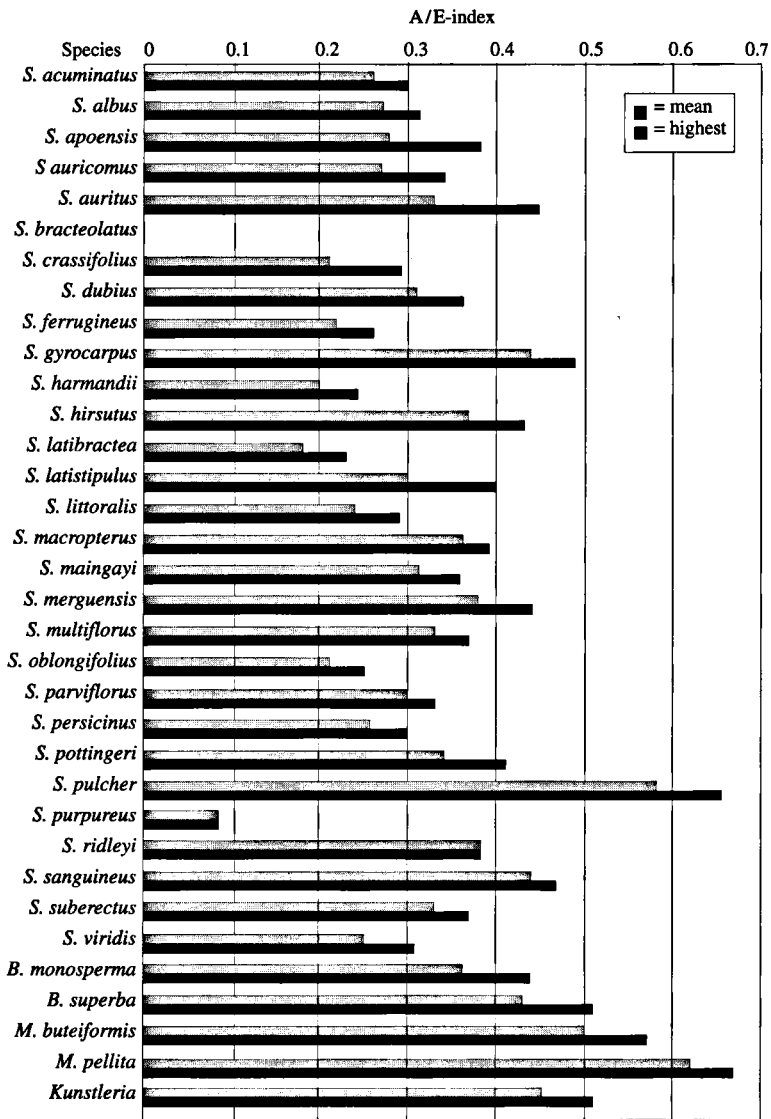
A/E-index

Figure 2.23. A/E-index of the pollen grains. Pollen of *Spatholobus bracteolatus* was not available.

than half the endexine, even sometimes thicker than the endexine, was found in *Kunst-leria* and some other species of *Spatholobus*. The foot layer–endexine ratio of the mean values of foot layer and endexine was used in the analysis (Fig. 2.24; only species of which a TEM section was available are included).

The infratectal layer [97] is a difficult character to code, resulting in most species being polymorphic for two or three states. Especially when the infratectal layer is thin,

Relative thickness of foot layer

Species	0	0.2	0.4	0.6	0.8	1	1.2	1.4	1.6

S. acuminatus
S. albus
S. apoensis
S auricomus
S. auritus
S. bracteolatus
S. crassifolius
S. dubius
S. ferrugineus
S. gyrocarpus
S. harmandii
S. hirsutus
S. latibractea
S. latistipulus
S. littoralis
S. macropterus
S. maingayi
S. merguensis
S. multiflorus
S. oblongifolius
S. parviflorus
S. persicinus
S. pottingeri
S. pulcher
S. purpureus
S. ridleyi
S. sanguineus
S. suberectus
S. viridis
B. monosperma
B. superba
M. buteiformis
M. pellita
Kunstleria

Figure 2.24. Thickness of the foot layer relative to the endexine. Values are given only for species of which TEM data are available.

which is so in most species, the columellae will be short and the difference between a granular and a columellate infratectal layer is not easy to see (Plate 2.2h).

Mesocolpial pouches [96] can be found in most species. In *Butea*, *Meizotropis*, *Spatholobus parviflorus* and *S. pulcher* this feature was present in very few grains. It is possible that in the case of a thin and flexible pollen wall, the wall may fold more easily into mesocolpial pouches.
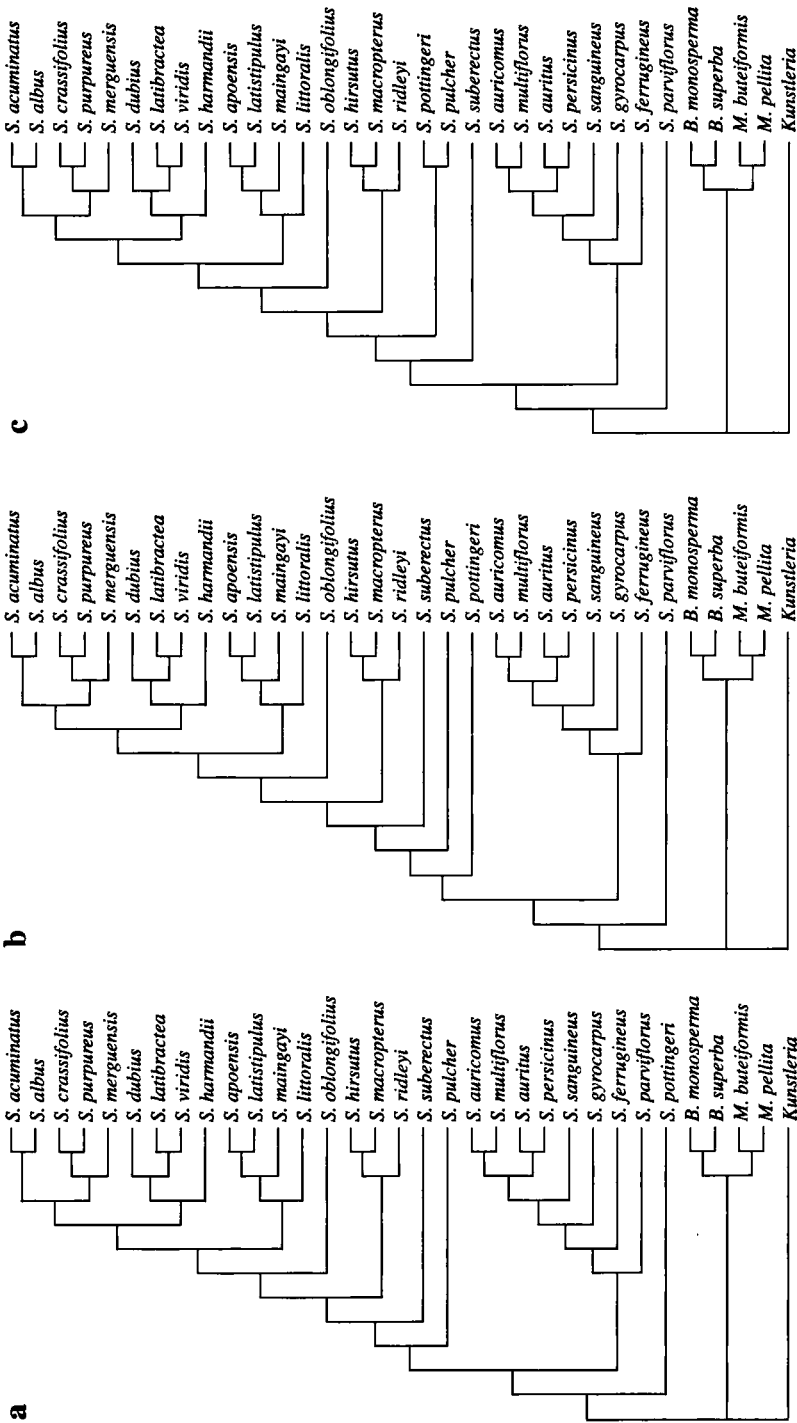
Figure 2.25. All three most parsimonious trees found by using PAUP under the heuristic search option, 'stepwise addition sequence random', tree-bisection-reconnections (TBR); all characters analysed unordered, uninformative characters ignored and characters with multiple states treated as polymorphisms; length 589, c.i. 0.46. On each of the branches the amount of change is shown. a = tree 1; b = tree 2; c = tree 3.

RESULTS

Finding the set of most parsimonious trees

Following the phases of preliminary analyses, checking and rechecking data, coding and recoding characters, a final phylogenetic analysis was performed. This analysis was carried out using PAUP under the heuristic search option with an addition sequence random, and the branch-swapping procedure TBR, using *Kunstleria* as the outgroup. One species, *Spatholobus bracteolatus*, was excluded from the analysis because of the lack of sufficient data.

The analysis resulted in three most parsimonious trees (MPT) with a length of 589 steps, and a consistency index of 0.46 (Fig. 2.25). The consistency index 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 gave a frequency distribution of the tree length in number of steps as shown in Figure 2.26. The three MPT's (length = 589 steps) found were much
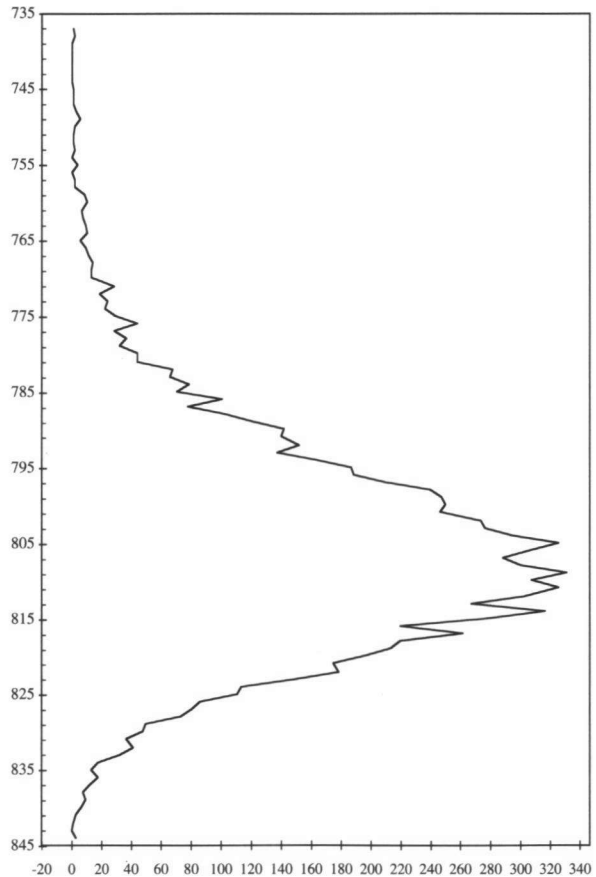
Figure 2.26. Frequency distribution of lengths of 10,000 random trees (mean = 805.6, sd = 13.7, g1 = –0.57, g2 = 0.783).

shorter than the random tree set, which had a mean value of 805.6 steps, and a standard deviation of 13.7. It is unlikely that the MPT's are randomly found trees, and it is very probable that the data set has more structure than would be expected by chance alone.

Another type of analysis is the parsimony analysis with implied weights. In the computer program PeeWee (Goloboff, 1993) the trees with the lowest number of extra steps in a character (best fit) are selected instead of the ones with the lowest number of steps (most parsimonious trees). Weighting in this way is carried out during the analysis. With this program the data were analysed using three different types of concaveness: 1, 3, and 6. However, it is difficult to know which concavity index to use [see also the discussion in Turner (1995) and Turner & Zandee (1995)]. The fit of the three trees found with concaveness 3 was 447.4, that of the two trees resulting from the analysis with concaveness 6 was 567.2, and that of the one tree found with concaveness 1 (which is equal to not weighting) was 285.8. When the statistics of MacClade where used to make it comparable to the most parsimonious trees found with PAUP these resulted in trees with length 827 and 823, and $ci = 0.35$. These lengths are nearly within the range of the mean value of random tree lengths that was found during evaluation of 10,000 random trees. The trees have some interesting features, but most of the clades seem to be very unnatural. The genera in the analysis turn out to be not monophyletic as one of the two species of *Butea* is placed as sister to *Spatholobus ferrugineus* halfway through the tree, and the other at the base as sister to one of the two species of *Meizotropis*. The other species of *Meizotropis* is placed as sister to *Kunstleria*. This outcome is very improbable, because in my view the monophyly of these two small genera is not in dispute.

Choice among the most parsimonious trees

The result of extensive reciprocal illumination and the running of several analyses turned out to be in certain respects rather stable. Mostly changes in the data matrix resulted in different trees. However, in most MPT's found during several trials the following more or less identical groups of species were found:

Spatholobus apoensis, *S. latistipulus*, *S. littoralis*, and *S. maingayi*,
S. acuminatus and *S. albus*,
S. crassifolius, *S. merguensis* (and often *S. purpureus*),
S. dubius, *S. harmandii*, *S. latibractea*, and *S. viridis*,
S. hirsutus, *S. macropterus*, *S. ridleyi*, sometimes including *S. oblongifolius* and
    S. pottingeri,
S. auricomus and *S. multiflorus*,
S. ferrugineus, *S. gyrocarpus*, and *S. sanguineus*,
Butea and *Meizotropis*.

Spatholobus parviflorus was always present near the base of the *Spatholobus* part of the cladogram. A few species and small clades, however, occurred in different places in the different cladograms (probably due to missing data or polymorphic states). Wandering species and small groups were *S. auritus*, *S. persicinus*, *S. pottingeri*, *S. pulcher* and *S. suberectus*, and the twins *S. auricomus* and *S. multiflorus*. The wanderers were

usually placed in the lower half of the cladogram, and the twins have been placed either near the top of the cladogram (mostly in the *S. harmandii*-clade) or at the end of the *S. ferrugineus*-clade.

The MPT's found in the final analysis show large similarities regarding the groups mentioned (Fig. 2.25). In one of the three trees (Fig. 2.25a) *S. pottingeri* is placed in a basal position and *S. parviflorus* is inserted into the clade of *S. ferrugineus*. However, on account of similarities in leaves and pods, the position of *S. parviflorus* near the base of the cladogram next to the *Butea*-clade seems more acceptable to me than within the group of *S. ferrugineus*. Besides, the flower structure is quite different from that in the *S. ferrugineus*-group. Similarly, the basal position of *S. pottingeri* in the cladogram next to the *Butea*-clade and far from *S. suberectus*, which it resembles very much in overall characteristics, is not preferable. In the second and third cladogram (Fig. 2.25b & c) *S. parviflorus* is placed next to the *Butea*-clade in a solitary position, and *S. pottingeri* can be found in the middle of the cladogram next to *S. pulcher*, and only one node from *S. suberectus*. The other 'wanderers', the twins *S. auricomus* and *S. multiflorus*, and the species *S. auritus* and *S. persicinus*, are placed in the top of the *S. ferrugineus*-clade in all three trees. *Spatholobus auricomus* and *S. multiflorus* are species with extremely small flowers. *Spatholobus sanguineus* and *S. gyrocarpus*, both belonging to the *S. ferrugineus*-clade, have the same type of small flower. In this view one would expect these two species to be close to *S. sanguineus* and *S. gyrocarpus* as is the case in the MPT's in Figure 2.25.

There are several ways to choose between equally parsimonious trees. One of the often used methods is successive weighting. Successive weighting resulted in one tree slightly different from the set of three MPT's found as result of the initial analysis. The most parsimonious tree found by successive weighting (TBR, random 100 repetitions) is one step longer than the original set of most parsimonious trees: 590 versus 589 steps (Fig. 2.27). This tree is nearly identical to the second of the three MPT's found without weighting (Fig. 2.25b); the only difference is the position of the *S. maingayi*-clade between the *S. crassifolius*-group and the *S. acuminatus*-group. This indicates a preference for the second tree in Figure 2.25.

Figure 2.27. The most parsimonious tree obtained by successive weighting. Length 590, c.i. 0.46, r.i. 0.5, r.c. 0.23.
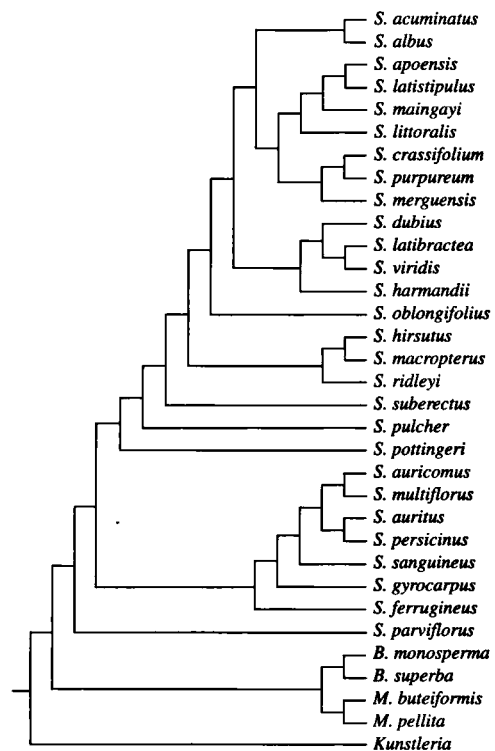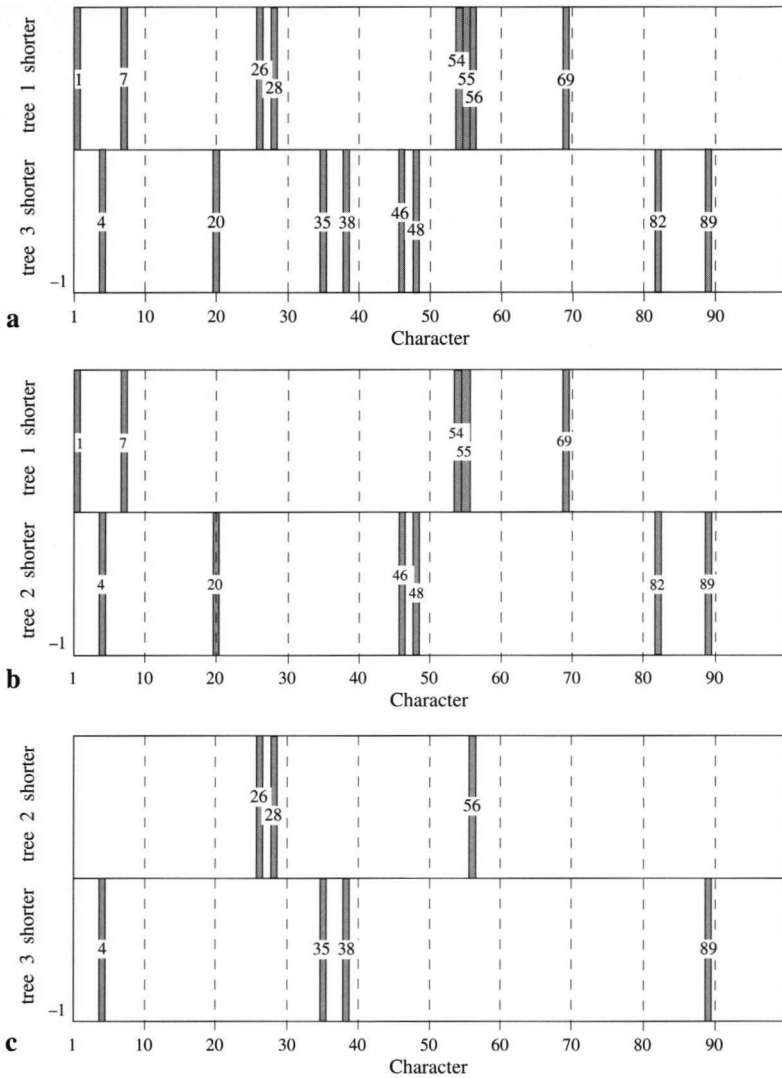
Figure 2.28. Differences between the MPT's in amount of change per character. a. Tree 1 compared with tree 3; b. tree 1 compared with tree 2; c. tree 2 compared with tree 3.

When taking into account the amount of support for the branches in the three different trees, there are no big differences (MacClade: Trace all changes and All change options: unambiguous changes only, graphics display: label by amount of change). Except for some other slight changes, tree two has more support for the first branch leading to the genus *Spatholobus*.

The difference between the three trees in amount of change per character is illustrated in Figure 2.28 (MacClade: Chart compare two trees). In this figure the differ-

ences between two trees in amount of steps per character are given. Compared with the first tree (= tree 1) the third tree (= tree 3) is one step shorter for 8 characters, in all other characters they have the same length. The characters for which tree 1 is shorter are: 1, 7, 26, 28, 54, 55, 56, 69. Tree 3 is one step shorter from tree 1 in the characters: 4, 20, 35, 38, 46, 48, 82, 89. Comparison between the second of the MPT's (= tree 2) and tree 3, shows that tree 2 is shorter for 3 characters (26, 28, 56). Tree 3 is different from tree 2 in 3 characters (4, 35, 38). The characters for which tree 2 is shorter than tree 1 are: 20, 46, 48, 82, 89. Tree 1 is shorter than tree 2 for the characters 1, 7, 54, 55, 69. Tree 2 is less different from the other two trees than the others are from each other.

Using the weighting method as described by Turner (1995), this gives for tree 1 W = 40.71, for tree 2 W = 40.63, and for tree 3 W = 40.76. This weighting method is in fact a comparison between the sum of the retention indices for all individual characters for each of the weighted trees:

$W = \sum ri$, where $ri = (Es_{i,max} - Es_i) / Es_{i,max}$

$Es_{i,max}$ = maximum number of extra steps for character i on the tree (i.e. maximum–minimum number of steps)

Es_i = observed number of extra steps for character i (i.e. observed number–minimum number of steps)

The tree with the highest fit ($ri = 1$, is the best fit; $ri = 0$, is the worst fit) will have the highest W, because the homoplasy is concentrated in the fewest characters. In this case tree 3 has the highest value of W. The values, however, do not differ very much. This is understandable, because in the tree comparison by amount of change (Fig. 2.28), none of the trees differ in the number of characters for which they are shorter than any of the other two trees. The homoplasy is concentrated in the same number of characters. The weighting method of Turner is not very discriminating in this case. In a former analysis with a slightly different data matrix, and which resulted in three equally parsimonious trees as well, there was a difference between the three trees in the number of characters in which the homoplasy was concentrated. In this case the tree that had the homoplasy concentrated in the fewest characters showed the highest value of W. In my view the two described methods above both end up with the same result, because they are both looking at the concentration of homoplasy in the MPT's, i.e. the higher the W the better the fit according to the method of Turner, and the fewer characters showing the homoplasy (= the fewer characters shorter for one of the MPT's) the better the fit of the tree according to the comparison of two trees in MacClade. The last method is very simple when few MPT's are involved, but Turner's method is easier with larger numbers of MPT's (in CAFCA this option is available).

As there are only three equal MPT's – two of which are hardly different – it may be possible to select one of the trees on morphological arguments. *Spatholobus parviflorus* differs from the other species in *Spatholobus*, and more closely resembles *Butea*. It is in various respects similar to *Butea*, e.g., a large pod, shape and structure of the leaves, extremely long calyx lobes, and a standard apex that is acute. Although in all other aspects 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 second and third cladogram it is placed at the base of the *Spatholobus* clade. The latter is preferable in my view. The other differences between the three MPT's concern the position of *S. pottingeri*. In the second and third cladogram this species is placed as sister to *S. pulcher*. In the first cladogram, however, *S. pottingeri* is placed basally in the *Spatholobus*-clade, while at the same time *S. parviflorus* occurs in the previously mentioned, less preferable position within the *S. ferrugineus*-clade. Based on overall similarity, but especially the general appearance of the flower (shape and size of calyx and petals), the species *S. pottingeri*, *S. pulcher* and *S. suberectus* appear to be closely related. At first sight it is not easy to tell them apart, but the differences become more apparent in detail. These considerations favour the choice for the second or third tree. Tree 2 and tree 3 only differ in the position of *S. pottingeri* with respect to *S. pulcher* and *S. suberectus*. There are as many morphological arguments to place these three species in the position in tree 2 as for the position they take in tree 3.

As a result of the considerations in this paragraph, especially the morphology and the result of weighting, tree 1 was discarded. Because there are no convincing arguments to chose between the remaining two, I accepted tree 2 as a working hypothesis (Fig. 2.25b).

Evaluation of the tree

Character support
Based on the arguments given above I accepted the second of the MPT's in Figure 2.25 as a working hypothesis. Several branches of smaller and larger parts of this tree (Fig. 2.29) are supported unambiguously by two or more characters. Most characters show parallellisms or reversals. Not many groups are supported by more than one synapomorphy. Because of the amount of homoplasy, detailed discussion of every character and state is avoided. Characters that turned out to be uninformative for the analysis are not considered here [i.e., characters 9, 57, 63, 64, 83, 85, 87]. Also the characters pertaining to the stigma [76] and leaf base [81] were not used in the analysis, because I considered these too subjective. The characters concerning the shape of the bracts [37] and the shape of the calyx lobes [44] were left unused, because in former analyses they seemed to create more noise than pattern. The support of the larger groups of the tree is evaluated below. Branch numbers refer to the numbers (in bold type) in Figure 2.29.

Branch 63 supports the *clade of Butea and Meizotropis*. There are five synapomorphies supporting this branch, all other characters on this branch show parallellisms with one or more species in the other part of the tree. Synapomorphies are: the presence of indumentum on the upper surface of the leaves [19], on the standard [45], on the inside of the wing petal [53; reversal in *M. pellita*], and on the filament sheath [66; outside this clade only found in *S. acuminatus* as polymorphy], and the size of the anthers [67]. Since the flowers of *Butea*, and *Meizotropis* as well, are rather large, the last character is, considering the small size of the flowers of *Spatholobus*, not really comparable within the group under study.

Figure 2.29. Phylogenetic tree of *Spatholobus* and allies. The numbers on the branches refer to the characters that change (see Table 2.1). Due to limited space the character states are not mentioned. Branch numbers are printed in bold type.

Figure 2.29 continued)
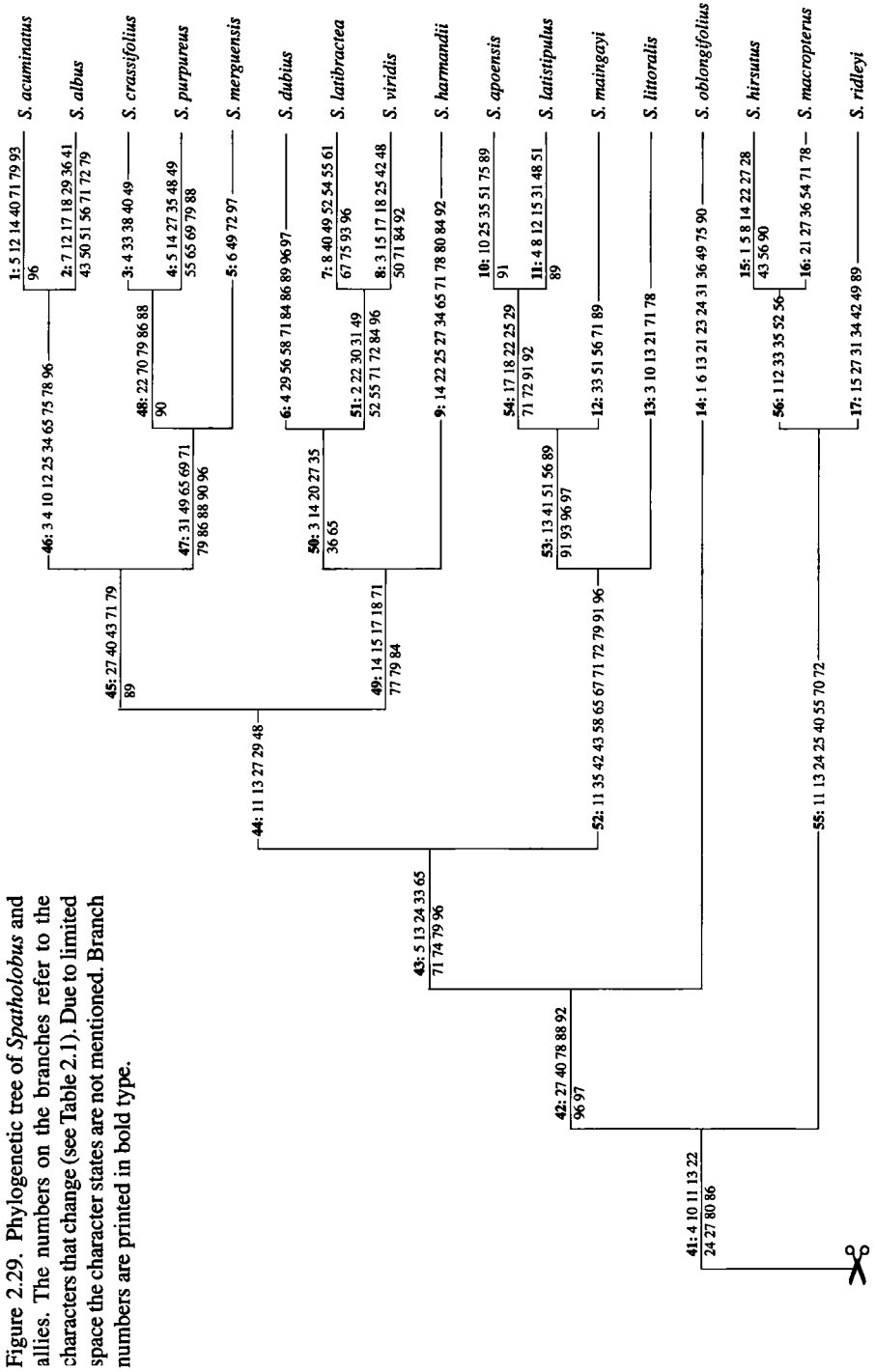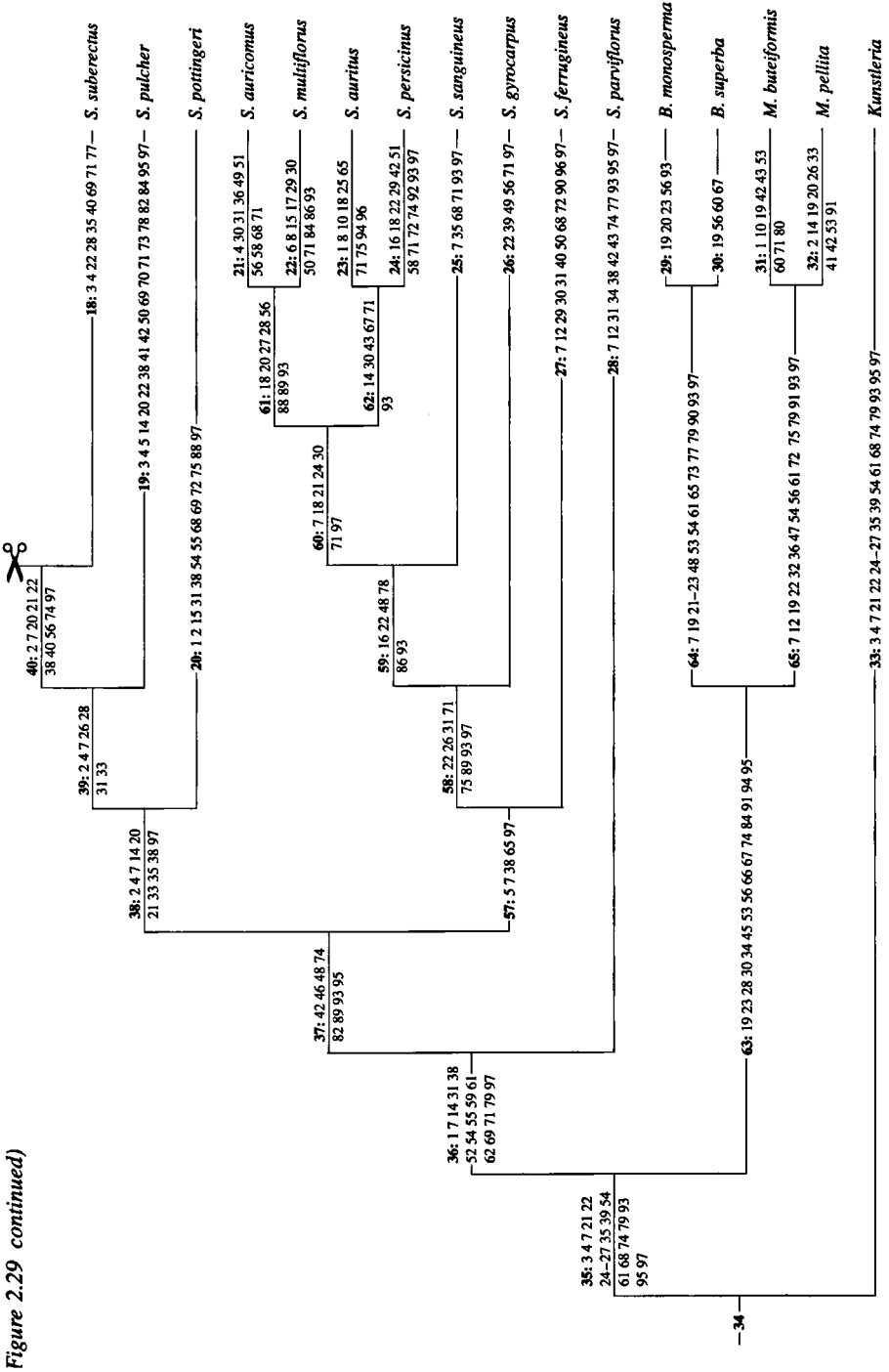
The other characters are the decurrent base of the leaflet [23; parallel in *S. oblongifolius*], the scalariform venation [28; parallel in *S. suberectus*], the secondary veins terminating in the margin [30; parallel in *S. ferrugineus*], the inflorescence with only first order side branches [34; parallel in the clade of *S. albus* and *S. acuminatus, S. harmandii, S. ridleyi* and polymorphic in *S. oblongifolius*], the absence of a dorsal auricle in the wing petal [56; parallel in several other species]; the medium position of the ovules in the ovary [74; parallel within the tree after node G, and the *S. ferrugineus*-clade], the curved anticlinal walls of the epidermis of the lower surface [84; parallel in *S. pulcher*, and polymorphic in *S. auricomus* and *S. ferrugineus*], the open ornamentation of the pollen grain [91; parallel with the *S. apoensis*-clade, and polymorphic in these species, and in *S. persicinus* and *S. latibractea*], the obtuse colpus ends [94; parallel with *S. pulcher*, and polymorphic in the *S. apoensis*-clade], the absence of mesocolpial pouches [95; parallel with *S. parviflorus* and *S. pulcher*].

The basal node [**branch 36**] of *Spatholobus* is supported by the following characters:
- the stem is not hollow [1], except for a reversal for the *S. macropterus*-clade;
- the wing petals are glabrous on the outside [52] as well as along the ventral margin [55], except for the *S. macropterus*-clade, *S. purpureus*, and *S. latibractea / S. viridis*;
- the outside and ventral margin of the keel petals are without indumentum [59, 62];
- the presence of usually 10 small nectary lobes [69]. *Spatholobus crassifolius, S. merguensis* and *S. pottingeri* show a reversal for the last character, and have no lobes, but only slightly thickened filament bases as in *Butea, Meizotropis* and *Kunstleria*.

Other characters are a synapomorphy for the genus *Spatholobus*, but change later in the rest of the tree (i.e. reversal or new apomorphies):
- a densely pubescent pulvinus [14], later becoming glabrous and reversing again to not densely pubescent;
- the number of pairs of nerves [31]; more than 8, many reversals in the rest of the tree to the plesiomorphic state of 5–8 pairs of nerves;
- the presence of two bracts at the base of the second order side branch of the inflorescence [38]; this is only the case in a few species (*S. crassifolius, S. parviflorus, S. pottingeri*, and *S. pulcher*), with reversals later to the plesiomorphic state of one bract at the base of the second order side branch;
- the indumentum on the ovary not very dense [71], later on larger parts of the tree reversal to plesiomorphic state of a densely hairy ovary.

Branch 37 supports the **genus without S. parviflorus**. Four characters support this node with an apomorphic character state (i.e. a synapomorphy for *Spatholobus* from this point on, without *S. parviflorus*):
- the apex of the standard is emarginate [46];
- the base of the standard decurrent [48, with reversals later on];
- a bulbous septate hair base [82] is present;
- tannin is absent from the phloem in the main nerve, but present between phloem and xylem, or in the xylem itself [89].

A character state developed parallel with *Butea* is the footlayer/endexine ratio [93] being between 0.6 and 0.1; a few reversals to a thicker endexine occur.

A reversal to the presence of mesocolpial pouches [95] is also found at this point.

The *group of S. ferrugineus* on *branch 57* is supported by three apomorphic characters, all showing parallel developments in other groups: the bark of the branches is smooth [5; parallel with the top of the tree after *S. oblongifolius*, and with *S. hirsutus* and *S. pulcher*]; the filaments are connate only up to half of the total length of the filaments [65; parallel with the group after *S. oblongifolius* [branch 43]]. The character on the A/E-index [97] may have in this clade all three possible states.

The rest of the tree (from *branch 38* on) involves character states changing for, among others, several indumentum characters. With some exceptions, the species before branch 38 are more hairy than the species occurring in the top of the tree. The stem [2] is glabrous/glabrescent (with some exceptions, e.g., *S. pottingeri*), the pulvinus [14] is glabrous in most species (but reversals do occur), and the indumentum on the lower surface of the leaflets [20] is absent or nearly so (again reversals are found). The inflorescence [33], however, is more hairy (apomorphy) after branch 38 than before, and after *S. oblongifolius* the inflorescences are glabrous again (reversal). The presence of brachyblasts [35] is after branch 38 reversed to the plesiomorphic state (i.e. solitary flowers), but frequent changes to the apomorphic state (i.e. brachyblasts) occur. The shape of the leaflets [21] is in most species elliptic. From branch 38 on, no ovate leaflets are present, except for a few reversals. A few species, however, have obovate leaflets as well.

Branch 41 supports the second half of the tree. Reversals to the plesiomorphic states are the lateral leaflets [24] being symmetrical, except for *S. oblongifolius*, and the secondary venation [27] versus the venation as well being prominent at the lower surface of the leaflets; higher in the cladogram this character is changing to the apomorphic state of only a prominent midrib. Other changes are:

- the stipules with clearly visible nerves [10], a few reversals are present higher up;
- the stipules are glabrous [11], but only for the species up to the *S. maingayi*-clade; further on the other species are grouped by a reversal to an indument on the stipules;
- the colour of the pulvinus [13] shows the same pattern as the former character: only the species up to the *S. maingayi*-clade have a dark pulvinus;
- the apex of the leaflets [22] is now more strictly acute, although leaflets with acuminate apices still occur;
- the indumentum of the pod [80] is puberulous or nearly glabrous instead of densely pubescent; some reversals do occur;
- the presence of adaxial stomata [86] is a feature developed parallel with the upper part of the *S.ferrugineus*-clade.

The *group of S. macropterus* [branch 55] is supported unambiguously by the following character states:

- the midrib is flat or sunken on the upper surface of the leaflets [25]; this reversal is present in some other species as well;
- the bracteoles are placed immediately below the calyx cup [40], a plesiomorphic feature present in the largest part of the cladogram, except in the middle [branch 40–44];
- an indumentum on the ventral part of the wing petal [55; parallel in *S. purpureus, S. latibractea, S. viridis* and *S. ferrugineus*, in the last two only polymorphic]; this is a reversal also occurring in *Butea* and *Meizotropis*;
- an indument on the nectary [70]; this feature occurs in parallel in *S. crassifolius, S. pulcher* and *S. purpureus*;
- an indumentum halfway up the style [72]. It is an apomorphic state found in parallel in *S. ferrugineus, S. latibractea*, the *S. maingayi*-clade, *S. merguensis, S. pottingeri* and *S. viridis*. The majority of the species of *Spatholobus* have the indumentum up to the base of the style.

The *S. maingayi-clade* [branch 52] is supported by the following characters:

- brachyblasts present [35]; this is a reversal to an earlier apomorphic state in *Spatholobus*, brachyblasts are present in the majority of the species;
- a vexillary lobe that is not emarginate [42]; parallel with a few other species of *Spatholobus*;
- calyx lobes that are less than half the length of the calyx cup [43]; developed in parallel in *Spatholobus*, in *S. albus, S. hirsutus, S. auritus, S. persicinus*, although in these species they are perhaps not as extremely short as in the *S. maingayi*-clade;
- the absence of a lateral pocket on the keel [58]; parallel with *S. dubius, S. auritus, S. persicinus*; in all others the presence of pockets in both keel and wing petal is a plesiomorphic character;
- the anthers ranging in size from 0.5–1 mm [67]; parallel with *S. latibractea, S. auritus, S. persicinus*; the plesiomorphic state is less than 0.5 mm long;
- open ornamentation of the pollen wall [91]; although the clade is polymorphic for this character, it is the only clade with this feature within the genus, which also occurs as a parallelism in the *Butea*-clade.

The *S. harmandii-group* [branch 49] is supported unambiguously by five characters:

- a reversal to a pubescent pulvinus [14];
- the presence of more or less persistent stipellae [15]; parallel with *S. latistipulus, S. multiflorus, S. pottingeri, S. ridleyi*; although it is difficult, because in the outgroup *Kunstleria* stipellae are absent, this seems to be an apomorphy over the plesiomorphic early caducous stipellae.
- a glaucous upper surface of the leaves [17]; parallel with *S. apoensis, S. latistipulus, S. albus, S. multiflorus*, and polymorphic for *S. purpureus* and *S. merguensis*;
- and a brown lower surface of the leaves [18]; parallel with *S. apoensis, S. latistipulus, S. albus, S. auricomus, S. multiflorus*, and *S. persicinus*. These two states [17 and 18] are most probably related to each other;
- pod with a stipe [77]; parallelisms for *S. suberectus, S. parviflorus*, and *Butea*. Pods are not known from two species within the clade, *S. latibractea* and *S. viridis*;

- the wing of the pod is wider than the apex [79]; in this clade the apomorphic state of the whole genus is present versus the reversed state of the top of the tree after branch 43;
- the strongly undulated anticlinal cell walls [84]; this apomorphic state is present in a few other species, *S. ferrugineus*, *S. latistipulus* and *S. multiflorus*, which show this features occasionally.

Branch 45 connects the last two clades in the cladogram, those of *S. acuminatus* and *S. crassifolius*, and is supported by:

- a reversal to the state in which the bracteoles are placed immediately below the calyx cup [40]; *S. acuminatus* and *S. crassifolius*, however, have their bracteoles placed lower on the pedicel;
- the vexillary calyx lobe [43] is as long as the calyx cup; this is an apomorphic state shared with *S. parviflorus*;
- the indumentum of the ovary [71] reversed to the apomorphic state in the genus of a pubescent ovary; a reversal in some groups to a plesiomorphic densely hairy ovary took place earlier in the cladogram;
- the absence of the tannin (?) layer in the vascular bundle of the midrib [89]; this feature is shared with some other species: *S. apoensis*, *S. maingayi*, *S. ridleyi* and part of the *S. ferrugineus*-clade.

Summary of the character evaluation

In Table 2.3 an evaluation of all characters is presented. In order to avoid a long enumeration of characters, some characters are selected for a short discussion.

The species of *Spatholobus*, *Butea* and *Meizotropis* in the basal part of the cladogram (Fig. 2.29) are more hairy than *Kunstleria*. The species in the upper part of the cladogram are more glabrous than those of the lower part including *Kunstleria*.

In the second half of the cladogram: the shape of the leaflets [21] becomes elliptic, the apex of the leaflets [22] acute only, the lateral leaflets symmetric [24], with 5–8 pairs of nerves [31], brachyblasts are present [35], a well developed dorsal auricle on the keel petal is absent [56], the filaments are connate for less than half their length [65], the style remnant of the pod is bent downwards [or up; 78], adaxial stomata are present [86], transcurrent veins are absent [88], tannin is lacking in the vascular bundle [89], the infratectal layer is more granular [96], and the grains have a very small A/E-index [97]. Some of these character states are reversals, others synapomorphies.

There is a correlation between the size of the anthers [67] and pollen ornamentation [91]. Although the species with open ornamentation are polymorphic for this character, no other species in *Spatholobus* have this character state. In this analysis the species with the larger anthers are those with an ornamentation showing the sexine elements through the pores.

A very small A/E-index [97] is usually correlated with fused colpi, but this is not always the case, e. g., in *S. ferrugineus*, where the A/E-index is very small and no pollen grains with fused colpi were found.

Table 2.3. Character evaluation.

For each character the number of steps, the minimum/maximum number of possible steps, the retention index, the plesiomorphic state of the characters as optimized on the outgroup node, the apomorphic states, and remarks with possible transformation series of the states is given.

Abbreviations: (syn./aut.)apo. = (syn/aut)apomorphy, par. = parallelism, rev. = reversal, ples. = plesiomorphy, B. = Butea, M. = Meizotropis, S. = Spatholobus.

Character	Steps	Min/Max	RI	Plesiomorphic state	Apomorphic state	Remarks
1. Stem hollow	8	3–10	0.29	1 = yes	2 = no	synapo. S.
2. Indumentum	6	4–18	0.86	2 = pubescent / puberulous / sericeous	1 = sparse / not pubescent; 3 = hirsute / strigose / pilose	2→3→1; glabrous from S. pulcher on.
3. Lenticels	7	2–9	0.29	2 = wart-like	1 = not conspicuous / small; 3 = elongated	synapo. for S., B., M.; a few rev., a few par. to state 3.
4. Exudate	10	3–16	0.46	2 = absent	1 = present	synapo. for S., B., M.; later rev. in S.
5. Bark	8	3–15	0.58	2 = with ridges / wrinkles	1 = smooth	some par. within S., after S. oblongifolius all state 1.
6. Ultrajugal part of the rachis	4	2–4	0.00	2 = ultrajugal part more than 1/10	1 = less than 1/10 of the rachis / no ultrajugal part	parallel in a few species.
7. Stipules	6	2–7	0.20	2 = not recurving	1 = recurving	synapo. B. and S.; early rev. in S. and also for M.
8. Stipules	5	1–5	0.00	1 = (early) caducous	2 = more or less persistent	a few parallelisms.
(9) Stipules symmetrical	1	1	0.00	1 = yes	2 = no (asymmetrical)	not informative.
10. Stipules nerves	6	1–12	0.55	2 = no visible nerves	1 = nerves visible	synapo. for S. after S. suberectus; M. buteiformis and S. auritus par.
11. Stipules indumentum	2	1–7	0.83	2 = hairy	1 = glabrous / glabrescent	synapo. after S. macropterus-clade; rev. after S. maingayi-clade.
12. Stipule length	7	2–9	0.29	2 = 2 or 3 times as long as wide	1 = as long as wide; 3 = 4 or more times as long as wide	most species ples.; some either state 1 or state 3.
13. Pulvinus colur	4	2–8	0.67	2 = same colour as rachis	1 = black / darker than rachis	the same as character 11, some more par.
14. Pulvinus indumentum	10	2–20	0.56	2 = pubescent / hirsute	1 = glabrous / glabrescent / sparsely hairy; 3 = densely pubescent / strigose	2→3→1; more glabrous after S. potingeri; also rev.
15. Stipellae caducous	6	1–7	0.17	1 = (early) caducous	2 = more or less persistent	most ples., a few apo., including S. harmandii-clade.
16. Stipellae length	4	3–6	0.67	1 = up to the length of the petiolule	2 = conspicuously longer than the petiolule	a few apo., most within S. ferrugineus-clade.
17. Upper surface colour	7	3–9	0.33	1 = green / brownish (dried colour)	2 = greyish blue (glaucous)	most ples., a few apo., including S. harmandii-clade.
18. Lower surface colour	6	1–9	0.38	1 = green / brownish (dried colour)	2 = always brown	idem.
19. Upper surface indumentum	5	4–5	0.00	1 = glabrous to sparsely pubescent	2 = pubescent (dense); 3 = sericeous; 4 = hirsute / strigose	synapo. for B. and M.
20. Lower surface indumentum	11	8–21	0.77	2 = pubescent (dense)	1 = glabrous to sparsely pubescent; 3 = sericeous; 4 = hirsute / strigose	2→4→1 or 2→3: synapo. after S. pulcher for state 1.

(Table 2.3 continued)

Character	Steps	Min/Max	RI	Plesiomorphic state	Apomorphic state	Remarks
21. Shape of top leaflet	10	4-15	0.45	1 = only elliptic	2 = ovate to elliptic; 3 = obovate to elliptic	1→2→3→1; state 2 synapo. for *S.*, *B.* and *M.*, later to 3; rev. to 1 after *S. pulcher.*
22. Apex leaflet	17	8-24	0.44	2 = acuminate / cuspidate	1 = acute; 3 = emarginate / rounded; 4 = abruptly acuminate	many polymorphisms, state 1 after *S. suberectus.*
23. Base leaflet	6	5-6	0.00	1 = acute / obtuse / subcordate	2 = decurrent	only apo. for *B.*, *M.* and *S. oblongifolius.*
24. Lateral leaflet symmetrical	4	1-12	0.73	1 = more or less symmetrical	2 = strongly asymmetrical	synapo. for *S.*, *B.* and *M.*; rev. in *S.* after *S. suberectus* and in the *S. ferrugineus*-clade.
25. Main nerve	10	4-12	0.25	1 = sunken or flat	2 = raised	synapo. for *S.*, *B.* and *M.*; some rev. later.
26. Secondary nerves at upper surface	4	1-6	0.40	1 = flat	2 = raised	synapo. for *S.*, *B.* and *M.*; rev. from *S. pulcher* on and within the *S. ferrugineus*-clade.
27. Nerves at lower surface	9	3-19	0.63	2 = midrib and secondary nerves prominent	1 = only midrib prominent; 3 = venation also prominent	2→3→2→1; synapo. for state 3 in *S.*, *B.* and *M.*, later in *S.* rev. to 2, and in top apo. state 1.
28. Venation	8	5-16	0.73	2 = reticulate-scalariform	3 = scalariform; 1 = reticulate	2→3 and 2→1; state 3 synapo. for *S. suberectus*, *B.* and *M.*; state 1 synapo. after *S. pottingeri*, par. within the *S. ferrugineus*-clade.
29. Angle secondary nerves with midrib (average)	7	1-12	0.45	1 = up to 45°	2 = more than 45°	synapo. for top after *S. maingayi*-clade, a few par.
30. Secondary nerves terminate	5	2-10	0.63	1 = diffusely	2 = in the margin; 3 = forming marginal arches	state 2 synapo. for *B.* and *M.*, par. with *S. ferrugineus*, state 3 a few species in *S.*
31. Pairs of secondary nerves (average)	9	1-15	0.43	1 = 5–8	2 = more than 8	apo. for *S.*, but rev. after *S. pottingeri.*
32. Place of inflorescence	1	1-2	1.00	1 = axillary / terminally	2 = terminally	synapo. for *M.*
33. Indumentum of inflorescence	9	5-10	0.20	1 = puberulous / pubescent	2 = hirsute / sericeous; 3 = (nearly) glabrous	state 2 in part of *S.*, state 3 autapo. for *S. maingayi.*
34. Number of branches	7	4-11	0.57	2 = main axis with secondary and tertiary branches / fascicles	1 = main axis with (secondary) side branches / fascicles; 3 = main axis with secondary, tertiary and quaternary branches / fascicles	state 2 for *B.* and *M.* and a few *S.*; state 3 for *S. parviflorus* and *S. ferrugineus* p. p.
35. Brachyblasts	13	5-16	0.27	2 = absent, flowers solitary	1 = present	synapo. for *S.*, *B.* and *M.*; later rev. after *S. pottingeri.*
36. Number of bracts of the first order (= secondary) side branch	6	1-9	0.38	2 = two bracts	1 = one bract	apo. for a few species in *S.*
(37) Shape of the bracts	11	4-11	0.00	2 = triangular	1 = linear; 3 = broadly ovate; 4 = elliptic, surrounding the bud	left out of analysis.

(Table 2.3 continued)

Character	Steps	Min/Max	RI	Plesiomorphic state	Apomorphic state	Remarks
38. Number of bracts of the tertiary branch / flower	4	1-4	0.00	1 = one bract	2 = two bracts	most ples., apo. only basal Asian species in S.
39. Length of the pedicel	3	2-3	0.00	1 = very short, up to 1 mm; flower nearly sessile	2 = pedicel > 1 mm; flower not nearly sessile	synapo. for S., B. and M.; ples. S. sanguineus / S. gyrocarpus.
40. Place of the bracteoles	10	5-15	0.50	1 = immediately below the calyx	2 = on the upper half of the pedicel 3 = on the lower half of the pedicel	synapo. from S. suberectus on, state 3 only S. acuminatus and S. latibractea.
41. Indumentum of the calyx	4	2-6	0.50	2 = pubescent / sericeous	1 = sparsely pubescent / nearly glabrous 3 = hirsute	both apo. and par. in small groups.
42. Top of the vexillary lobe	13	7-16	0.33	equivocal	1 = emarginate 2 = not emarginate	only in S. state 1 ples.
43. Length of the vexillary lobe	9	4-16	0.58	2 = about half the length of the cup	1 = as long as the cup 3 = less than half the length of the cup	both apomorphic states present in but a few small groups.
(44) Shape of the other calyx lobes	12	3-13	0.10	3 = more or less rhomboid	1 = triangular 2 = truncate / somewhat rounded 4 = with a rounded apex	left out of analysis.
45. Indumentum on standard	1	1-4	1.00	2 = absent	1 = present	synapo. for B. and M.
46. Apex of the standard	1	1-6	1.00	2 = not emarginate	1 = emarginate	synapo. for S. after S. parviflorus.
47. Standard with auricles	3	3-4	1.00	2 = absent	1 = present	synapo. for M.
48. Base of the standard blade	11	5-18	0.54	2 = truncate	1 = decurrent into the claw	synapo. for S. after S. parviflorus; later rev. in tree and top S. ferrugineus-clade.
49. Dorsal auricle on wing	8	2-8	0.00	1 = present	2 = absent	par. in a few species of S.
50. Ventral auricle on wing	5	1-5	0.00	2 = absent	1 = present	idem.
51. Wing with lateral pocket	5	1-5	0.00	1 = present	2 = absent	idem.
52. Wing with indumentum outside	4	2-9	0.71	1 = present	2 = absent	synapo. for S., with a few rev.
53. Wing with indumentum inside	2	1-3	0.50	2 = absent	1 = present	synapo. for B. and M.
54. Wing with indumentum on dorsal auricle/margin	5	1-6	0.20	1 = present	2 = absent	synpo. for all except B. and some species of S.
55. Wing with indumentum on ventral auricle/margin	7	3-13	0.60	1 = present	2 = absent	synpo. for S., some rev. later.
56. Keel with a dorsal auricle	14	6-18	0.33	1 - present	2 = absent	par. in B., M., S. pulcher and top S. ferrugineus-clade.
(57) Keel with a ventral auricle				1 = present	2 = absent	left out of analysis.
58. Keel with a lateral pocket	4	1-7	0.50	1 = present	2 = absent	par. in a few species, including S. maingayi-clade.

(Table 2.3 continued)

Character	Steps	Min/Max	RI	Plesiomorphic state	Apomorphic state	Remarks
59. Keel with indumentum outside	2	2–6	1.00	1 = present	2 = absent	synpo. S.
60. Keel with indumentum inside	2	1–2	0.00	2 = absent	1 = present	only in B. superba and M. buteiformis.
61. Keel with indumentum on dorsal auricle/margin	3	1–4	0.33	1 = present	2 = absent	synapo. for all except B. and S. latibractea.
62. Keel with indumentum on ventral auricle/margin	1	1–5	1.00	1 = present	2 = absent	synpo. for S.
(64) Vexillary filament	1	1	0.00	2 = connate to the claw of the standard	1 = free	uninformative.
65. Filaments connate for	9	4–18	0.64	3 = more than half, but less than 3/4 of their length	1 = less than half of their length; 2 = more than 3/4 of their length	par. after S. oblongifolius and the S. ferrugineus-clade.
66. Indumentum on filament sheath	2	2–5	1.00	1 = absent	2 = present	synapo. for B. and M.
67. Size of the anthers	5	3–11	0.75	1 = less than 0.5 mm	2 = more than 0.5 mm, but less than 1 mm; 3 = more than 1 mm, but less than 2 mm; 4 = more than 2 mm	par. in S. maingayi-clade and S. aurius, S. persicinus and S. latibractea; states 3 & 4 synapo. for B. and M.
68. Anthers	5	2–5	0.00	2 = fertile and alternately larger and smaller	1 = fertile and equal; 3 = alternately fertile and sterile	state 1 synapo. for all; state 3 par. in a few basal species.
69. Nectary glands	6	3–11	0.63	4 = 10 thickened filament bases	1 = 10; 2 = 5, all equal; 3 = connate, no separate lobes	state 1 synapo. for S., state 2 par. in S. purpureus and S. pulcher, state 3 autapo. in S. suberectus.
70. Nectary with indum.	5	3–7	0.50	1 = absent	2 = present	par. in just a few species of S.
71. Indumentum of the ovary	15	3–18	0.20	2 = very densely pubescent / woolly	1 = pubescent / sericeous; 3 = sparsely hairy	synapo. for S., with many rev., and some species with state 3.
72. Indumentum on the style	10	2–16	0.43	2 = at the base	1 = up to halfway; 3 = up to at least 3/4	most ples., some state 1 or 3 par.
73. Number of ovules	2	2–3	1.00	1 = 2	2 = 2–4; 3 = more than 4	state 2 autapo. for S. pulcher, state 3 synapo. for B.
74. Place of the ovules	6	2–8	0.33	1 = basal	2 = in the middle / apical	synapo. for B., M. and S.
75. Stipe of ovary present	8	1–13	0.42	2 = yes	1 = no	most ples., some par. state 1.
(76) Stigma	14	5–18	0.31	2 = capitate	1 = flat; 3 = elongated	left out of analysis.
77. Stipe of pod exceeding calyx	6	3–8	0.40	2 = no	1 = yes	par. in B., S. parviflorus, S. suberectus and S. harmandii-clade.
78. Top of the pod	7	2–11	0.44	2 = with the style remnant pointing	3 = with the style remnant bent downwards; 1 = with the style remnant bent upwards	2–3→1; synapo. from S. oblongifolius on, par. with top of S. ferrugineus-clade; par. in S. acuminatus-clade and S. macropterus state 1.

(Table 2.3 continued)

Character	Steps	Min/Max	RI	Plesiomorphic state	Apomorphic state	Remarks
79. Shape of the wing	5	1–8	0.43	1 = straight, as narrow as the seed-bearing part	2 = wider than the seed-bearing part	synapo. for all, but top tree and *M.* rev.
80. Indumentum of pod	3	1–12	0.82	2 = densely pubescent	1 = puberulous or nearly glabrous	synapo. for *S.* after *S. suberectus*.
(81) Hair base	15	14–19	0.31	1 = basal cell not in palisade layer	2 = basal cell in palisade layer	left out of analysis.
82. Bulbous septate hair base	3	2–6	0.75	1 = absent	2 = present	synapo. for *S.* / rev. for *S. pulcher*.
(83) Glandular hair	2	2	0.00	2 = stalk 2–5, head 4–8 cells	1 = stalk 1–2, head 2–6 cells; 3 = head cup-shaped	uninformative.
84. Epidermis lower surface	10	7–11	0.25	3 = undulate	1 = straight; 2 = curved cell walls; 4 = strongly undulate	state 2 par. in *B.*, *M.* and *S. pulcher*; state 4 synapo. for *S. harmandii*-clade.
(85) Hypodermis	7	7	0.00	1 = absent; 2 = only near larger veins	3 = present throughout leaves	left out of analysis.
86. Stomata adaxial	9	5–17	0.67	1 = absent	2 = present	par. in *S.* after *S. suberectus* and in top *S. ferrugineus*-clade.
(87) Vascular bundle in midrib	5	5	0.00	1 = open	2 = closed / semi-closed	left out of analysis.
88. Veins transcurrent	12	9–19	0.70	2 = present	1 = absent (smaller veins palisade layer continuous)	synapo. for *S.* after *S. oblongifolius*, a few earlier par.
89. Tannin (?) containing cell layer between phloem and xylem	10	4–20	0.63	1 = present	2 = absent; 3 = in xylem itself	$1 \to 3 \to 2$; synapo. for *S.*, some rev.; state 2 par. in top tree and *S. ferrugineus*-clade.
90. Tannin in bundle sheath	5	1–7	0.33	2 = absent	1 = present	par. in a few species of *S.*
91. Ornamentation pollen	13	12–13	0.00	1 = closed ornamentation (rugulate, psilate-perforate, fossulate)	2 = microreticulate / coarse perforate; 3 = verrucate	par. in *B.*, *M.*, *S. maingayi*-clade; *S. latibractea* and *S. persicinus* polymorphic.
92. Fused colpi	5	2–13	0.73	1 = absent	2 = yes, sometimes; 3 = often	synapo. after *S. oblongifolius*, some have state 3.
93. Foot layer / endexine ratio	8	2–10	0.25	1 = more than 0.6	2 = less than 0.6 and more than 0.1; 3 = less than 0.1	state 2 synapo. for *S.*, with some rev.; state 3 par. in *M.* and *S. parviflorus*.
94. Colpus ends	6	5–9	0.75	1 = acute	2 = obtuse	synapo. for *B.*, *M.*, par. with *S. auritus*.
95. Mesocolpial pouches	3	1–6	0.60	1 = present	2 = absent	synapo. for *B.*, *M.*, *S. parviflorus*, par. with *S. auritus*.
96. Infratectal layer	32	30–34	0.50	2 = irregular (short) columellae	1 = well-spaced columellae; 3 = granules; 4 = indistinct / dense	many polymorphisms, after *S. oblongifolius* state 3 better represented.
97. A/E	11	2–17	0.40	3 = mean > 0.4	1 = mean < 0.28, max ≤ 0.31; 2 = 0.28 ≤ mean < 0.4	$3 \to 2 \to 1$; synapo. state 2 for all, with rev. to state 3 (among others *M.*); after *S. oblongifolius* state 1.

APPENDIX

For the study of the leaf anatomy, the following material was used
(from L, unless stated otherwise)

Butea monosperma: Backer 3424, 16773, 26695 (all Java), Chevalier 31338 (Viet-
   nam, P), Dickason 6939 (Myanmar), Jacobs 4920 (Java), Kostermans 24393, 28597
   (both Sri Lanka), Magnen, Gourgand, Châtillon s.n. (Cambodia), Teijsmann 1867
   (Hort. Bog.), Thwaites 1465 (Sri Lanka, K).
Butea superba: Poilane 12288 (Vietnam), 14959 (Cambodia) (both P).
Meizotropis buteiformis: L herbarium sheet nr. 908.112-159, Griffith K.D. 1679 (East
   Bengal), Koelz 28394, 28408 (both India).
Kunstleria curtisii: KL 3428 (T & P 828) (Malay Peninsula).
Kunstleria forbesii: Elmer 13105 (Philippines, K), 21322 (Borneo), 21605 (Borneo),
   Forbes 3241 (Sumatra), Meijer 2256 (Borneo), SAN 37083, 39227, 89034, 89128
   (all Borneo).
Kunstleria geesinkii: SAN 31574, 52944, 54866 (all Borneo, K).
Kunstleria kingii: FRI 13056 (Malay Peninsula, K), King's collector 3830 (Malay
   Peninsula, K).
Kunstleria philippinensis: BS 16144 (Philippines, US), Wenzel 818 (Philippines, US).
Kunstleria ridleyi: Elmer 21494 (Borneo), FRI 8360, 10518, 16919 (all Malay Penin-
   sula), Hort. Bog. XVII.F.13, XVII.F.36, Kostermans 6569 (Borneo), Maingay
   1168 (K.D.609) (Malay Peninsula), NBFD 4905 (Borneo), Niga Nangkat NN 193
   (Borneo), S 15769 (Borneo).
Kunstleria sarawakensis: S 18036 (Borneo).
Spatholobus acuminatus: Lace 3033 (Myanmar, K), Langlassé 507 (Singapore, P),
   Maxwell 75-197 (Thailand), Wallich 5443 (India, K).
Spatholobus albus: S 23683, 32206, 32363, 32829 (all Borneo).
Spatholobus apoensis: Elmer 11795, 13300 (both Philippines).
Spatholobus auricomus: S 22446, 22517, 23063 (all Borneo).
Spatholobus crassifolius: Griffith 1826 (India, K).
Spatholobus dubius: Curtis s.n., April 1893 (Singapore, K).
Spatholobus ferrugineus: van Balgooy 3977 (Sulawesi), Blume s.n., 1284 (both Java),
   Boerlage s.n. (Java), Elsener H88 (Borneo), Hallier 1382 (Borneo), Maingay 530
   (Malay Peninsula), Schiffner 2188 (Java), SF 40687 (Singapore), Teijsmann s.n.
   (Sumatra), de Vriese 66 (Borneo), Wiriadinata 3530, 3596 (both Borneo).
Spatholobus gyrocarpus: KL 2758, 3392 (both Malay Peninsula), Maxwell 86-530
   (Thailand).
Spatholobus harmandii: BKF s.n. (Sangkhachand 238) (Thailand), F.C. How 72999
   (Hainan, P), Lei 80 (Hainan), Maxwell 71-733 (Thailand), Pierre s.n., July 1866
   (Vietnam), Poilane 11856 (Laos, P), 19757 (Vietnam, P), SF 23060 (Henderson)
   (Malay Peninsula, K), Tsang, Wai-Tak 288 (Hainan, P).
Spatholobus hirsutus: Endert 5162 (Borneo), Kato & Wiriadinata B.7001 (E Borneo),
   Kostermans 13652 (Borneo), Mogea 4085 (Borneo), Nieuwenhuis 948, 1079, 1440,
   1444 (all Borneo), S 41420 (Borneo), SAN 76943 (Borneo).

Spatholobus latibractea: SAN 97466 (Borneo).

Spatholobus latistipulus: Elmer 21439 (Borneo), SAN 65877 (Borneo), Wiriadinata 3397 (Borneo).

Spatholobus littoralis: Backer 10099, 11016, 17061 (all Java), Blume s.n., 1723(?) (both Java), BS 28217, 30947 (both Philippines), Junghuhn 259 (Java), de Voogd 526 (Sumatra, BO), Winckel 325b, 488b (both Java).

Spatholobus macropterus: BRUN (Ashton) 3320 (Borneo), Elmer 21175 (Borneo), Forbes 3243 (Sumatra), FRI 10529 (Malay Peninsula), Kostermans 6872 (Borneo), Meijer 2508 (Borneo), PNH 23077 (Philippines), SAN 16421, 18841, 22567, 31293, 66164, 67684, 89836, 97576 (all Borneo).

Spatholobus maingayi: Elmer 17642 (Philippines), FRI 8373 (Malay Peninsula), PNH 2911 (Philippines), SAN 30594, 34322, 76900 (all Borneo), Santos 4064 (Philippines).

Spatholobus multiflorus: S 32370 (Borneo), SAN 91834, 96975, 110486 (all Borneo).

Spatholobus oblongifolius: Clemens 26354 (Borneo), Kostermans 13688 (Borneo), SAN 19832, 27454, 50481, 55708, 97669, 99420, 117192 (all Borneo).

Spatholobus parviflorus: Beusekom et al. 3607 (Thailand), BKF 37911 (Thailand), Hort. Bog. XVIII.D.23 (India), Kostermans 1171 (Thailand), Larsen et al. 31677 (Thailand), Maxwell 74-746 (Thailand), Murata T-17277 (Thailand), Pierre s.n. (Vietnam), Smitinand 4815 (Thailand).

Spatholobus persicinus: Endert 5410 (Borneo, BO), Kostermans 7108 (Borneo), Motley 734 (Borneo, K), Nooteboom 4374 (Borneo).

Spatholobus pottingeri: BKF 37401 (Thailand), Poilane 20366 (Laos, P), Thakur Rup Chand 6853a (India).

Spatholobus pulcher: Henry 12780B (China).

Spatholobus purpureus: Ridsdale 611 (India).

Spatholobus ridleyi: Forbes 3195 (Sumatra), Ridley 6401 (Singapore, K).

Spatholobus sanguineus: Elmer 17984, 18250 (both Philippines), Kostermans 21244 (Borneo), SAN 32504, 74457, 88852 (all Borneo), Wenzel 989 (Philippines).

Spatholobus suberectus: Poilane 15432 (Laos, P), 15870 (Laos, K), 25579 (Vietnam, P).

Spatholobus viridis: Kostermans 6586, 21654 (both Borneo), Meijer 2458 (Borneo, BO), SAN 97423, 110263 (both Borneo).

Chapter 3

OVERVIEW OF THE GEOLOGICAL HISTORY
OF SOUTHEAST ASIA

INTRODUCTION

In a historical biogeographical study the first question that comes to mind relates to the origin of the species. As De Jong (1987) stated: "What are the present-day ecological factors, and what are the historical ones? The range of a species can be changed actively by the organisms themselves or by external factors such as geographical or geological ones."

I think it is unsatisfactory to rely on the outcome of the analyses of area cladograms – based on the phylogeny and distribution of extant taxa – without some knowledge of the geology in the region. The area cladograms will probably indicate a common distribution pattern, but this does not explain the cause of that pattern. In historical biogeography the main assumption is that such a common pattern in distribution of different groups of organisms is related to geological or geographical (vicariant) events. These events may have caused isolation of species or an enlargement of the area. It is important, however, to specify the age and impact of the geological events before assigning them a role in the speciation of the groups studied. Whitmore (1981), e.g., states that, although the warm Tertiary climate influenced the flora and fauna in the Malay Archipelago, the most important climatic changes are those of the last two Ma. As an example of an ancient pattern, he cites the distribution of monsoon climate plant species, which have a very wide but disjunct distribution. This still reflects the more continuous range of distribution that was caused by a more seasonal climate in the now everwet parts in the past (for distribution patterns see also Van Steenis, 1961, 1979).

To get some idea about the geological history of Southeast Asia, it is necessary to study its fossil record, its palaeoclimatology, and its palaeogeography. A synthesis of the outcome of the cladistic analysis and the geological information may yield a reconstruction of the historical development of the distribution of the present day taxa.

This overview is based on literature, which is cited in the text. The part on the geology is a summary (and synthesis) of several articles and books of Hamilton (1973, 1979, 1988), Hutchison (1989a, 1989b, 1992, 1996), and Metcalfe (1988, 1990, 1991, 1994a, 1994b, 1996). These are mostly not cited individually to avoid a text unreadable by the amount of citations. Additional literature is cited separately. The overview presented here is restricted to the region of occurrence of the genera *Spatholobus*, *Butea*, *Meizotropis* and *Kunstleria*: Southeast Asia (from the Himalayas and Yunnan to southern India and Indochina), and the western Malesian Archipelago (including Sulawesi and the Philippines) (Fig. 3.1). In Table 3.1 some of the characteristics of each period and some of the tectonic events are listed.
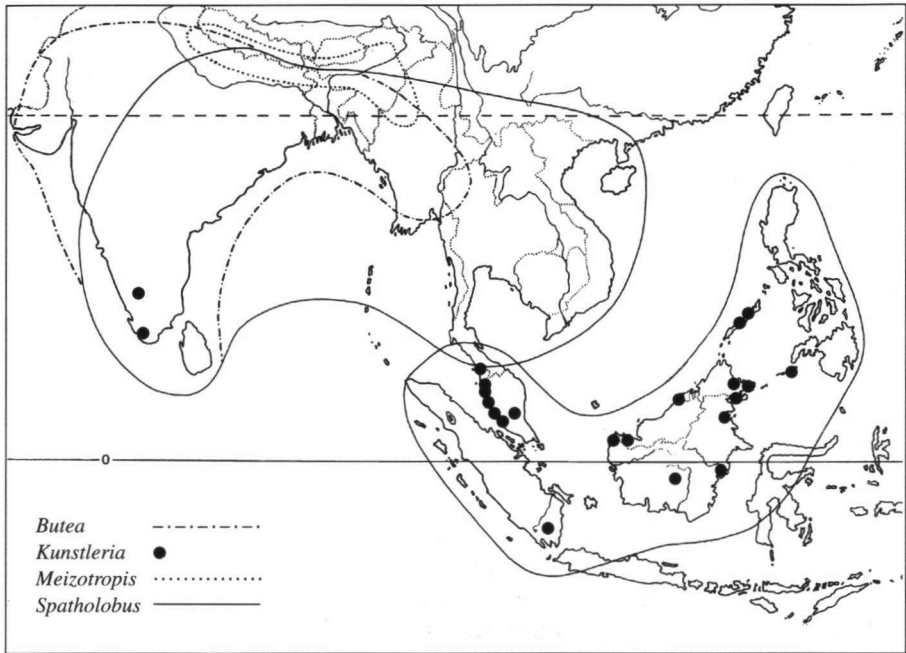
Figure 3.1. Map of Southeast Asia and the West Malesian Archipelago showing the distribution of the genera *Butea, Kunstleria, Meizotropis,* and *Spatholobus.*

FOSSIL EVIDENCE OF LEGUMINOSAE IN SOUTHEAST ASIA

The first angiosperms probably appeared in the Southeast Asian region in the Early Cretaceous (Wing & Sues, 1992). They already had undergone significant diversification in the lower latitudes, but were generally still rare or absent in mid- and higher latitudes. During the Late Cretaceous, the number of angiosperms increased considerably, and by the end of that epoch 50% to 80% of the vascular plant species were flowering plants. In the opinion of Wing and Sues the early angiosperms probably were weedy plants or small trees that flourished in disturbed settings or undergrowth of forests dominated by large coniferous trees. During the Early Eocene angiosperm-dominated forest was at the height of its distribution, subtropical forest may have reached up to 60° N and tropical rain forest occurred as far north as 30° N.

On account of the presumed unlikelihood of long dispersal occurring in many disjunct genera, Walker (1982) states that angiosperms must already have been in existence since the Late Jurassic (135 Ma). However, there is no fossil evidence for this. He suggests that *Kingiodendron* (Leguminosae), a genus with a very disjunct distribution from India over the Philippines into Fiji, might be an example of this.

Raven and Polhill (1981) mention the Maastrichtian (Upper Cretaceous) as being where the first records of the Leguminosae (both pollen and macrofossils) were found. The Upper Cretaceous records of fossil wood and pollen are regarded as unreliable by

Table 3.1. Schematic overview of geological events in relation to Southeast Asia.

Time	Events	Sea level / Climate	Fossils / Flora
Palaeozoic (600–225 Ma).	SE Asia part of Gondwanaland (northern Australia).		
Silurian/Ordovician or Carboniferous (Upper lower Palaeozoic, 500–400 Ma or up to 280 Ma).	Blocks (Yangzi, Phu Hoat, North China and South China (Metcalfe), Indochina/Eastern Malaya, West Borneo Basement) rifting away from Gondwana in sets. *Burrett: this event in Cambrian (600–500 Ma).*		
Early Carboniferous (340 Ma).	South China welded with Indochina/East Malaya to form Cathaysialand. Blocks are in equatorial part. Still close to Gondwana are Lhasa, Himalaya, Shillong, Indian platform, Burma Plate, Sinoburmalaya (Sibumasu), Shan-Tai.		Cathaysian flora (not glacial) for the equatorial blocks, the other blocks remained under influence of Gondwanaland in Carbo-Permian times, including glaciation.
Early Permian (270 Ma).	Rifting of Cimmerian continent off Gondwana (among others Sibumasu).		
Late Permian/Early Triassic (240–220 Ma).	Collision of Sinoburmalaya (Sibumasu) with Asia (and Indosinia).	Up to now Eurasian Plate marine.	
Triassic (225–195 Ma).	North China welded with Cathaysia. Burman Plate present as island arc in front of future Southeast Asia.		
Early Jurassic (195 Ma).	*Acc. to Audley-Charles, rifting of Tibet, Burma, Thailand, Malaya, Sumatra.* Opening of Proto-South China Sea and rifting of West Borneo from Indosinia. Separation of India from Gondwanaland.	Eurasian Plate above sea level.	
Mid-Jurassic.	Western Burman Plate collided with Asian Plate. Closure of Tethys Ocean. East margin of China volcanic arc up to Indosinia.		

(Table 3.1 continued)

Time	Events	Sea level / Climate	Fossils / Flora
Late Jurassic.	*Acc. to Audley-Charles collision of blocks mentioned above with Asia.*		
Cretaceous (135–65 Ma).	Burman Plate was island arc on the Asian margin. *Burrett 1990: South Sumatra and South Kalimantan still close to Australia.*		
Late Cretaceous.	Collision of Burman Plate with Asia (Shan states). Arrival of Woyla terranes Sumatra.	Sea level up to +350 m.	First records of Leguminosae (Raven & Polhill, 1981) unreliable records for India and China.
Early Tertiary (65 Ma onwards).	Oceanic crust Philippine Sea Basin began forming at the southern boundary of the Pacific Plate.		
Palaeocene (65–54 Ma).	Opening of the Makassar Basin; West Sulawesi rifting off SE Borneo. Deltas (Baram, Tarakan) develop. Formation of sediments of Northwest Borneo Geosyncline (Rajang group). Borneo south and southeast of Rajang group form landmass together with West Sulawesi and Java Sea.	Tropical monsoon. Episodes of lower sea levels.	Fossils indicating presence of Caesalpinioideae and Mimosoideae (Herendeen et al. 1992).
Early Eocene (53 Ma).	Indian collision and subduction below Burma (uplift of Indo-Burman Ranges). Spreading after separation of Australia from Antarctica. Start of subduction of Australian Plate in Sunda Trench. *Burrett, 1990: collision of S Sumatra and S Kalimantan with SE Asia.* Final collision Indian Plate with Eurasia (Himalaya). Philippine Sea Basin rotate clockwise and drift northward.		
Middle Eocene.		Tropical monsoon episodes of lower sea level.	All three subfamilies are represented in fossil record.
Late Eocene (45 Ma).			

(Table 3.1 continued)

Time	Events	Sea level / Climate	Fossils / Flora
Oligocene (38–26 Ma).	Opening of the South China Sea (32–17 Ma); rifting of blocks towards Borneo from Chinese margin. South China Sea. Start of rift of fragments of Chinese continental margin.	Wet tropical monsoon or tropical rain forest. Sea level fall of –250 m (Late Oligocene).	Legume species known from Yunnan and India.
Miocene (26–7 Ma).	Java becomes part of the active plate margin. Spreading in Philippine Sea Basin ceased 26 Ma.	Tropical monsoon.	Fossils identified up to generic level in China and India. Migration from Legumes into India from Africa and South-
Middle Miocene.	Opening of Andaman Sea (13 Ma) as result of the rotation of the Malay Peninsula. End of spreading activity in South China Sea by collision of Palawan with West Philippines block. Volcanic arc in N Sulawesi active (east facing before rotating later). Collision of Banggai-Sula with Sulawesi Trench.	Mid-Miocene sea level changes in three stages to +220 m. Tropical monsoon.	east Asia well documented (Awashti, 1992). Legumes dominant in India.
Late Miocene-Pliocene.	Volcanic arc active in Philippines. Uplift of Meratus Mts and Semitau Range (other mountains Cretaceous). Collision of Australian continental shelf with Timor.		
Pliocene (7–2 Ma).		Sea level rise to +140 m.	Fossil record more scanty (drier period/lack of studies).
Pleistocene.		Many glacial periods.	

Herendeen et al. (1992), because they cannot unequivocally be assigned to the Leguminosae (see also Wheeler & Baas, 1992). The Palaeocene fossils (pollen as well as fruit and wood) are more informative, however, and suggest the presence of Caesalpinioideae and Mimosoideae. In the Eocene both subfamilies were abundant. The origin of the Papilionoideae is unknown, but by the Middle Eocene they were diverse. From the Middle Eocene onwards all three subfamilies are represented.

Modern legume groups originated by the end of the Cretaceous, when Eurasia was still in contact with Africa, and there were still overland connections between North America and Europe (Raven & Polhill, 1981). These authors suggest that Africa has been a prime area for the early radiation and evolution of Leguminosae, based on both the geographical relationships and the common occurrence of many legumes in moist and dry forests in Africa. They explain the relatively poor fossil record of Eurasia and the less abundant current occurrence in tropical Asia (as opposed to that of Africa, Madagascar and Latin America) by the existence of a post-Palaeocene water barrier between Africa and Eurasia. Later, when exchange was possible, difficulties in penetrating forests containing competitive groups may have prohibited further migration.

Probably due to climatic factors several taxa were more widespread than they are today. The limited fossil record in New Zealand, Australia, China and India, however, may indicate that these areas were reached relatively late (Herendeen et al., 1992; Polhill & Raven, 1981). Fossil data as well as data from extant taxa indicate that the family has had a long evolutionary history in tropical America and Africa/Madagascar. Despite water barriers, there has been a floristic exchange between Africa/Madagascar and the Americas, between Africa and Europe, and between South and North America.

A tropical North American origin has been assigned to the Papilionoideae by Lavin (1995). During the Early Tertiary they could have spread out over North America and Eurasia before both continents were separated. The latter suggestion, also known as the Boreotropics hypothesis (Lavin & Luckow, 1993), more readily explains the occurrence of relatives in Southeast Asia, Africa and South America than by direct exchanges (e.g., between South America and Africa) (Fig. 3.2). In addition, the hypothesis satisfactorily explains the occurrence of fossils in southeastern North America, whose closest relatives are living in tropical South America (Herendeen et al., 1992). The disjunct occurrence of the closely allied Southeast Asian genera *Derris* and "American *Derris*" (*lonchocarpus*) (Geesink, 1984) may be explained by this theory as well.

In China and India reliable fossil records of the Leguminosae extend as far back as the Eocene (Guo & Zhou, 1992; Awasthi, 1992); from the Late Cretaceous there are a few unreliable records only from both China and India. There are two legume species known from the Oligocene of Yunnan. Leguminosae are well represented, however, in the Miocene fossil record throughout China, and have often been identified up to generic level (e.g., *Dalbergia, Desmodium, Gleditsia, Pueraria, Sophora*). Probably due to a lack of comprehensive studies little is known from the Pliocene and Quaternary of China.
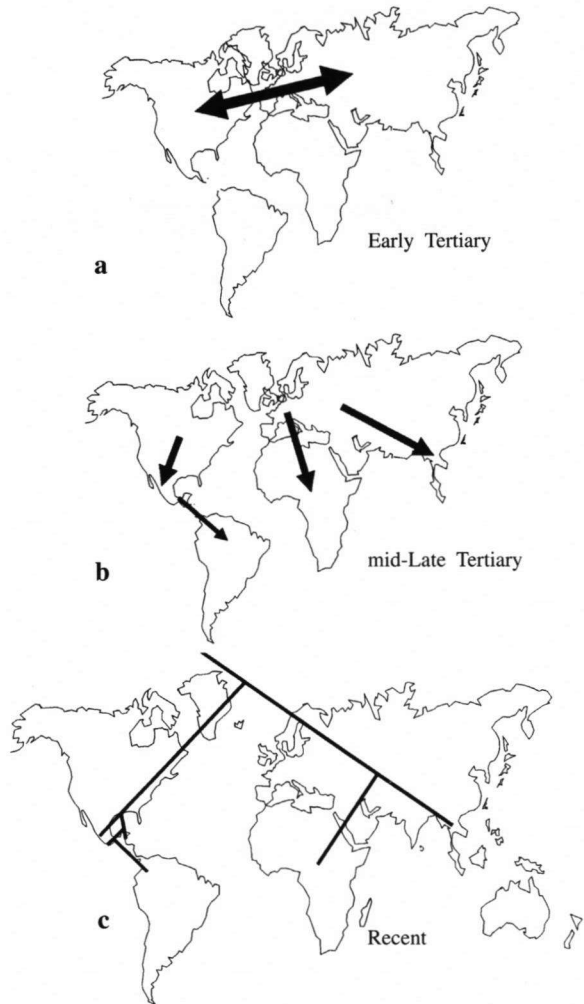
Figure 3.2. Maps illustrating the Boreotropics hypothesis (after Lavin, 1995).

a: Arrow suggesting direct interchange of tropical biotas during the Early Tertiary.

b: Arrows suggesting movement of Early Tertiary northern tropical elements with the onset of mid-Tertiary climatic cooling and separation of the North Atlantic.

c: 'Area cladogram' of present-day remnants of Early Tertiary north tropical groups predicted by the Boreotropics hypothesis.

In northeastern India legumes are present in the fossil flora since the Late Palaeocene. During the Oligocene and Early Miocene they are also found throughout peninsular India. Migration of legumes into India from Africa (indirect) and Southeast Asia, and *vice versa*, is well documented since the Miocene. By the Middle Miocene legumes were dominant in India. They reached a maximum diversity and were one of the major components of the tropical evergreen forest. By the end of the Pliocene, as the climate became drier, the tropical evergreen forest diminished and many taxa became extinct. Some taxa survived, however, in the evergreen forests that remained in the Western Ghats and northeastern India. The deciduous legumes living today in India may be regarded as the result of adaptations to a drier climate.

CLIMATE

During the Mesozoic-Early Cenozoic, annual rainfall was relatively high at the mid-latitudes. The equatorial region, however, was drier, and characterised by higher temperatures and light levels (Wing & Sues, 1992). The temperature reached peak values during the Early Eocene. A cooling and drying trend followed during the mid-Oligocene transgression. From the Early Miocene on the climate was warmer again, but the overall trend during the Late Cenozoic is a cooler and drier climate, although this has alternated with warmer temperatures. A decline in temperature after the mid-Miocene (13 Ma) is associated with a retreat of the palaeotropic flora and expansion of deciduous forests and grasslands (Potts & Behrensmeyer, 1992).

During the Tertiary and Quaternary, climatic pulses of temperature resulted in an expansion of new unexplored environments. This led to an increase in the diversity of Leguminosae from drier environments (with many herbaceous Papilionoideae) to tropical regions (rich in Caesalpinioideae, Mimosoideae and woody Papilionoideae). Processes that indirectly affected the climate are plate tectonics, mountain building, glaciation and sea level changes, and volcanism. The tropical region became progressively warmer and drier during the Miocene (Axelrod, 1992), resulting in the growth of savannahs and grassland in which tropical legume species could adapt to drier conditions.

During the periods with a drier climate, the evergreen forests were restricted to only certain parts of India. The species were forced to adapt to drier conditions or disappear (Awasthi, 1992). The South China Sea region, Borneo, and Brunei became more seasonal (Morley & Flenley, 1987; Van Steenis, 1961). During the Pleistocene these authors suggest a 'savannah corridor' connected the Malay Peninsula and Sumatra with South Borneo (Fig. 3.3). In this reconstruction the northern part of Borneo remains everwet. The temperature was lower and resulted in a forest limit that was about 1700 m below the present one. The Pleistocene glaciations resulted in eustatic low sea levels that profoundly changed the shape of the Malay Archipelago. The existence of a 'savannah corridor' was mentioned by Van Steenis (1961) in connection with the now disjunct areas of several drought plants. Verstappen (1980) adds that drier conditions were also inferred from fossils of grazing animals found on Java and other islands. The savannah corridor was bordered by monsoon tropical forest during periods of low sea level (Adams, 1995). Van der Kaars and Dam (1995) provide data from the Bandung area covering the last 135,000 years. They found dry conditions around 135,000 years B.P., warm and humid ones during the interglacial between 126,000 and 81,000 years B.P.; the climate became dry again between 81,000 and 74,000 yr B.P., but later it became more wet. The last drier and cooler period was between 47,000 and 20,000 yr B.P, during the Last Glacial Maximum.

Southwest China had a tropical monsoon climate during the Palaeocene, as indicated by the presence of megafossils (Guo, 1993). The climate was a little drier during the Eocene, but tropical monsoon forests were still present. During the Oligocene the climate was warmer and more humid, characterised by a wet tropical monsoon or tropical rain climate. Towards the end of the Oligocene climatic conditions were drier, and at the beginning of the Miocene also cooler. This change may be the result of uplifted
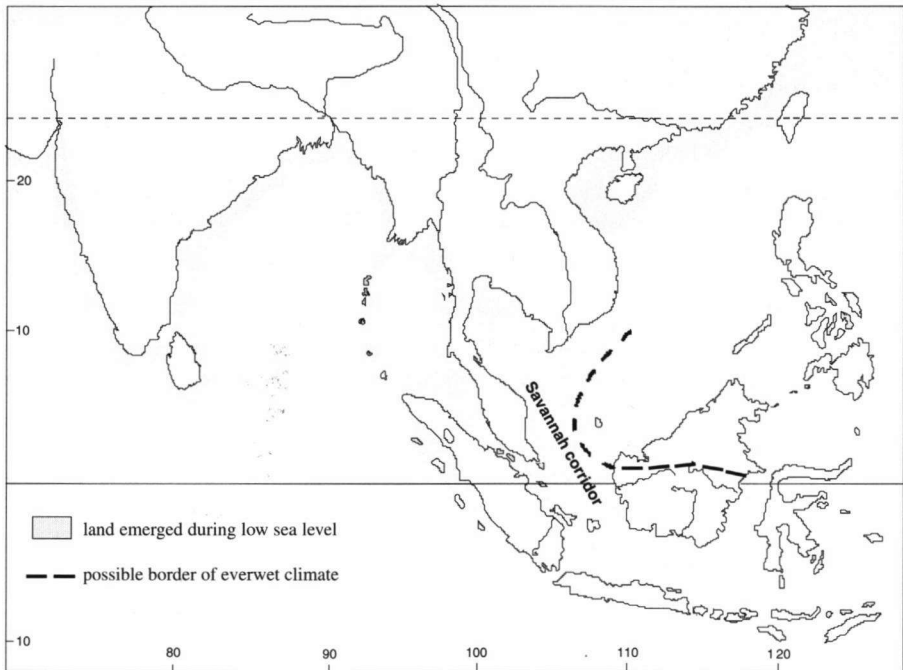
Figure 3.3. Map illustrating the Malesian Archipelago during low sea level. Modified after Morley & Flenley (1987) and Verstappen (1975).

plateaus (Himalayas and others). On plains and hills a tropical monsoon climate prevailed, with the Leguminosae as one of the dominant families. In the Pliocene a montane tropical monsoon climate was present in NW Yunnan and to the north in S Sichuan.

According to Ferguson (1993) the climate in northern China was modified by the rapid uplift since the Pleistocene of the mountain plateaus that threw a rainshadow over the area. It became more extreme: colder and drier during the glacials, warmer and moister during the interglacials. Even in the south and southwest of China this was felt, but it was less pronounced. Yunnan had a stable flora and fauna up to the Pleistocene, and was later affected by the influence of a drier climate.

EUSTATIC SEA LEVEL CHANGES

Eustatic sea level variations have a profound impact on the environment and are particularly important for the West Malesian area. A lowering of the sea level (Table 3.1) enabled a periodic exchange between regions that were otherwise isolated.

From the Jurassic to the Cretaceous large parts of South Tibet, Indochina, and probably Sumatra were exposed (Audley-Charles, 1987). During the late Cretaceous and Palaeocene (85–55 Ma), sea levels reached an all time high of 350 m above the present level (Hutchison, 1989a; Dercourt et al., 1993). It stayed high until the Late Oligocene except for some episodes of lower sea levels during the Late Palaeocene, and the Lower

and Upper Eocene. During the Late Oligocene a spectacular fall in sea level to 250 m below the present level exposed the entire landmass of Sundaland. From then on the sea level rose again up to 220 m above the present level in mid-Miocene times, and the Indian continent and the Himalayas (before the real uplift) were only joined by an isthmus (Cavelier et al., 1993). This was followed by a drop in sea level that occurred in three phases to 220 m below its present level from the Middle to the Late Miocene. Again the Sundaland Plateau was exposed. At the beginning of the Pliocene a rise to 140 m above present-day sea level occurred. During the Pleistocene, changes in sea level were more frequent, but less spectacular.

During the Pleistocene, glacial periods occurred for longer periods than the interglacials (Morley & Flenley, 1987). There is a coincidence between climatic changes and the rise and fall of the sea level. On the continent an increase in drier conditions occurs when the sea level is low, and presently inundated parts of Sundaland become inhabited by landplants from the now drier continent. The newly formed landmass created a corridor with savannah vegetation in its central part, and monsoon forest along the edges. Land bridges allowed plants and animals to migrate from Thailand to Sulawesi. The existence of a savannah corridor (Fig. 3.3) was already mentioned by Van Steenis (1961, 1979) in his articles on vegetation types in the Malesian Archipelago. He suggested that during the Pleistocene Ice Ages the seasonal monsoon climate zones were extended, providing a pathway from the Southeast Asian mainland into the Malesian Archipelago (and even into Australia).

Plate tectonic reconstructions often do not adequately demonstrate the land–sea distribution. Maps that show clear coastal outlines are important for biogeographical reasons, however. Colour maps with indications which areas have been above sea level in certain periods have been published by, e.g., Rangin et al. (1990b) and Dercourt
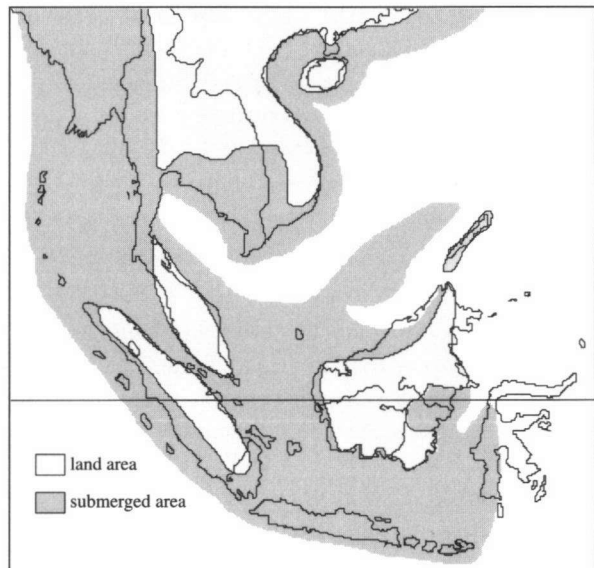
Figure 3.4. Map of the emerged parts of Southeast Asia during high sea levels in Middle Eocene to Late Miocene times. Modified and simplified after Rangin et al. (1990b).

land area

submerged area

et al. (1993). The reconstructions of Rangin (Eocene to Present) show the Malesian area during high sea level, and it is remarkable to see that the area is divided into a few larger emergent landmasses: Borneo, the Malay Peninsula, Sumatra (in part) and West Java. Figure 3.4 shows the emergent landmasses during high sea levels in Middle Eocene to Late Miocene times. In the Pliocene the emergent parts are similar to the mountain ranges presently occurring, including the mountains west of Phnom Penh.

GEOLOGY

Southeast Asia represents a complex region that is influenced by the convergence of four major lithospheric plates: The Eurasian Plate, the Indo-Australian Plate, the Pacific Plate and the smaller Philippine Sea Plate. The region is further complicated by the presence of numerous smaller continental fragments and island arcs that are caught between these plates (Fig. 3.5).

The geology of the region has been summarised in comprehensive studies by Hamilton (1973, 1979, 1988), Hutchison (1989a, 1989b, 1992, 1996), and Metcalfe (1988, 1990, 1991, 1994a, 1994b, 1996). Geological evidence on which this overview is based can be found in these references. Additional references are mentioned where necessary in the text. Biogeographical studies of the East Malesian Archipelago, including an overview of the geological history with emphasis on New Guinea, can be found in De Boer (1995), Turner (1995), and Vermeulen (1993). De Jong and Treadaway (1994) discussed the biogeography and geology of the Philippines.

Tectonic mechanisms

Although there were scientists (Lam, 1930; and references cited by him) who adopted the theories of continental drift at an early stage, it was not until the sixties that the theories of Alfred Wegener (1915) became widely accepted. Since then a wealth of geological information has been acquired using highly specialised disciplines such as palaeomagnetics, seismology, isotope stratigraphy and palaeontology. This has contributed to the elaboration of the plate tectonic concept.

The surface of the earth is covered by lithospheric plates that may be continental or oceanic (or both) in origin. Plates move relative to one another along plate boundaries (Fig. 3.5). Plate boundaries are convergent (active) when one plate is moving below the other (subduction). Divergent plate boundaries (the mid-oceanic spreading ridges) are located at the position where two plates move apart.

The subduction of one plate below another results in characteristic geological features more extensively explained in Hamilton (1988) and Daly et al. (1991); some are shown in Figure 3.6. At convergent margins, sediments may be scraped off the subducting plate and welded against the overlaying margin where they form an accretionary wedge. At the zone where the plate is subducted to depths greater than 600 km, the high temperature causes the sinking slab to melt. Volcanic arcs develop on top of the overriding plate. Between the accretionary wedge and the volcanic arc the fore-arc basin is situated, usually a sub-marine basin that originated due to extension of the overriding plate. At the other side of the volcanic arc a back-arc basin may be present.
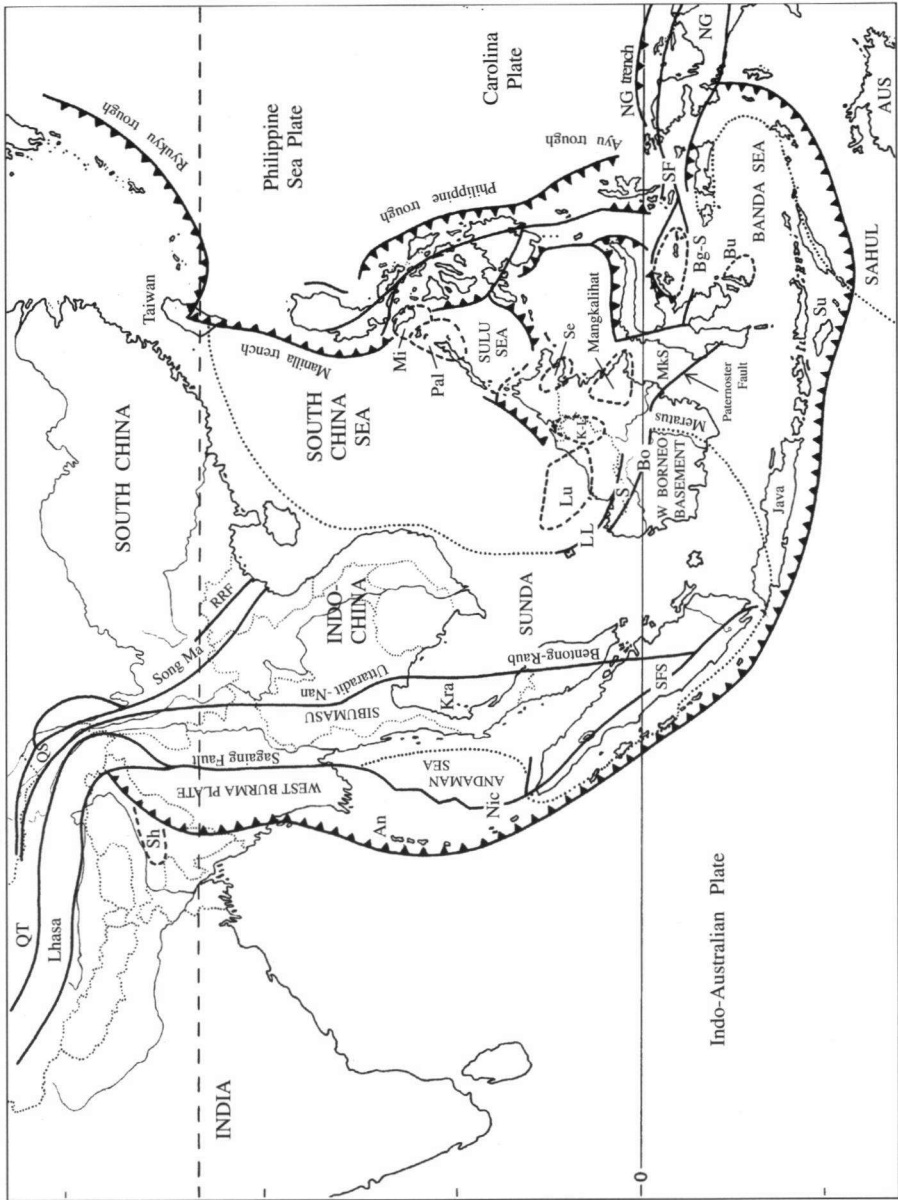
Figure 3.5. Map of SE Asia showing the main geological features. Heavy lines represent fault systems, indented lines show plate margins with the indentation on the overriding plate, and dotted (bold) lines represent the border of Sahul and Sunda platform.

An   Andaman Islands
AUS Australia
Bg-S Banggai-Sula
K-L Kelabit-Longbowan
Kra Isthmus of Kra
LL   Lupar Line
Lu   Luconia
Mg   Mangkalihat
Mi   Mindoro
MkS Makassar Strait
NG   New Guinea / Irian Jaya
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
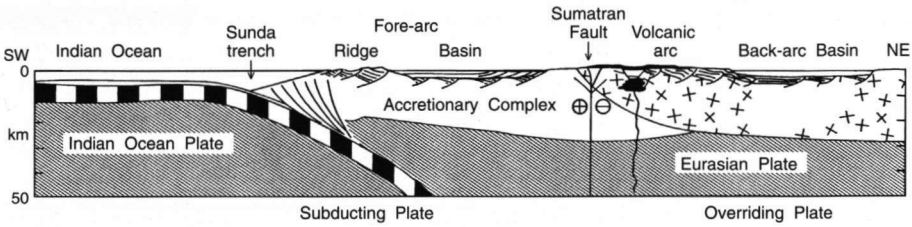
Figure 3.6. Schematic cross section of a subduction zone (after Simandjuntak & Barber, 1996)..

Plates do not always approach each other in a perpendicular fashion. Oblique subduction or strike-slip movement between plates are more common, and may result in large faults (e. g., the Sumatran Fault). The rigid subducted slab is reflected by a high density of earthquakes known as the Benioff Zone.

During their origin, rocks may become magnetised by the earth's magnetic field and may then receive a polarisation corresponding to the direction of the earth magnetic field at that time. The earths magnetic field is considered to be a dipole field, the axis of which has an average position parallel to the rotation axis of the earth. Because continents may have moved since, palaeomagnetism can give valuable information on their original latitudinal position.

Present situation

The Southeast Asian part of the Eurasian Plate represents an assemblage of larger and smaller continental fragments that probably originated from Gondwanaland. The region can be divided into several structural units: India and the Himalayas, West Burma, Sinoburmalaya (Hutchison) or Sibumasu (Metcalfe), South China, Indochina and East Malaya, and several smaller fragments (Fig. 3.5).

India is part of the Indo-Australian Plate and collided with the Eurasian Plate during the Late Eocene resulting in the formation of the Himalaya mountains. Early collision events during the Early Eocene between India and Burma caused the uplift of the Indo-Burman Ranges. The West Burman Plate represents a narrow plate extending from the Indo-Burman Ranges to the Shan and Sagaing Faults (Fig. 3.5, 3.13).

Sundaland itself is composed of a complex of cratonic terranes (= structural units of the earth's crust) and younger orogenic belts that developed since the Late Triassic. There is no seismic activity except along some Cenozoic faults (e. g. the Red River Fault). Sundaland is bordered by the Shan Boundary and Sagaing Fault in Burma, and its outlines continue southwards along the Andaman–Nicobar Ridge and offshore to the west of Sumatra. On West Java it extends eastwards and continues (in a fragmented way) to the Meratus Mountains in SE Borneo. West Sulawesi represents a piece of Sundaland that drifted away from the southeastern margin of Borneo in the Early Tertiary opening up the Makassar Strait. On Borneo, the margin of Sundaland can be traced along the Lupar Line, east of Kuching, and extends into the South China Sea along the Natuna Ridge, and off the coast of Vietnam towards the Song Ma Suture. The Song Ma Suture represents the area where the blocks of South China and Indochina

are welded. The Sunda shelf is the extension below sea level of the continent, connecting Borneo, Java, and Sumatra. The maximum depth of the continental shelf is 200 m.

The greater part of the Philippines is composed of a separate block which is enclosed between the Pacific and Eurasian Plates. In the west, the South China Sea Basin (Eurasian Plate) is subducting below the Philippines along the Manila Trench. In the east, the Pacific Plate is subducted along the Philippine Trench. The Philippines consist partly of continental fragments that were separated from China after opening of the South China Sea Basin.

Australia, including the Sahul shelf and New Guinea, is presently colliding with Indonesia. Fragments of this shelf are found in several parts of the East Malesian Archipelago.

The major rifting events

There is much evidence that most Southeast Asian terranes formed an integral part of Gondwanaland in the Palaeozoic. I follow Metcalfe, who summarised the dispersal of the fragments as three separate rifting events:

- (Early) Palaeozoic rifting of, among others, N China, S China, Indochina and E Malaya, and the Tarim terrane (Fig. 3.7).
- Early to Middle Permian rifting of Sibumasu, Qiantang, Iran and Turkey (together forming the Cimmerian continent). The continental sliver disintegrated, after which Sibumasu, Qiantang, Iran and Turkey travelled rapidly to the north during the Permo-Triassic (Fig. 3.8).
- Late Triassic rifting of Lhasa to Late Jurassic rifting of W Burma, Woyla (Sikuleh and Natal in Sumatra), and Mangkalihat (part of E Borneo), W Sulawesi and Banda allochton (Fig. 3.9).
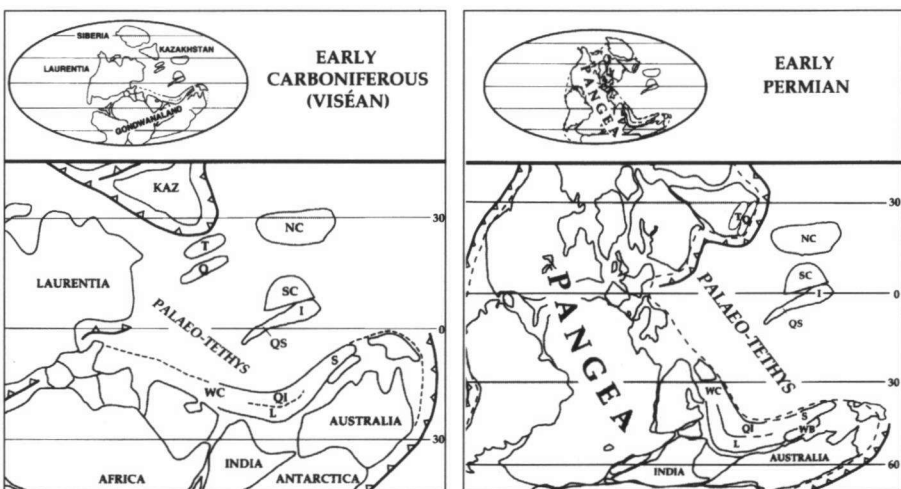
Figure 3.7. Maps of the Early Carboniferous and Early Permian showing the first rifting phase (Metcalfe, 1996).

Abbreviations in Fig. 3.7–3.9: Ba: Banda allochton; Ba-Su: Banggai-Sula; B-S: Buru-Seram; BU: Buton; C: Cimmerian continent; ES: E Sulawesi; I: Indochina; L: Lhasa; M: Mangkalihat; N: Natal; NC: N China; O: Obi-Bacan; QS: Qamdo-Simao; QT: Qiangtang; S: Sibumasu; SC: S China; SG: Songpan-Ganzi; Si: Sikuleh; Sm: Sumba; SWB: SW Borneo; T: Tarim; WB: W Burma; WC: W Cimmerian; WIJ: W Irian Jaya; WS: W Sulawesi;
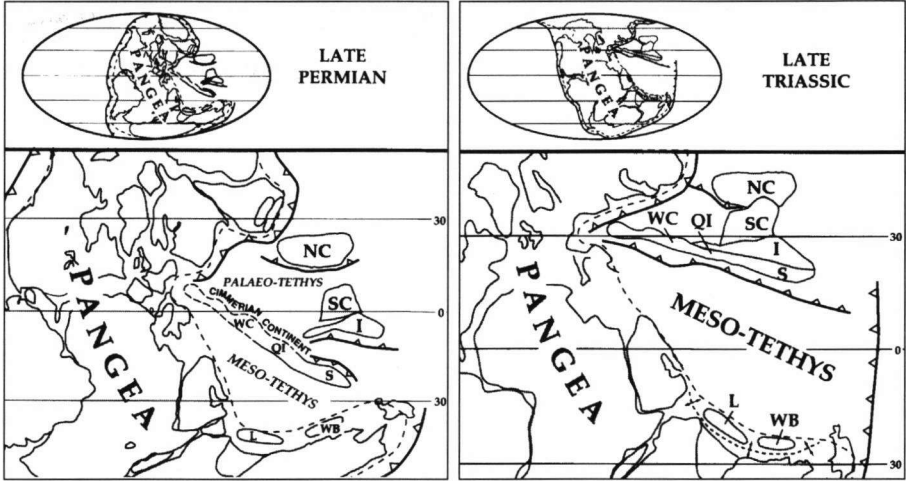
Figure 3.8. Maps of the Late Permian and Late Triassic showing the second rifting phase (Metcalfe, 1996).
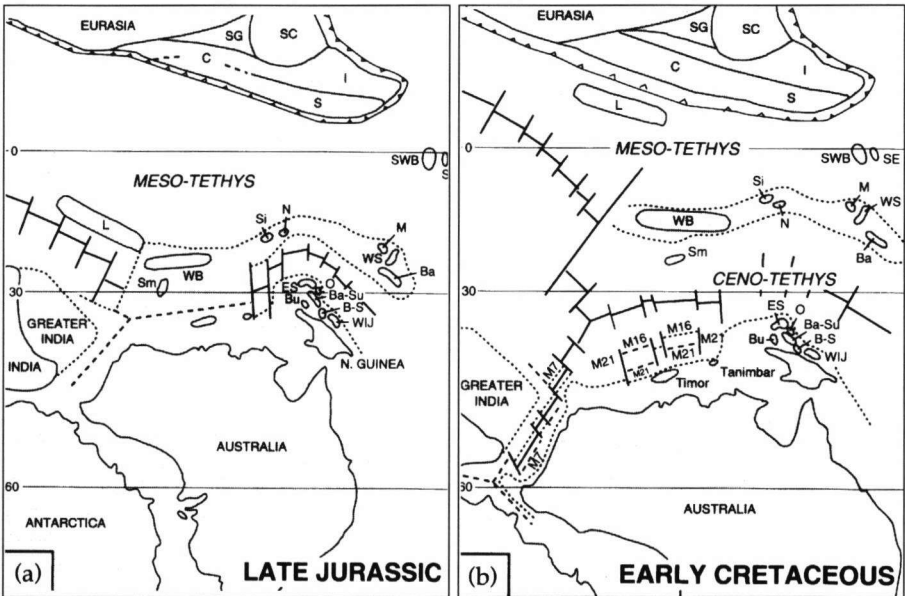
Figure 3.9. Maps of the Late Jurassic (a) and Early Cretaceous (b) showing the third rifting phase (Metcalfe, 1996).
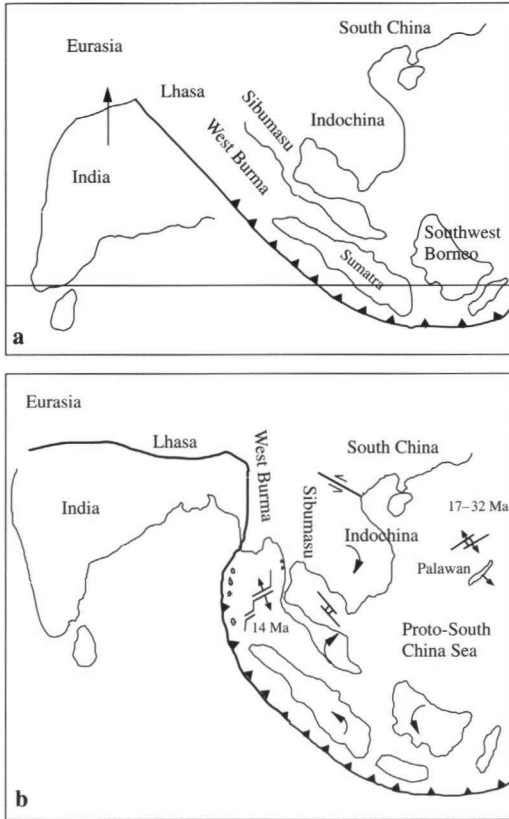
Figure 3.10. – a: Beginning of collision of India with Eurasia. – b: Some of the geological events that happened after the indentation of India into Eurasia. Timing is not necessarily the same for all events. Note that the West Burma Plate has moved northward, several basins have opened, and some parts of Southeast Asia have rotated clockwise or counterclockwise.

India initially also separated during the Late Jurassic (160 Ma). The onset of its collision (50 Ma) was probably the major cause for the clockwise rotation of Indochina, whereas the greater part of Sundaland performed a counterclockwise rotation (Fig. 3.10). Several basins and faults in SE Asia came into existence. This process was interrupted during the Middle Miocene by the collision of Australia with SE Asia (Rangin et al., 1990a, 1990b).

Other opinions on the major rifting events are of Audley-Charles (1987; et al., 1988) and Burrett et al. (1991). The latter placed the first rifting event of N and S China, Indochina and E Malaya in the Cambrian, the rifting of Sibumasu (also called Shan-Tai or Sinoburmalaya) in the Permian, and the last more continuous rifting phase in Cretaceous-Jurassic times. Audley-Charles (1987; et al., 1988), on the other hand, suggests that rifting occurred in later times: Burma, Thailand and Malaya, Sumatra and S Tibet separated from Gondwanaland in Early Jurassic times and collided with Asia at about 160 Ma. These land masses probably were exposed during most of the Jurassic and Cretaceous. The Late Cretaceous major eustatic sea level rise inundated large parts of the continents. However, Australia and the already rifted fragments remained largely above sea level.

Each collision event was accompanied by the closure of an existing (Palaeo-)Tethys Ocean, while each rifting event was followed by the opening of a new (Neo-)Tethys Ocean (Metcalfe, 1994b, 1996; Audley-Charles, 1987). The Uttaradit-Nan and Raub-Bentong line (Fig. 3.5), along which Indochina/East Malaya and Sinoburmalaya were sutured during the Late Permian/Early Triassic, can be regarded as the position of the former Palaeo-Tethys Ocean. To the north of the Himalayas, the Lancangjiang suture between the Qamdo-Simao and Qiangtang terranes (Fig. 3.5) represents another rem-

nant of the closed Palaeo-Tethys. The Song Ma line (Fig. 3.5) is the suture along which Indochina/E Malaya welded with S China, together called Cathaysia (see Metcalfe) in the Early Carboniferous, before their collision with Eurasia. Cathaysia and N China were at that time located at low northern to equatorial latitudes.

A Permian Cathaysian flora of equatorial climate developed on blocks that were rifted during the first Palaezoic rifting event. Other blocks that remained close to Gondwanaland were influenced in Carbo-Permian times by cooler climatic factors, such as glaciation. Blocks that remained longer under Gondwanaland influence are: Lhasa (Tibet), Himalayas (part of Indian Plate), Shillong massif and Indian platform, Burma Plate, Sinoburmalaya and Shan-Tai (Sibumasu). Blocks of Cathaysian affinity are: Yangzi Platform (S China), Phu Hoat microcontinent (between S China and Indochina), Indochina and E Malaya, which is a continuation of Indochina beneath the South China Sea, and the West Borneo Basement (the terranes mentioned above in the first rifting phase). Sumatra probably has a mixed affinity: the Djambi province in S Sumatra with a Cathaysian type flora is probably a displaced part of the eastern Malay Peninsula, while northern Sumatra shows affinities with the western Malay Peninsula. Metcalfe regards northern Sumatra as part of Sibumasu, and southern Sumatra as belonging to E Malaya (Fig. 3.11).
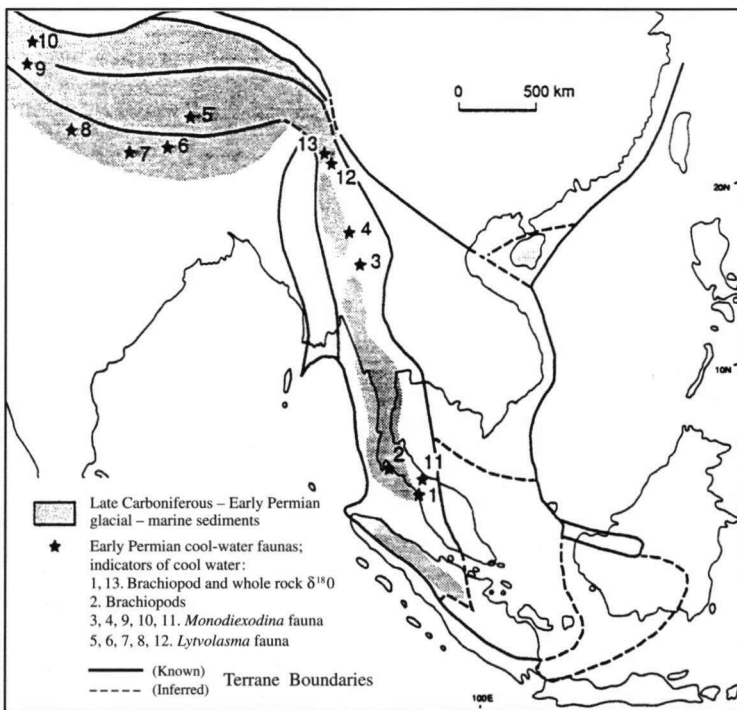
Figure 3.11. Map showing the distribution of cool-water indicators and glacial marine sediments in Southeast Asia and the Tibet-Himalaya region (Metcalfe, 1994a).
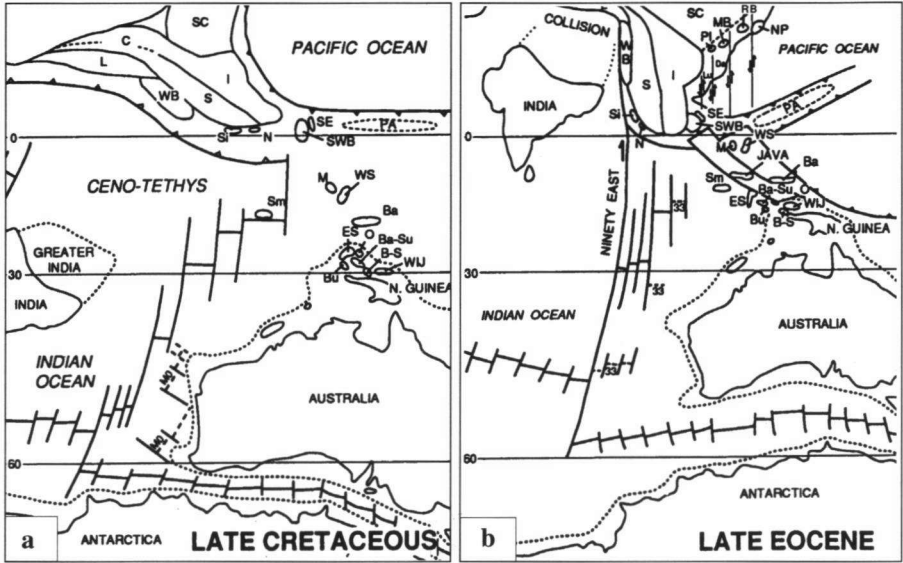
Figure 3.12. Maps of the Late Cretaceous (a) and Late Eocene (b) showing the rifting of India and Australia, and the collision of India (Metcalfe, 1994a). — For abbreviations, see page 79.

India

The initial separation of India from Gondwanaland (between the western margin of the Australian craton and the eastern margin of Africa) began in the Jurassic (Fig. 3.9). India moved northwest until 90 Ma due to sea floor spreading in the Argo Abyssal Plain (the oceanic part of the Indo-Australian Plate). Evidence from magnetic anomalies in the ocean floor shows a change in direction of the spreading just south of the Argo Abyssal Plain.

After 90 Ma, plate margins were reorganized, and Australia began to separate from Antarctica (see also Veevers, 1991). India rapidly moved (10 cm/year) with a changed direction northwards until 53 Ma (Early Eocene) when it started colliding with the Eurasian Plate (Fig. 3.12).

Weijermars (1989) in his reconstructions places India close to Africa during the Upper Cretaceous, whereas others isolate India during its rift towards Eurasia (see for discussion Briggs, 1989; Patterson & Owen, 1991; Thewissen & McKenna, 1992). These different views have implications concerning the development of a flora in India during its northward rift.

Until the collision of India with Eurasia, the Tethyan ocean (in fact Tethys III or Ceno-Tethys) subducted below Tibet; it was closed with the arrival of India. The Indus Yarlung Zangbo suture is a remnant of the closed Tethys (Fig. 3.5). At 45 Ma a major plate reorganization took place, and spreading in the Indian Ocean switched from northeast to southeast (Hutchison, 1992).

It is possible that spreading continued east of the Ninety East Ridge until 32 Ma, after which the Indian Plate and the Australian Plate were welded into one plate. The

Ninety East Ridge (Fig. 3.12) may be interpreted as the trace of the east margin of the Indian Plate; the Ridge has been built up of basalts, as the plate moved northwards over the Kerguelen hotspot.

The collision of India with the Eurasian Plate took part in two stages, a first one in the Early Eocene and a stronger one in the Late Eocene (45 Ma). The last one resulted in several major tectonic events such as the uplift of the Himalayas, the movements along pre-existing faults (Red River Fault), the clockwise rotation of Indochina and the subsequent opening of basins as the Gulf of Thailand as well as the Andaman Sea (Fig. 3.10). A large part of Sundaland, including the Malay Peninsula, Borneo and W Sulawesi, performed a counterclockwise rotation.

Burma

Before collision of the Indian continent eastward subduction occurred along the margin of the Asian Plate beneath the Burman Volcanic Arc, which became extinct after the collision of India with the Eurasian Plate (Fig. 3.5). The Indo-Burman Ranges, which represent an accretionary wedge formed during subduction of the Indian Plate below the Asian Plate, was uplifted during the Early Eocene as a result of the collision between India and Eurasia.

The West Burman Plate (also called Mount Victorialand) lay about 450 km south of its present location (Fig. 3.13). At this moment the small plate lies east to the Indo-Burman Ranges and west of the Sagaing-Namyin Fault. In the Early Mesozoic, the West Burman Plate probably formed an island arc which was separated by oceanic crust from the Asian Plate. The oceanic basin closed in the Late Cretaceous, and the island arc collided with Asia (Shan States, Sibumasu). Metcalfe (1994b) concludes that, although the origin of this block is not known, it might as well be part of a continental sliver that rifted off Gondwanaland in the Late Jurassic (WB in Fig. 3.9). During the Late Cenozoic the plate moved 450 km northwards along the Sagaing Fault. At that time the Andaman Sea was not yet formed.

The opening of the Andaman Sea started in the Middle Miocene (13 Ma) as the result of the oblique subduction of the Indian Plate.
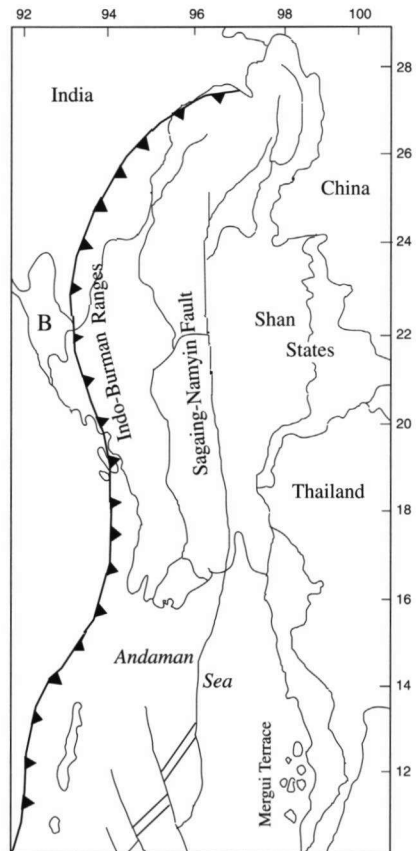
Figure 3.13. Map of Burma (redrawn after Hutchison, 1992). B = Bangladesh.

Before opening, the Andaman Sea probably represented a fore-arc basin in connection with the Andaman–Nicobar arc, the outer-arc ridge below which the Indian Plate is subducting. The Mergui Terrace (Fig. 3.13), adjacent to the Andaman Sea, represents a shelf extension of the Thai–Malay Peninsula block and is of continental crust. Some authors suggest that the Mergui area was a small continental fragment itself; Metcalfe feels there is little basis for this (references in Metcalfe, 1996). McCourt et al. (1996) indicate an extension of this microplate into W Sumatra.

Sinoburmalaya

Sinoburmalaya (or Sibumasu) started to separate from northern Gondwanaland together with other parts of the Cimmerian continent about 300 Ma (Fig. 3.8). Sinoburmalaya moved towards the Southeast Asian continent (at that moment consisting of Cathaysia), closing the Palaeo-Tethys Ocean that was located in between. The collision occurred during either the Late-Triassic or the Late Permian / Early Triassic and resulted in a fold belt that extends from the Malay Peninsula into Thailand and Yunnan along the Uttaradit-Nan and the Bentong-Raub Sutures (Fig. 3.5).

In the Jurassic the Eurasian Plate was above sea level. Afterwards it subsided resulting in the deposition of marine sediments in the Late Mesozoic. The plate was bordered in the south by a convergent margin (a volcanic arc) that extended from Sumatra through the Java Sea into the Meratus on Borneo.

Since the Late Eocene a clockwise rotation of at least 10° of Indochina and the Malay Peninsula occurred as the result of the collision of India with the Eurasian Plate. This same event is held responsible for the opening of the South China Sea and the Thai and Malay Basins.

Other scientists, however, regard the subduction of the Proto-South China Sea below Borneo as the major cause of opening of the South China Sea (Hall, 1995).
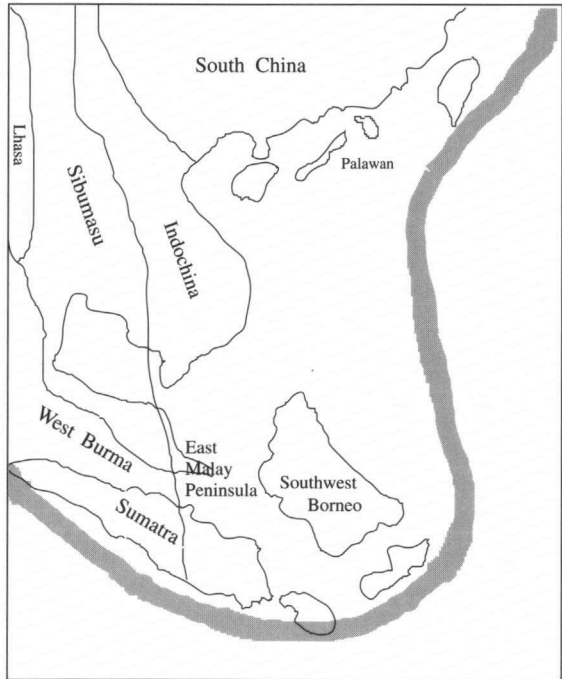
Figure 3.14. Simplified map of the ancient volcanic arc along the margin of the Asian Plate during the Cretaceous. The small West Burma Plate is shown to the east of Sibumasu.

The South China Sea region

A volcanic arc developed from the Mid-Jurassic to Mid-Cretaceous along the eastern margin of China. The arc extended from Hainan to Hong Kong and terminated in the east of Indochina (Fig. 3.14). Subduction occurred along this margin, but ceased before the onset of the Tertiary, after which the margin started to break up.

During the Jurassic the West Borneo Basement (Schwaner Block) separated from the Southeast Asian continent during the opening of the Proto-South China Sea. In the reconstructions of Metcalfe, however, SW Borneo and the Semitau remain at an equatorial latitude from the Late Jurassic onwards (Fig. 3.9).

The collision of India with Eurasia resulted in pericollisional extension in Southeast Asia, which led to the opening of the South China Sea (Fig. 3.15). As mentioned in the section on Sinoburmalaya, the opening of the South China Sea can also be explained by the pull forces of the subducting slab of the Proto-South China Sea below Borneo and the Philippine Sea Plate that resulted in stretching of the Eurasian margin (Hall, 1995, 1996; Hall et al., 1995). The South China Sea showed spreading activity from the Palaeocene or from the Mid-Oligocene to Early Miocene (32–17 Ma). The Proto-South China Sea subducted below Borneo and S Chinese continental fragments moved towards the island, which at that time performed an anticlockwise rotation of up to 50°.

Rifted fragments (Fig. 3.5) that are partly located above sea level, are represented by the Spratley Islands, Dangerous Grounds and the Reed Bank, and North Palawan and Mindoro (the Calamian group). The latter fragments form the oldest rocks of the Philippines. Other fragments are found on Borneo. Barber and Hall (1995) stressed the fact that, although in literature there is reference to fragments or blocks rifted off the South China margin, it is in fact one block that rifted southwards.
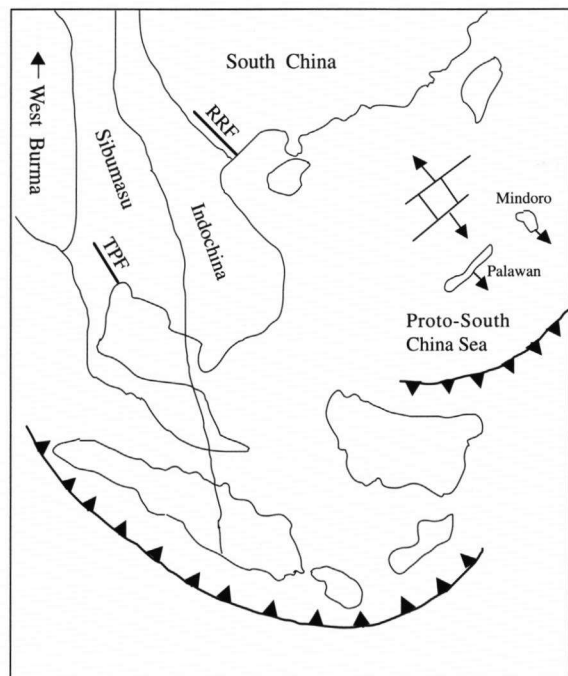
Figure 3.15. Schematic map of the opening of the South China Sea starting 17 Ma. Fragments of the Chinese continental margin move towards Borneo. Of the fragments only Palawan and Mindoro are shown. RRF= Red River Fault, TPF = Three Pagodas Fault.

The Proto-South China Sea was mainly consumed in the Palawan Trough according to Lee and Lawver (1992). The collision of the North Palawan microcontinent with the Cagayan ridge (West Philippines Block) in the Early Miocene stopped the opening of the South China Sea (Hall, 1996). After this collision subduction switched to the Sulu Sea, but was halted by the collision between the Sulu Ridge and Mindanao in the Late Miocene.
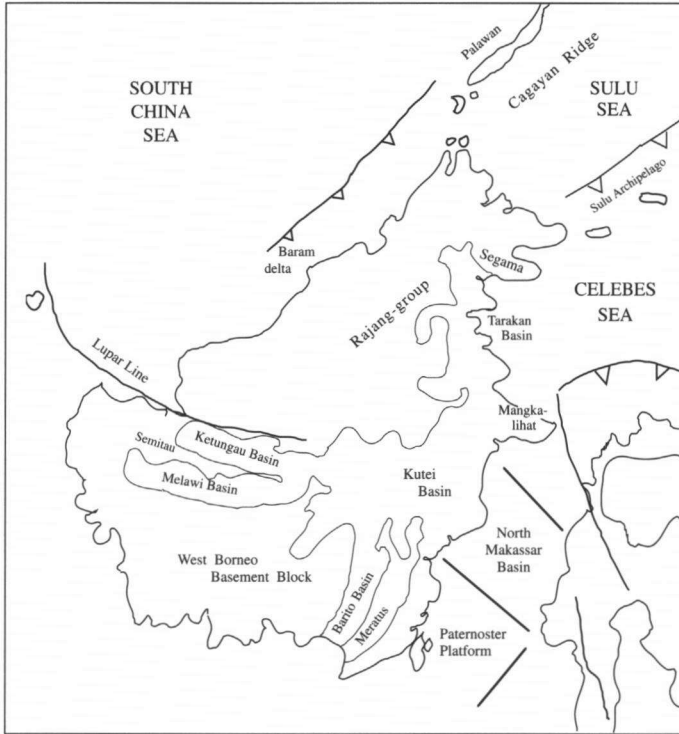
Figure 3.16. Map of Borneo showing major faults and basins.

Borneo

The island of Borneo is represented by a number of cratonic terranes that are separated by faults and younger orogenes, which stabilised during the Late Triassic. The Paternoster (Transform) Fault borders the Tertiary Kutei Basin towards the southern part of Borneo (Fig. 3.16). The West Borneo Basement Block is separated by the Boyan Suture from the Semitau terrane, which in turn is separated by the Lupar Line from the Northwest Borneo Geosyncline (Sarawak). The Boyan Suture is of Cretaceous age and represents the collision of the Semitau terrane and the (South) West Borneo Basement.

The West Borneo Basement is regarded by Hutchison as a displaced part of Indochina, which started rifting due to the opening of the Proto-South China Sea. Hamilton and Metcalfe placed this part of Borneo (SW Borneo and Semitau) in the Late Jurassic at equatorial latitude. Rangin et al. (1990b) suggest that the volcanic arc of the Meratus range (and E Java and Sumatra) was once continuous with the South China magmatic belt (Fig. 3.14). In their opinion Sundaland as a whole was displaced during the Late Cretaceous/Early Palaeocene along the Lupar line, which, in their view, is a continuation of the Three Pagodas Fault. Lorenz et al. (1993) accept a displacement of Indochina and Borneo of 700 km along the Red River.

In the Late Cretaceous continental fragments of the Chinese margin started to rift (see also Taylor & Hayes, 1983). As mentioned in the former paragraph, these fragments were rifting towards Borneo beneath which the Proto-South China Sea subducted. Partly incorporated in Borneo are (Fig. 3.5): The Luconia-Balingian block, for the largest part submerged off the coast of Borneo and reaching up to the Tinjar Fault, the Kelabit Highlands-Long Bawan province, and the Segama block near Tawau.

The Mangkalihat Peninsula block, lying between the Kutei and the Tarakan Basin (Fig. 3.16), is of different origin. According to Metcalfe it is part of the continental fragments (among them W Sulawesi) which rifted off the Gondwanaland margin in the Late Jurassic (M in Fig. 3.9), and contains the oldest fossils known from Borneo (Early Devonian corals).

In Palaeocene times (Hutchison, 1992) all of Borneo south and southeast of the Rajang Group was an extensive landmass together with what is now West Sulawesi and the area below the Java Sea.

The Kutei Basin was formed after the Early Tertiary opening of the Makassar Basin which rifted away the eastern part of Borneo to become what is now the west part of Sulawesi. The Melawi and Ketungai (Mandai) basins on the continental landmass of the West Borneo Basement are from the same period. In the northwest, the Rajang Basin (the now uplifted parts of Sarawak and Sabah) was a northwards directed gulf of the Proto-South China Sea in the Palaeocene and was uplifted probably in the Early Miocene. The Crocker Range represents the accretionary complex, and deltas (Baram, Tarakan) developed which received sediments from the uplifted parts of Borneo and probably from the Indochina part of the Sundashelf as well.

In Late Oligocene times a marine transgression phase is represented by the shallow marine carbonate platform south and east of the Rajang Basin.

Up to the Oligocene the Meratus Mountains in the southeast were not uplifted, but continuous with the basins at both sides. Only in the Late Miocene-Pliocene a rapid uplift of the Meratus Mountains took place.

At the same time the West Borneo Basement Block, dominated by the Schwaner Mountains, rotated counterclockwise about 50°.

To the northeast two island arcs bridge the gap between Borneo and the Philippines. The northwest one consists of Palawan and some other smaller islands, and belongs to the part of the southeast Chinese margin rifted off the Asian continent. To the southeast of these islands is the Sulu Sea. This sea is floored in the northern part by continental crust, to the south of the Cagayan ridge with ocean floor (Hall, 1995). Part of the Sulu

Sea subducted between 15 and 10 Ma in the south under the Sulu Archipelago. This forms the other island arc bridging Borneo and the Philippines, a now almost extinct volcanic arc.

Java

Java consists mainly of Cenozoic volcanic rocks with a marine basement. Continental crust is located in a broad belt in the Java Sea extending towards the Meratus Mountains in SE Borneo. East of this line there are no pre-Tertiary rocks. The belt may be regarded as a relict subduction zone that bounded the continent along its margin.

South of Java the Indian Plate is converging nearly perpendicular to the Java Trench. This trench is more than 6 km deep. The outer arc ridge is completely submerged, and the fore-arc basin is well developed.

From the Late Oligocene onwards, Java became part of the presently active arc/trench system that extends from the Indoburman Ranges to Java. The islands located to the east of Java (including East Java) are of Neogene age and are built on top of oceanic crust. The Sunda arc becomes younger towards the east, and continues as the Banda Arc.

Sumatra

The continental crust of Sumatra is built up of rocks of Lower Palaeozoic age. The volcanic arc extends parallel to the right lateral Semangko Fault system that can be regarded as the continuation of the West Andaman and the Sagaing-Namyin Faults. These faults originated due to the strong oblique subduction of the Indian Plate.

Northern Sumatra belonged to the Sinoburmalaya block, which collided with Indochina in the Late Triassic or Late Permian/Early Triassic (Fig. 3.8). Southern Sumatra, however, formed part of East Malaya and was welded to the Southeast Asian craton in the Early Carboniferous (Fig. 3.7).

Metcalfe describes two small terranes, Sikuleh and Natal (Woyla; Fig. 3.5), that rifted during the Late Jurassic off the Australian margin. These two terranes collided with North Sumatra in the Late Cretaceous.

To the west of Sumatra the accretionary wedge is visible by a chain of small islands on top of the ridge. This ridge continues towards the north as the Andaman–Nicobar Ridge.

In the Cenozoic Sumatra underwent a slight clockwise rotation.

The Philippines

The Philippines (Fig. 3.17) consist of a collage of blocks of diverse origin, amalgamated between two active arc-trench subduction systems. These are, respectively, the westward facing Manila trench in the west (subduction of South China Sea Basin) and the eastward facing Philippines Trench and East Luzon Trough system in the east (subduction of the West Philippines Sea Basin).

The Philippines do not consist of a single plate, but are the product of a diffuse deformation zone between the Philippine and the Eurasian Plate. Most of the islands
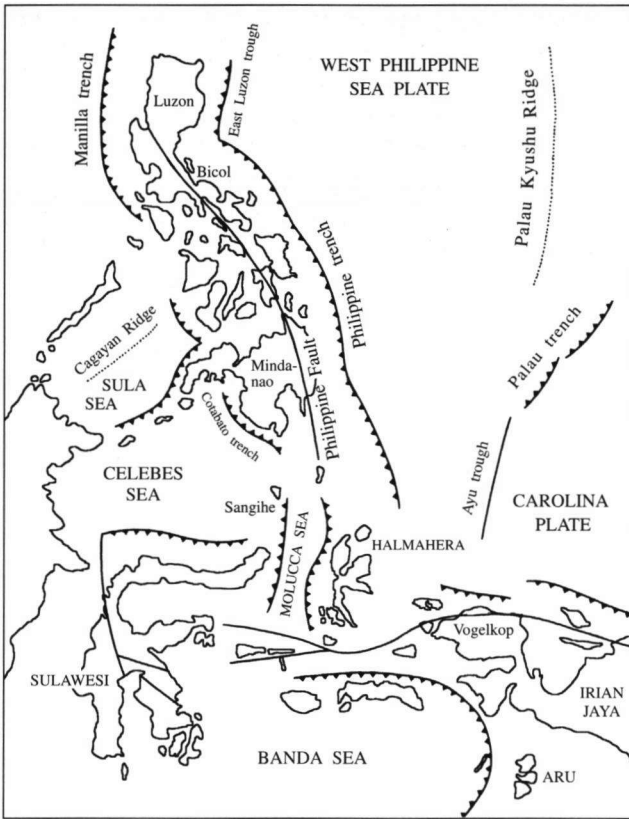
Figure 3.17. Geological map of the Philippine and Molucca region.

originally formed part of an arc at the southern edge of the Philippine Sea Plate. The Philippine Sea Plate has a Palaeocene age, and was formed at a spreading ridge at the southern boundary of the Pacific Plate. The Pacific Plate is moving to the northwest and subducting below Eurasia. Daly et al. (1991) suggest that spreading started 42 Ma ago, when the Pacific Plate motion changed from NNW to WNW. Spreading ceased at about 26 Ma. It is possible that the Central Basin Ridge is the fossil spreading centre of this Plate.

Since 35–40 Ma the Philippine Sea Basin has undergone a clockwise rotation of 50° and a northward drift. The Palau-Kyushu Ridge (volcanic arc) forms the eastern margin of the basin. The margin may continue into the Palau and Ayu Troughs which separate the Philippine Basin from the Carolina Plate (a small plate in the southwest of the large Pacific Plate). Subduction of the Carolina Plate beneath the Philippine Sea Basin has ceased or nearly so (Rangin et al., 1990a, 1990b). Hall (1995) placed the rotation of the plate before 40 Ma, after which rotation ceased and the spreading of the West Philippines Sea extended to the Celebes Sea and the Makassar Strait.

The eastern part of the Philippines (Luzon, Bicol, East and Central Mindanao) existed as a volcanic island arc which continues to Halmahera, and which is located more to the south along the margin of the West Philippine Sea Plate. The western Philippines (West Mindanao, Zambales) may be regarded as an extension of the volcanic arc that is located on the margin of the Eurasian Plate. Hall (1995) suggests that these western Philippine parts are from the Middle Eocene onwards (40 Ma) part of the Philippine Sea Plate, and that the Philippines are not the result of a collision of two opposite arcs.

In the Miocene the Philippines collided with the Eurasian margin. For a more extensive review of the Philippines see Hall (1995, 1996), Hall et al. (1995), and Rangin et al. (1990a, 1990b).

The Philippine Sea Plate rotated after the Miocene, and there was subduction at the Manilla Trench. Luzon subsequently collided with Taiwan. At present subduction probably ceased in the Manila Trench due to the collision of Taiwan with China. At the same time subduction begins at the Philippine Trench at the end of the Miocene. Plate consumption now only occurs along the Philippine Trench.

Sulawesi

The island of Sulawesi represents a very complex structure that originated from different sources. It is surrounded by arc-trench systems and sea basins.

West Sulawesi rifted from the eastern margin of Borneo in the Late Eocene (Fig. 3.16). The Paternoster Platform, which is located in the southern part of Makassar Strait, represents the part of Borneo to which the western arm of Sulawesi was connected. Metcalfe suggests in his reconstructions that West Sulawesi rifted from the Gondwanaland margin in Late Jurassic times. Masse et al. (1993) and Butterlin et al. (1993) describe the Paternoster Platform as a continental fragment (Argo) from the Australian Plate, which collided with Borneo in the Eocene. There is, however, no good evidence for this (Wensink, personal comm.). New insights on the evolution of the Makassar Strait are presented by Bergman et al. (1996).

West Sulawesi may be divided into two different terranes: a northern volcanic arc, and a western part that rifted from Borneo. Prior to the opening of Makassar Strait, the old Sulawesi subduction complex was assumed to be continuous with that of the Java Sea and Java (Fig. 3.14). The part that rifted from Borneo is of a continental nature and, before rifting, was volcanic during the period when it formed part of the subduction complex. This boundary is now obscured by the collision of ophiolitic masses and associated melanges, and some Australian continental fragments, e.g., Banggai-Sula and Buton (Wensink, 1996). The north arm of Sulawesi was part of the margin beneath which the northwards moving Indian–Australian Plate was subducting until the Early Miocene. From the Middle Miocene to the Quaternary, volcanism resumed and was accompanied by folding, faulting and uplift of the region. After spreading in the Celebes Sea, the arm began to rotate clockwise. At present the oceanic crust of the Celebes Sea is subducting southwards beneath Sulawesi's north arm.

The northeastern part of the Celebes Sea is subducting into the Cotabato Trench (below SW Mindanao). The Sangihe volcanic arc is located to the east of this basin, and continues into the northern arm of Sulawesi. This east facing arc has been active

since Early or Middle Miocene. The Molluca Sea represents a separated part of the Indian Ocean lithosphere that was trapped by the northwards movement of the Australian continent. It is subducting both to the west under the Sangihe arc and to the east under the Halmahera arc, which is part of the Philippine Sea Plate. In fact the Molluca Sea Plate itself is probably almost completely subducted by the Philippine Sea Plate, which itself is subducting under the Eurasian Plate (Hall, 1995; Barber & Hall, 1995).

East Sulawesi contains suits of ophiolites of probably Indian Ocean origin. Buton and the Banggai-Sula spur located to the southeast and east of Sulawesi are continental fragments of the Australian Plate that were translated westwards from the Bird's Head of New Guinea along the Sorong Fault System. Burrett et al. (1991) show that Buton is a detached part of the Australian Plate that collided with the Sulawesi Trench 18 Ma ago. After this collision extension of the Banda arc began. The Banggai-Sula spur collided with the Sulawesi Trench in the Middle Miocene (10 Ma). The island arc of Sulawesi was bent by those collisions. Banggai-Sula subducted beneath Sulawesi's east arm.

The Australian margin

Separation of Australia from Antarctica occurred 53 Ma ago. The Australian Plate subducted and collided with the Banda arc trench system since the Middle-Late Miocene. At present the Australian Plate is underlying Timor, Sumba and the microcontinent of Buru-Seram, at the same time enclosing the Banda Sea from three sides. The heavy oceanic slab has been detached from the Australian continent below Timor, thus causing (by the diminished weight) a strong uplift of these islands (Burrett et al., 1991; Van der Werff, 1995).

New Guinea is located on the northern margin of Australia, and has accreted several terranes of Pacific origin. For a more extensive review, see Pigram & Davies (1987), Daly et al. (1991), and Rangin et al. (1990a, 1990b). An overview of the geological history of Australia is presented by Veevers (1991).

Chapter 4

HISTORICAL BIOGEOGRAPHY

INTRODUCTION

In this chapter the cladistic reconstruction of *Spatholobus* and allies, together with the cladograms of three other genera, will be used to construct a general area cladogram that gives information on the overall pattern of speciation (at least for these genera) in Southeast Asia, and in this way reflects the vicariance events and the history of the areas involved. In addition, an attempt has been made to use the cladogram of *Spatholobus* together with the general area cladogram to show the specific history of speciation and distribution of this genus within SE Asia.

Considerable research has been undertaken to find the most appropriate methods for analysis of data provided by phylogenies of taxa and their distribution. Several methods and criticisms on these methods have been given, in, e.g., Bremer (1992, 1995), Brooks (1990), Brooks & McLennan (1991), Cracraft (1983, 1988), Morrone & Carpenter (1994), Nelson & Ladiges (1991), Page (1988, 1990), Turner (1995a, 1995b), Van Welzen (1992), Wiley (1981, 1987), and Zandee & Roos (1987). Several computer programs are available to analyse taxon-area cladograms; most of these are in use for phylogenetic analyses as well. The best known of these are PAUP (Swofford, 1991, 1993, 1996) and Hennig86 (Farris, 1988) for BPA (Brooks Parsimony Analysis), CAFCA (Zandee, 1995) for CCA (Component Compatibility Analysis), COMPONENT (Page, 1993) for Component Analysis, and TAS (Nelson & Ladiges, 1992) for Three-Area Statements. Despite all efforts, however, all these methods and programs retain more or less serious flaws and "it must be admitted that current computer implementations of the methods remain unsatisfactory" (Morrone & Carpenter, 1994).

Apart from the flaws in the computer implementations, there are limitations in choice of the groups that can be used for the historical biogeographical analysis. In order to avoid comparing cladograms that reflect different time spans, it is best to use groups of organisms that have developed in the same time. Such groups may be expected to show the same vicariance events. Another important factor in the choice of the groups is the similar distribution pattern, especially in the Malesian area, where it is possible that plants have migrated from SE Asia into the archipelago eastward, or from the east towards SE Asia. If comparing opposite patterns, it is possible that the analysis will eliminate both patterns ('wave extinction') and reflect nothing. With these limitations in mind I used the results of the cladistic analysis of *Spatholobus* and allies, and those of the other groups, and compared these with the geological information as presented in Chapter 3. For practical reasons (computer equipment and time) I had to restrict myself to BPA and CCA analyses.

DATA

The data used for the biogeographical analysis were the phylogenies of *Spatholobus* and allies (Chapter 2), of *Fordia* (Schot, 1991), of *Genianthus* (Klackenberg, 1995), and of *Xanthophytum* (Axelius, 1990). The phylogenies of all these genera were generated using morphological characters, and parsimony analysis was undertaken with either Hennig86 or PAUP. The cladograms of the different genera are shown in Figure 4.1. The genera occur in the same region as *Spatholobus*: continental Southeast Asia and the West Malesian Archipelago (Fig. 4.2). Only *Xanthophytum* has species in New Guinea. This small monophyletic part in the cladogram was removed during the analysis to facilitate comparison with the other genera. The distribution data for each species per genus are given in Table 4.1.

METHODS

The first step was the delimitation of the areas used in the biogeographical analysis. For this step the distribution of all species of the genera *Spatholobus*, *Butea*, *Meizotropis*, *Xanthophytum*, *Fordia*, and *Genianthus* were taken into consideration. Although the genera occur more or less in the same region, there are differences in, e.g., the range of distribution (Fig. 4.2). There are widespread species and also species with very restricted areas within the genera. To facilitate comparison of the different area cladograms, areas were recognised based on the distribution of the species within each of the genera. These are not areas of endemism, but areas of distribution as described by Axelius (1991). Some areas contain endemics (= only occurring in the chosen area), other areas are composed of overlapping distributions of non-endemic species. Some authors, e.g. Sosef (1994), state that each area should at least contain one endemic, and that these 'remnant areas' (without endemics) are not informative. In my opinion, however, this is not necessary, and it is at least not feasible and practical to use only those areas which contain endemics. The species occurring in an area – endemic or not – will reflect their relation to other species in the coding of the areas, and thus a solution for placement of these 'remnant areas' is also possible. As a result of using these areas, it is possible that some end-branches will be empty, because the species coding for the area that is represented by the end-branch, is optimised on a node lower in the cladogram. On the other hand, difficulties may also arise with areas occupied by an endemic species having relations with species in different areas.

   It is not always easy to decide on the delimitation of the areas, as it depends on the number of species present in an area. When there are too few species in an area (e.g., Sri Lanka) problems may arise during analysis. These areas often turn up basally in the cladogram due to lack of data (many zeroes in the area-taxon matrix), especially when an all zero outgroup is postulated, as is the case in BPA analysis. Furthermore, the delimitation of areas is related to their size. When the size chosen is too large (e.g., continental SE Asia) the results will remain uninformative. It is clear that by adding other genera to the analysis, the delimitation of the areas has to be reviewed and changed where necessary (e.g., more precise distribution areas within Sulawesi or East India/ Burma and Indochina). Figure 4.3 shows the basic geographic entities delimited for this study.

a (Butea, Meizotropis, Spatholobus cladogram)

- A64 — S. acuminatus
- S. albus
- A63, A61 — S. crassifolius
- A62 — S. purpureus
- A60 — S. merguensis
- S. dubius
- A58 — S. latibractea
- A59, A57 — S. viridis
- A56 — S. harmandii
- A34 — S. apoensis
- A35 — S. latistipulus
- A36 — S. maingayi
- A55 — S. littoralis
- A54 — S. oblongifolius
- A52 — S. hirsutus
- A51, A53 — S. macropterus
- A50 — S. ridleyi
- S. suberectus
- A49 — S. pulcher
- S. pottingeri
- A37 — S. auricomus
- A39 — S. multiflorus
- A38 — S. auritus
- A40 — S. persicinus
- A41 — S. sanguineus
- A48, A42 — S. gyrocarpus
- S. ferrugineus
- A47 — S. parviflorus
- A43 — B. monosperma
- A45 — B. superba
- A44 — M. buteiformis
- A46 — M. pellita
- Kunstleria

b (Fordia cladogram)

- FA19 — F. bracteolata
- FA20 — F. albiflora
- FA22 — F. unifoliolata
- FA23, FA21 — F. incredibilis
- FA25 — F. spec. a
- F. leptobotrys
- FA26, FA24 — F. ngii
- F. nivea
- FA27 — F. johorensis
- FA28 — F. pauciflora
- FA29 — F. lanceolata
- FA30 — F. ophirensis
- FA33 — F. cauliflora
- FA31 — F. brachybotrys
- FA34, FA32 — F. splendidissima
- F. stipularis
- F. rheophytica
- outgroup

c (Genianthus cladogram)

- GA17 — G. laurifolius
- GA19 — G. bicoronatus
- GA20, GA18 — G. aurantiacus
- G. siamicus
- GA23 — G. hastatus
- GA22 — G. ellipticus
- GA21 — G. valvatus
- G. rectinervis
- GA29 — G. rufo-velutinus
- GA25 — G. crassifolius
- GA26, GA24 — G. macrophyllus
- GA27 — G. maingayi
- GA28 — G. nicobarensis
- G. ridleyi
- G. subpeltatus
- outgroup

d (Xanthophytum cladogram)

- X. magnisepalum
- X. grandiflorum
- X. papuanum
- X. nitens
- X. calycinum
- X. balansae
- XA44 — X. polyanthum
- XA43 — X. attopavense
- XA42 — X. kwangtungense
- X. johannus-winkleri
- X. pubistylosum
- XA38 — X. fruticulosum
- XA39 — X. ferrugineum
- XA41 — X. borneense
- XA40 — X. olivaceum
- XA37 — X. setosum
- X. capitatum
- XA45 — X. longipedunculatum
- XA36, XA35 — X. glabrum
- X. brookei
- X. alopecurum
- XA32 — X. cylindricum
- XA33 — X. grandifolium
- XA31 — X. foliaceum
- XA34, XA30 — X. semiorbiculare
- X. glomeratum
- XA46 — X. minus
- X. sessile
- X. involucratum
- outgroup

Figure 4.1. Cladograms of **a**: *Butea, Meizotropis,* and *Spatholobus,* **b**: *Fordia* (Schot, 1991), **c**: *Genianthus* (Klackenberg, 1995), **d**: *Xanthophytum* (Axelius, 1990). Numbers in the cladograms refer to the numbering of the ancestors used for compiling the area-taxon datamatrix.

Figure 4.2. Distribution maps of the genera *Butea, Meizotropis, Spatholobus* (**a**), and *Fordia* (**b**).

Figure 4.2. Distribution maps of the genera *Genianthus* (**c**) and *Xanthophytum* (**d**).

Table 4.1. Distribution of the species of *Butea, Fordia, Genianthus, Kunstleria, Meizotropis, Spatholobus,* and *Xanthophytum.*

Species	Areas of distribution	Species	Areas of distribution
Butea monosperma	1, 2, 3, 4, 5	*Spatholobus latibractea*	21, 22
Butea superba	2, 4, 5	*Spatholobus latistipulus*	19, 23, 24
Fordia albiflora	12, 13	*Spatholobus littoralis*	15, 18, 25, 27
Fordia brachybotrys	19, 20, 21, 22, 23, 24, 25, 28	*Spatholobus macropterus*	12,13,15,19,20,21, 22, 23, 24
Fordia bracteolata	12	*Spatholobus maingayi*	8, 12, 13, 14, 19, 20, 22, 23, 24, 27, 28
Fordia cauliflora	6		
Fordia incredibilis	14	*Spatholobus merguensis*	7
Fordia johorensis	14	*Spatholobus multiflorus*	21, 22, 23, 24
Fordia lanceolata	12	*Spatholobus oblongifolius*	21, 22, 23, 24
Fordia leptobotrys	5	*Spatholobus parviflorus*	1, 2, 3, 4, 5, 6
Fordia ngii	13	*Spatholobus persicinus*	19,20,21,22, 24, 25
Fordia nivea	15	*Spatholobus pottingeri*	4, 5
Fordia ophirensis	12	*Spatholobus pulcher*	5
Fordia pauciflora	8, 11	*Spatholobus purpureus*	1
Fordia rheophyta	22, 23	*Spatholobus ridleyi*	14, 15
Fordia spec. a	14	*Spatholobus sanguineus*	22, 23, 24, 27
Fordia splendidissima	19,20,21,22,23,24,25	*Spatholobus suberectus*	5
Fordia stipularis	15	*Spatholobus viridis*	20, 21, 22, 23, 24
Fordia unifoliolata	12	*Xanthophytum alopecurum*	21
Genianthus aurantiacus	4, 5	*Xanthophytum attopavense*	5, 6
Genianthus bicoronatus	5	*Xanthophytum balansae*	6
Genianthus crassifolius	4, 6, 12, 15, 18, 22, 23	*Xanthophytum borneense*	21, 22, 24
Genianthus ellipticus	18, 21, 24, 27, 29	*Xanthophytum brookei*	21, 22
Genianthus hastatus	5	*Xanthophytum calycinum*	New Hebrides
Genianthus laurifolius	1, 6	*Xanthophytum capitatum*	19, 22, 23, 25
Genianthus macrophyllus	18	*Xanthophytum cylindricum*	21
Genianthus maingayi	12, 14, 20	*Xanthophytum ferrugineum*	13, 17, 26, 27, 28
Genianthus nicobarensis	10	*Xanthophytum foliaceum*	24
Genianthus rectinervis	27, 28	*Xanthophytum fruticulosum*	15, 18
Genianthus ridleyi	12	*Xanthophytum glabrum*	21, 22
Genianthus rufo-velutinus	12, 13	*Xanthophytum glomeratum*	21
Genianthus siamicus	6	*Xanthophytum grandiflorum*	New Guinea
Genianthus subpeltatus	12	*Xanthophytum grandifolium*	21
Genianthus valvatus	24	*Xanthophytum involucratum*	20
Kunstleria	1, 11–15, 20–28	*Xanthophytum johannis-winkleri*	19
Meizotropis buteiformis	2, 3, 4		
Meizotropis pellita	3	*Xanthophytum kwantungense*	5, 6
Spatholobus acuminatus	2, 4, 5, 6, 8, 9, 11	*Xanthophytum longipeduncu-latum*	23
Spatholobus albus	21, 22, 23		
Spatholobus apoensis	20, 28	*Xanthophytum magnisepalum*	New Guinea
Spatholobus auricomus	21, 21, 22	*Xanthophytum minus*	21
Spatholobus auritus	11, 19	*Xanthophytum nitens*	New Guinea
Spatholobus bracteolatus	7, 12	*Xanthophytum olivaceum*	19, 20
Spatholobus crassifolius	2, 4, 6, 11	*Xanthophytum papuanum*	New Guinea
Spatholobus dubius	11, 12	*Xanthophytum polyanthum*	6
Spatholobus ferrugineus	8, 11–26, 29	*Xanthophytum pubistylosum*	19, 20, 24
Spatholobus gyrocarpus	5, 8, 11, 12, 13, 16	*Xanthophytum semiorbiculare*	19, 21, 22, 24
Spatholobus harmandii	5, 6, 8	*Xanthophytum sessile*	20
Spatholobus hirsutus	19, 21, 22, 23, 24	*Xanthophytum setosum*	20

An area-taxon matrix (Table 4.2) was based on the available cladograms (Fig. 4.1) and the distributions (Table 4.1). The area-taxon matrix gives the presence (or absence) in a distribution 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 zeroes), 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 & Roos, 1987) considers missing data as primitively absent. In this case missing data are coded as zero. Assumption 1 and 2 (Nelson & Platnick, 1981) treat them as uninformative. Under these assumptions missing data are coded as '?' (see in Table 4.2, e.g., Nicobar Islands for *Spatholobus*). In this analysis missing taxa were treated both under assumption 0 and assumption 1; widespread species were only treated under assumption 0, i.e., starting from the assumption that the areas inhabited by the widespread species formed one single area in the past (monophyletic origin). Under assumptions 1 and 2 the information given by the distribution of the widespread species is considered not as fully informative as under assumption 0 (mono- or paraphyletic origin, and in case of assumption 2 even polyphyletic).

The matrices used for each of the two methods differ slightly from each other (Table 4.2). BPA needs an artificial (all-zero) outgroup, and the area-taxon matrices of the genera have to be combined into one large matrix (30 areas, 170 taxa and ancestor taxa; as in Table 4.2). CCA needs no outgroup, but the matrices of each genus have to be entered separately for the analysis. In BPA the clades can be defined by the absence of a taxon (as is possible for characters), thus sometimes causing very artificial situations (Van Welzen, 1989, 1992). In CCA, however, the components used for constructing the cladogram are defined only by the presence of taxa. Sosef (1994) states that CCA may not find the correct cliques when dispersal or extinction events have occurred. In his view, it is better to use BPA in case of many dispersal and extinction events and check for clades solely based on the absence of taxa.

BPA was performed with PAUP 3.1.1 (Swofford, 1993). The complete matrix (Table 4.2) was analysed under heuristic search (addition sequence random, 1000×). The analysis was executed both under assumption 0 and 1 for missing areas.

Table 4.2. Taxon-area matrix of *Spatholobus, Butea, Meizotropis, Xanthophytum, Fordia,* and *Genianthus.* An all-zero outgroup has to be added for analysis with BPA. For CCA an outgroup is not added, and the datamatrix is divided into the parts belonging to the different genera. For analysis under assumption 0 (missing taxa = 0), the '?' has to be replaced by a zero; analysis under assumption 1 (genus is missing from area = ?) needs a '?'.

	S. acu	S. alb	S. apo	S. auric	S. aurit	S. cra	S. dub	S. fer	S. gyr	S. har	S. hir	S. latib	S. latis	S. lit	S. mac	S. mai	S. mer	S. mul	S. obl	S. par	S. per	S. pot	S. pul	S. pur	S. rid	S. san	S. sub	S. vir
1 Kerala	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
2 India	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
3 W Nepal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
4 W Burma / E India	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
5 Yunnan / N Thailand	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0
6 Indochina	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
7 Mergui / Tenasserim	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
8 S Thailand	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
9 Andaman Is	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10 Nicobar Is	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11 Penang / Kedah	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12 W Malaya	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
13 E Malaya	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
14 Singapore	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
15 SE Sumatra	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0
16 N Sumatra	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17 Sumatra coast	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18 W Java	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
19 SW Borneo	0	0	0	0	1	0	0	1	0	0	1	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0
20 Semitau	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1
21 Sarawak / C Borneo	0	1	0	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	1
22 NW Borneo	0	1	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1
23 NE Borneo	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	1	1	0	0	0	0	0	1	0	0	1
24 CE Borneo	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	1	0	0	1
25 Meratus	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
26 Palawan	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
27 N Philippines	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0
28 S Philippines	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
29 Sulawesi	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30 Outgroup area	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	B. mon	B. sup	M. but	M. pel	A34	A35	A36	A37	A38	A39	A40	A41	A42	A43	A44	A45	A46	A47	A48	A49	A50	A51	A52	A53	A54	A55	A56	A57
1 Kerala	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	0	0	1	1	0
2 India	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	0	0	1	1	0
3 W Nepal	1	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
4 W Burma / E India	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1	0
5 Yunnan / N Thailand	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	0	0	1	1	0
6 Indochina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	1	1	1	0
7 Mergui / Tenasserim	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	1	1	1	0
8 S Thailand	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	0	0	1	1	0
9 Andaman Is	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	1	1	1	0
10 Nicobar Is	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	?	?	?	?	?	?	?
11 Penang / Kedah	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0
12 W Malaya	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0
13 E Malaya	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0
14 Singapore	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	1	1	1	0
15 SE Sumatra	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0
16 N Sumatra	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
17 Sumatra coast	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
18 W Java	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	0	0	1	1	0
19 SW Borneo	0	0	0	0	1	1	1	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
20 Semitau	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
21 Sarawak / C Borneo	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
22 NW Borneo	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
23 NE Borneo	0	0	0	0	1	1	1	1	0	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
24 CE Borneo	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
25 Meratus	0	0	0	0	0	0	1	0	1	1	1	1	1	0	0	0	1	1	1	1	1	0	0	1	1	1	0	0
26 Palawan	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
27 N Philippines	0	0	0	0	0	1	1	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1	0	0	1	1	1	0
28 S Philippines	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	1	1	0
29 Sulawesi	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0
30 Outgroup area	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(Table 4.2 continued)

	A58	A59	A60	A61	A62	A63	A64	X. alo	X. att	X. bal	X. bor	X. bro	X. cal	X. cap	X. cyl	X. fer	X. fol	X. fru	X. gla	X. gra. fl	X. gra. fo	X. glo	X. inv	X. joh	X. kwa	X. lon	X. mag	X. min
1 Kerala	0	0	1	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
2 India	0	0	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
3 W Nepal	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
4 W Burma / E India	0	0	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
5 Yunnan / N Thailand	0	1	1	0	0	1	1	0	1	0	0	0	?	0	0	0	0	0	0	?	0	0	0	0	1	0	?	0
6 Indochina	0	1	1	1	1	1	1	0	1	1	0	0	?	0	0	0	0	0	0	?	0	0	0	0	1	0	?	0
7 Mergui / Tenasserim	0	0	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
8 S Thailand	0	1	1	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
9 Andaman Is	0	0	1	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
10 Nicobar Is	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11 Penang / Kedah	1	1	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12 W Malaya	1	1	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
13 E Malaya	0	0	0	0	0	0	0	?	?	?	?	?	?	?	0	0	1	0	0	?	0	0	0	0	0	0	?	0
14 Singapore	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
15 SE Sumatra	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	?	0	0	0	0	0	0	?	0
16 N Sumatra	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17 Sumatra coast	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	1	0	0	0	?	0	0	0	0	0	0	?	0
18 W Java	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	1	0	?	0	0	0	0	0	0	?	0
19 SW Borneo	0	0	0	0	0	0	0	0	0	0	0	0	?	1	0	0	0	0	0	?	0	0	1	0	0	0	?	0
20 Semitau	1	1	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	?	0	0	1	0	0	0	?	0
21 Sarawak / C Borneo	1	1	1	0	0	1	1	1	0	0	1	1	?	0	1	0	0	0	1	?	1	1	0	0	0	0	?	1
22 NW Borneo	1	1	1	0	0	1	1	0	0	0	1	1	?	1	0	0	0	0	1	?	0	0	0	0	0	0	?	0
23 NE Borneo	1	1	1	0	0	1	1	0	0	0	0	0	?	1	0	0	0	0	0	?	0	0	0	0	0	1	?	0
24 CE Borneo	1	1	1	0	0	1	1	0	0	0	0	1	?	0	0	0	0	1	0	?	0	0	0	0	0	0	?	0
25 Meratus	0	0	0	0	0	0	0	0	0	0	0	0	?	1	0	0	0	0	0	?	0	0	0	0	0	0	?	0
26 Palawan	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	1	0	0	0	?	0	0	0	0	0	0	?	0
27 N Philippines	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	1	0	0	0	?	0	0	0	0	0	0	?	0
28 S Philippines	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	1	0	0	0	?	0	0	0	0	0	0	?	0
29 Sulawesi	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30 Outgroup area	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	?	0	0	0	0	0	0	?	0

	X. nit	X. oli	X. pap	X. pol	X. pub	X. sem	X. ses	X. set	XA30	XA31	XA32	XA33	XA34	XA35	XA36	XA37	XA38	XA39	XA40	XA41	XA42	XA43	XA44	XA45	XA46	F. alb	F. brach	F. bract
1 Kerala	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
2 India	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
3 W Nepal	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
4 W Burma / E India	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
5 Yunnan / N Thailand	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0
6 Indochina	?	0	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0
7 Mergui / Tenasserim	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
8 S Thailand	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0
9 Andaman Is	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
10 Nicobar Is	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11 Penang / Kedah	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0
12 W Malaya	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1
13 E Malaya	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	1	0	0
14 Singapore	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0
15 SE Sumatra	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	0	0
16 N Sumatra	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17 Sumatra coast	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	?	?	?
18 W Java	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	?	?	?
19 SW Borneo	?	1	?	0	1	0	0	1	1	0	1	1	0	0	0	1	0	1	1	1	0	0	0	1	1	0	1	0
20 Semitau	?	1	?	0	1	0	1	1	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	1	1	0	1	0
21 Sarawak / C Borneo	?	0	?	0	0	1	0	0	1	1	1	1	1	1	1	0	0	1	1	1	0	0	0	1	1	0	1	0
22 NW Borneo	?	0	?	0	0	1	0	0	1	1	0	1	1	1	1	1	0	1	1	1	0	0	0	1	1	0	1	0
23 NE Borneo	?	0	?	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0	0	1	1	0	1	0
24 CE Borneo	?	0	?	0	1	1	0	0	0	1	1	0	1	1	0	0	0	1	1	1	0	0	0	1	1	0	1	0
25 Meratus	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	1	0	1	0
26 Palawan	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	?	?	?
27 N Philippines	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	?	?	?
28 S Philippines	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	1	0
29 Sulawesi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30 Outgroup area	?	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(Table 4.2 continued)

	F. cau	F. inc	F. joh	F. lan	F. lep	F. ngii	F. niv	F. oph	F. pau	F. spl	F. rhe	F. sti	F. uni	F. spec.	FA19	FA20	FA21	FA22	FA23	FA24	FA25	FA26	FA27	FA28	FA29	FA30	FA31	FA32	FA33
1 Kerala	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
2 India	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
3 W Nepal	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
4 W Burma / E India	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
5 Yunnan/N Thailand	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	1
6 Indochina	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
7 Mergui/Tenasserim	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
8 S Thailand	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1
9 Andaman Is	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
10 Nicobar Is	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11 Penang / Kedah	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1
12 W Malaya	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	1	1	0	0	1
13 E Malaya	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	0	0	1
14 Singapore	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	1	1	1	1	0	0	1
15 SE Sumatra	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1	1	1
16 N Sumatra	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17 Sumatra coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18 W Java	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19 SW Borneo	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
20 Semitau	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
21 Sarawak/C Borneo	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
22 NW Borneo	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
23 NE Borneo	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
24 CE Borneo	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
25 Meratus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
26 Palawan	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
27 N Philippines	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
28 S Philippines	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
29 Sulawesi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
30 Outgroup area	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	FA34	G. lau	G. bic	G. aur	G. sia	G. has	G. ell	G. val	G. rec	G. mac	G. mai	G. cra	G. rufo	G. nic	G. rid	G. sub	GA17	GA18	GA19	GA20	GA21	GA22	GA23	GA24	GA25	GA26	GA27	GA28	GA29
1 Kerala	?	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	1
2 India	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
3 W Nepal	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
4 W Burma / E India	?	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	1	1	1	1	1	1
5 Yunnan/N Thailand	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	1
6 Indochina	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	1	0	1	1	1	1	1
7 Mergui/Tenasserim	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
8 S Thailand	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
9 Andaman Is	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
10 Nicobar Is	?	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
11 Penang / Kedah	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12 W Malaya	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1
13 E Malaya	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
14 Singapore	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
15 SE Sumatra	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
16 N Sumatra	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17 Sumatra coast	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18 W Java	?	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
19 SW Borneo	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
20 Semitau	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
21 Sarawak/C Borneo	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1
22 NW Borneo	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
23 NE Borneo	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
24 CE Borneo	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1
25 Meratus	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26 Palawan	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
27 N Philippines	?	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1
28 S Philippines	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1
29 Sulawesi	?	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
30 Outgroup area	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

For CCA the computer program CAFCA was used (Zandee, 1995). The four matrices (for each group its own matrix) were analysed under the biogeographical run, generalised area cladogram, with as cladon option partial monothetic sets [defined by the unique occurrence of (at least one) monophyletic group of taxa], and as cladogram selection criterium the minimum amount of state changes (steps). Again the analysis was performed under both assumption 0 and 1.

<div align="center">AREAS</div>

The distribution areas shown in Figure 4.3 are based only on the distribution of the species. It is remarkable that a large part of these areas coincide with the tectonic terranes as described by, e.g., Metcalfe and Hutchison (see Chapter 3 and Figure 3.5).

In the text below, geological (and other historical) information on each of the separate areas is summarised. This summary is based on the information on the geological history of Southeast Asia, as provided in Chapter 3. Where necessary, the abbreviation of the name of the area (as used in the computer analyses) is given in parentheses. These abbreviations (versus the 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 species of the genera *Butea, Fordia, Genianthus, Meizotropis, Spatholobus* and *Xanthophytum* occurring in the areas are mentioned in the summary below.

1. *Kerala* 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.
   In Kerala, *S. purpureus* is endemic; *B. monosperma, G. laurifolius,* and *S. parviflorus* also occur here.
2. *India* (including Kerala, which is taken as a separate area) 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 (53 Ma), but the final collision took place in the Late Eocene (45 Ma). After this event the Himalayas were uplifted.
   In this large area both species of *Butea, M. buteiformis, S. acuminatus, S. crassifolius,* and *S. parviflorus* are found.
3. *West Nepal* and *Kumaon* (W Nepal) 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.
   Meizotropis pellita is endemic in this region. The other species occurring here are *B. monosperma, M. buteiformis,* and *S. parviflorus.*
4. *Bangladesh* and *eastern India up to Burma* (W Burma / E India). From a geological point of view, this area is composed of several parts. Bangladesh forms part of the Indian Plate; W Burma and the mountains of eastern India are part of the West Burma Plate, which was uplifted in the Early Eocene by the subducting Indian Plate. Later, during the Cenozoic, the small West Burma Plate moved northwards to its present position by the movement of the Indian Plate.
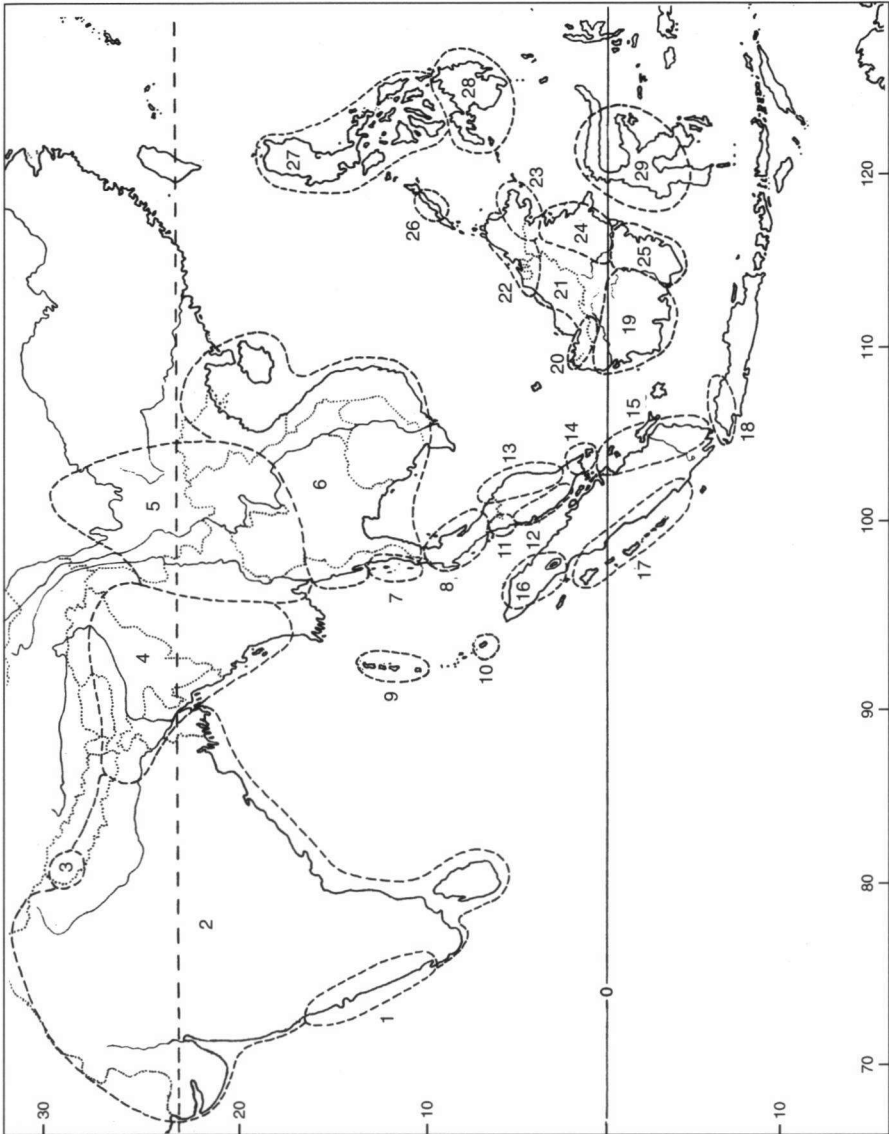
Figure 4.3. Map with basic geographic entities (areas of distribution).

1: Kerala. – **2**: India. – **3**: Kumaon & W Nepal. – **4**: Bangladesh & eastern India up to Burma. – **5**: E Burma, northern Thailand & 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 & 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.

Four species of *Spatholobus* occur (*S. acuminatus, S. crassifolius, S. parviflorus, S. pottingeri*), both *Butea* species, *G. aurantiacus, G. crassifolius*, and *M. buteiformis*.

5. **East Burma, northern Thailand, northern Laos** and **Yunnan** (Yunnan/N Thailand) are all part of 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. South China and Indochina rifted away from Gondwanaland in the Palaeozoic, and sutured along the Song Ma line in the Early Carboniferous. These parts developed a Cathaysian flora subject to an equatorial climate. Parts that remained near the Gondwana margin in Carbo-Permian times were influenced by the cooler climate. Sibumasu rifted off the Gondwana margin in a later phase, during the Early to Middle Permian. Here glacial-marine elements in the fossil fauna indicate an influence due to the cooler climate. Indochina and Sibumasu collided in the Late Permian/Early Triassic. It is clear that these parts have already been welded into one area for a long period.

  Endemic in the area are *F. leptobotrys, G. bicoronatus, G. hastatus, S. pulcher*, and *S. suberectus*. Species occurring here are both species of *Butea, G. auranticus, S. gyrocarpus, S. harmandii, S. pottingeri, X. attopavense*, and *X. kwantungense*.

6. **Indochina, Hainan, South Guangxi, Central Thailand** and **part of Burma** (Indochina) are parts of Indochina, South China, and Sibumasu. This composite area has a history comparable to area 5.

  Endemic in this area are *F. cauliflora, G. siamicus, X. balansae*, and *X. polyanthum*. Other species in this area are *S. acuminatus, S. crassifolius, S. harmandii, S. parviflorus, G. crassifolius, G. laurifolius*, and *X. attopavense*.

7. The **Mergui Archipelago** and **Tenasserim** (Mergui/Tenasserim) are part of Sibumasu. The Mergui Archipelago is in fact an extension of the continental shelf, while Tenasserim is part of the continent itself.

  Here only *S. merguensis* is endemic. The other species occurring here, *S. bracteolatus*, is not included in the analysis due to incompleteness of the available material.

8. **South Thailand** (S Thailand) is the narrow part of the country, near the Isthmus of Kra. It mainly represents the transition between the more seasonal and everwet climates during the present. This part has been inundated extensively in the past, during periods of high sea level (Chapter 3: Fig. 3.3). Tropical rain forest has established here at least 18,000 years ago. At that time the sea level was low and a savannah corridor from Indochina to Java was present, bordered by monsoon forest (Chapter 3: Fig. 3.3). 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.

  No endemics occur in this region. The species found here are *F. pauciflora , S. acuminatus, S. ferrugineus, S. gyrocarpus, S. harmandii*, and *S. maingayi*.

9 & 10. The *Andaman Islands* & *Nicobar Islands* represent the outer arc ridge, below which the Indian Plate subducted before the opening of the Andaman Sea in the Middle Miocene (13 Ma).

  On the Andaman Islands only the widespread *S. acuminatus* occurs; on the Nicobar Islands only the endemic species *G. nicobarensis* is present.

11, 12, & 16. *Penang & Kedah* (Penang/Kedah), the *West Malay Peninsula* (W Ma-
laya), & *North Sumatra* (N Sumatra) are part of Sibumasu (see also area 5). In area
11 (Penang/Kedah) no endemics are present. *Spatholobus auritus* is probably en-
demic in area 11, if the identification of the sterile specimen of *S. auritus* in SW
Borneo (area 19) is wrong. Other species occurring here are *F. pauciflora*, *S. acu-
minatus*, *S. crassifolius* (?), *S. dubius*, *S. ferrugineus*, and *S. gyrocarpus*. In area 12
(W Malaya) three species of *Fordia* are present as endemics: *F. lanceolata*, *F.
ophirensis*, and *F. unifoliolata*. Other species occurring here are *F. albiflora*, *S. brac-
teolatus*, *S. dubius*, *S. ferrugineus*, *S. gyrocarpus*, *S. macropterus*, and *S. maingayi*.
In area 16 (N Sumatra) *S. ferrugineus* and *S. gyrocarpus* are present.

13, 14, & 15. The *East Malay Peninsula* (E Malaya), *Singapore, & Southeast Sumatra*
(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). The whole part of
East and West Malaya has been rotated clockwise after the collision of India.

In area 13 (E Malaya) *F. ngii* is endemic. Other species in this area are *F. albiflora*,
S. ferrugineus, *S. gyrocarpus*, *S. macropterus*, *S. maingayi.*, and *X. ferrugineum*. In
area 14 (Singapore) three species of *Fordia* are endemic: *F. incredibilis*, *F. johorensis*,
and *F. spec. a*. Other species here are *G. maingayi*, *S. ferrugineus*, *S. maingayi*, and
S. ridleyi. In area 15 (SE Sumatra) *F. nivea* and *F. stipularis* are endemic. Other
species occurring in this area are *G. crassifolius*, *S. ferrugineus*, *S. littoralis*, *S. ma-
cropterus*, *S. ridleyi*, and *X. fruticulosum*.

17. The *west coast of Sumatra* (Sumatra coast) and its islands are largely the same as
the Woyla terranes of Metcalfe (Chapter 3). These terranes rifted in the Late Jurassic
from the Gondwana margin towards the Eurasian one.

Only *S. ferrugineus* and *X. ferrugineum* are found here.

18. *West Java* (W Java) has long been part of the continent under which the Indian
Plate was subducting. The remaining part of Java is Cenozoic volcanic rock on
marine basement, that developed as result of the eastward extending volcanic arc.
Genianthus macrophyllus is present as an endemic in this area. Other species occur-
ring here are *G. ellipticus*, *G. crassifolius*, *S. ferrugineus*, *S. littoralis*, and *X. fruticu-
losum*.

19. *Southwest Borneo* (SW Borneo) is in fact the oldest part of Borneo (Borneo Base-
ment). It rifted from the Eurasian margin in Jurassic times due to the opening of the
Proto-South China Sea.

In this area *X. johannis-winkleri* occurs as an endemic. Other species here are *F.
brachybotrys*, *F. splendidissima*, *S. auritus*, *S. ferrugineus*, *S. hirsutus*, *S. latistipulus*,
S. macropterus, *S. maingayi*, *S. persicinus*, *X. capitatum*, *X. olivaceum*, and *X. pubi-
stylosum*.

20. The *Semitau* (extended towards the region around Kuching) has a similar history
as SW Borneo, and collided with the Borneo Basement in the Cretaceous.

Endemics in this area are *X. involucratum*, *X. sessile*, and *X. setosum*. Other species
are *F. brachybotrys*, *F. splendidissima*, *G. maingayi*, *S. apoensis*, *S. auricomus*, *S.
ferrugineus*, *S. macropterus*, *S. maingayi*, *S. persicinus*, *S. viridis*, *X. olivaceum*, and
X. pubistylosum.

21 & 22. *Sarawak and the central mountain range of Borneo* (Sarawak/C Borneo) & *Northwest Borneo* (NW Borneo) are part of the Rajang-Crocker accretion that was uplifted in the Early Miocene, but before was part of a Gulf of the Proto-South China Sea. Since Palaeocene times the other parts of Borneo (also including W Sulawesi) were already land areas.

Fordia brachybotrys, F. splendidissima, S. albus, S. auricomus, S. ferrugineus, S. hirsutus, S. latibractea, S. macropterus, S. multiflorus, S. oblongifolius, S. persicinus, S. viridis, X. borneense, X. brookei, X. capitatum, X. glabrum, X. olivaceum, X. pubistylosum, and *X. semiorbiculare* are present in both areas. In addition *G. ellipticus* and *X. cylindricum* occur in area 21, and *G. crassifolius, S. maingayi,* and *S. sanguineus* in area 22. Endemic in area 21 are *X. alopecurum, X. glomeratum, X. grandifolium,* and *X. minus.* In area 22 there are no endemics.

23. *Northeast Borneo* (NE Borneo) is suggested by Hutchison (1989; Chapter 3) to be partly a continental fragment (Segama block), rifted off the Chinese margin in the Oligocene.

Fordia brachybotrys, F. splendidissima, F. rheophytica, S. albus, S. ferrugineus, S. hirsutus, S. latistipulus, S. macropterus, and *X. capitatum* are present. Endemic in this area is *X. longipediculatum.*

24. *Central East Borneo* (CE Borneo) consists of the continental fragment Mangkalihat, and the Kutei and Tarakan basins. This area originated after the opening of the Makassar Strait in the Early Tertiary. The Tarakan basin was a Miocene delta. Mangkalihat is regarded as a continental fragment rifted off Gondwana in the Late Jurassic together with W Sulawesi, and contains the oldest fossils of Borneo.

Fordia brachybotrys, F. splendidissima, G. ellipticus, S. ferrugineus, S. hirsutus, S. latistipulus, S. macropterus, S. maingayi, S. multiflorus, S. oblongifolius, S. persicinus, S. sanguineus, S. viridis, X. pubistylosum, and *X. semiorbiculare* are present. Endemic are *G. valvatus* and *X. foliaceum.*

25. The *Meratus* mountains have been uplifted rather late. Up to the Oligocene this part was continuous with the basins at both sides. It has been continuous with the South China magmatic belt (Chapter 3: Fig. 3.16), and consists of Cretaceous rocks. Together with the Semitau and SW Borneo, this is the oldest part of Borneo. The other parts of Borneo all accreted in later times, although some parts have a considerable age (see Mangkalihat in area 24).

Species occurring here are *F. brachybotrys, F. splendidissima, S. ferrugineus, S. littoralis, S. persicinus,* and *X. capitatum.*

26. *Palawan* is part of the displaced Chinese 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 17 Ma.

Here *S. ferrugineus* and *X. ferrugineum* are present.

27 & 28. *Northern Philippines* (N Philippines) & *southern Philippines* (S Philippines) are both part of a geological complex and active region. The geology indicates different origins of parts of the Philippines. Most of the southern part is 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. Part of Mindoro (see also Palawan) is part of the continental sliver that rifted from the Chinese continental margin.

Of the studied genera no endemic species are present in this region. Species occurring in area 27 are *G. ellipticus, G. rectinervis, S, maingayi, S, sanguineus,* and *X. ferrugineum*; in area 28 *F. brachybotrys, G. rectinervis, S. apoensis, S. maingayi,* and *X. ferrugineum* are present.

29. *Sulawesi* is geologically very complex. However, the groups studied are not well represented in this area and, consequently, no subdivision of Sulawesi can be made using the present data. West Sulawesi has been part of the east margin of Borneo, but rifted away after opening of the Makassar Strait. Other parts have been rifted from the Australian margin, and collided with the west of the island 10 Ma.

Only the widespread species *S. ferrugineus* and *G. ellipticus* occur on Sulawesi.

RESULTS

The results of the analysis with PAUP under assumption 0 are: 19 equally most parsimonious area cladograms with a length of 366 steps and a consistency index of 0.45 (h.i. = 0.55, r.i. = 0.66, r.c. = 0.3). The 50% majority rule consensus tree and the strict consensus tree of the 19 most parsimonious area cladograms are presented here in Figure 4.4; differences 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 Is), 3) the clade of Sumatra coast and Palawan, and N Sumatra. The percentages of the trees that support a particular branch are indicated in the cladogram, but this does not mean that they support all the branches at the same time.

Groups that can be recognised in the cladogram are:

1) A group of areas on the *continent of SE Asia*: Kerala, India, W Burma/E India, and Yunnan/N Thailand with as sister Indochina. India shows up with an empty branch, because there are no endemics in the area, and the species occurring in India are also present in other related areas. In the strict consensus and the Adams consensus tree this clade is collapsed, except for Yunnan/N Thailand and Indochina. The reason for this is that W Burma/E India can move around in this clade (Fig. 4.4). Mergui/Tenasserim and the Andaman Islands are connected to this continental SE Asian area-group, but in different ways. This is probably caused by the low number of taxa in these area.

2) A small clade of two areas on the *Isthmus of Kra*: S Thailand and Penang/Kedah. This clade is added to the base of the continental SE Asia clade.

3) A group of areas in *Borneo*: Meratus, SW Borneo, Semitau, NE Borneo, NW Borneo, CE Borneo, Sarawak/C Borneo. The area NW Borneo is inhabited only by species occurring in areas sister to this area; because it does not have endemics, it shows empty branches.

4) A group on the *Malay Peninsula* extending into Java: W Malaya, Singapore, E Malaya, SE Sumatra, W Java, and connected to this group the N Philippines and S Philippines as sister areas.
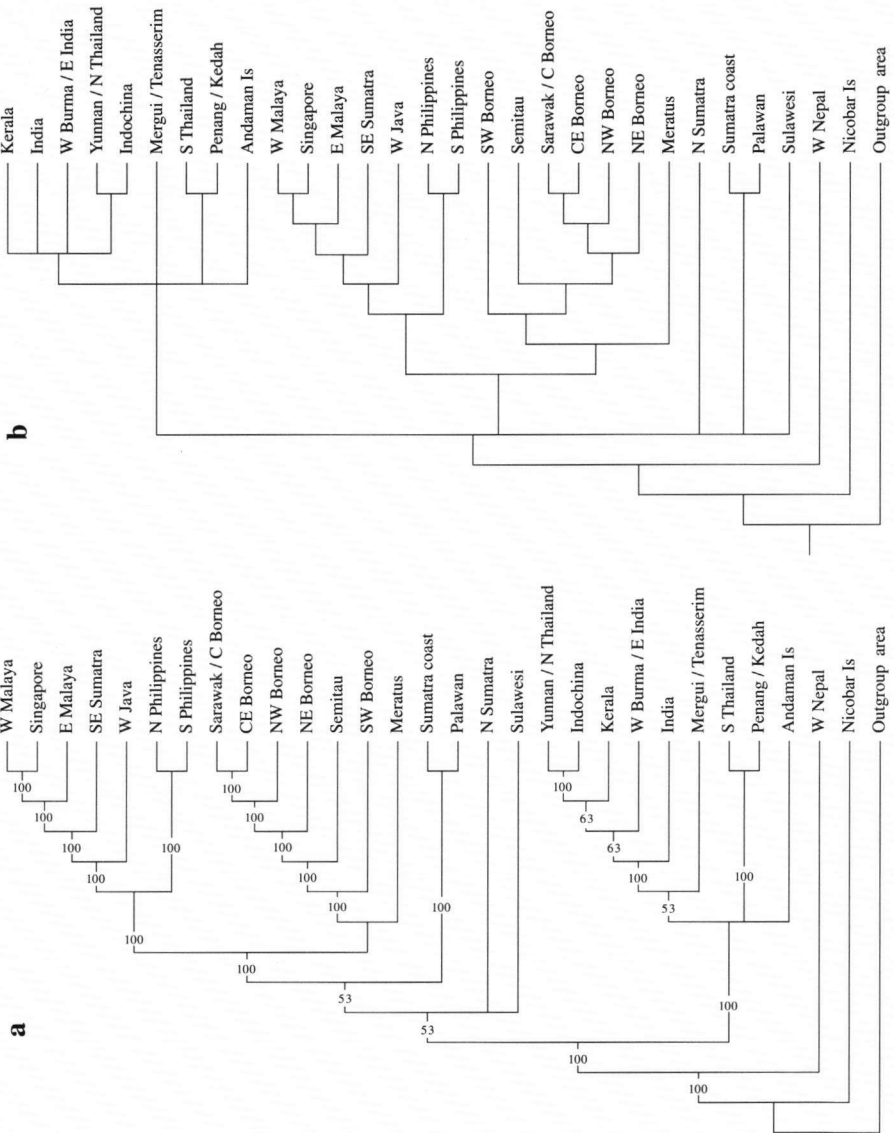
Figure 4.4. — **a**: 50% majority rule consensus tree of the nine-teen equally most parsimonious area cladograms obtained by analysis with PAUP of the area-taxon matrix of *Spatholobus, Butea, Meizotropis, Fordia, Genianthus,* and *Xanthophytum*, under assumption 0 (missing areas coded as 0). Values on the branches indicating 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 Is), 3) the clade of Sumatra coast and Palawan, and N Sumatra.
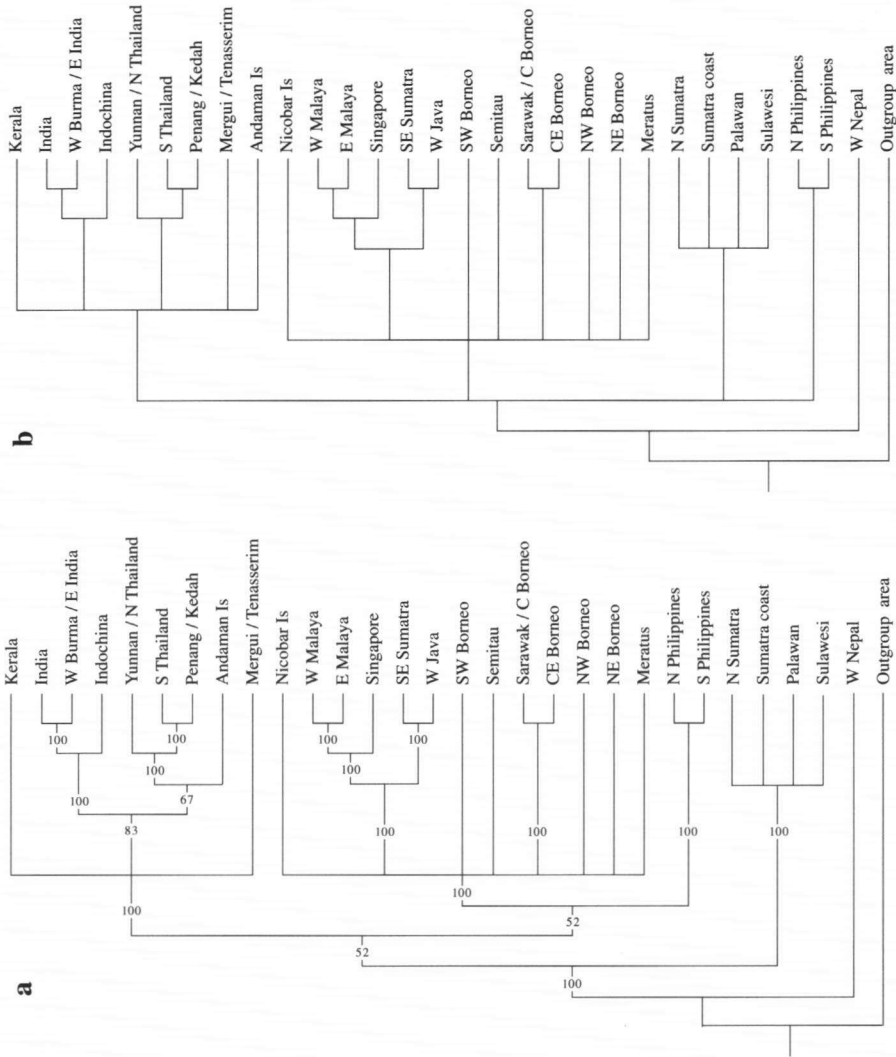
Figure 4.5. Consensus trees of all 324 equally most parsimonious area cladograms obtained by analysis of the area-taxon matrix of *Butea, Fordia, Genianthus Meizotropis, Spatholobus,* and *Xanthophytum* with PAUP, under assumption 1 (missing areas coded as ?). — **a**: majority rule consensus tree with indication of the percentage of trees supporting a specific clade. — **b**: strict consensus tree.

Some of the areas are placed low in the cladogram, probably due to lack of information: Nicobar Is, W Nepal, Sulawesi, Palawan, Sumatra coast, N Sumatra, and Andaman Is and Mergui/Tenasserim. The datamatrix shows, e.g., that on the Nicobar Islands only one species of *Genianthus* is present, and only one species of *Genianthus* and one of *Spatholobus* occur in Sulawesi. Palawan, Sumatra coast and N Sumatra are often connected to the Borneo and Malaya clades; the Andaman Is and Mergui/Tenasserim are often connected to the SE Asian continental clade.

Analysis under assumption 1 (missing areas coded as '?') resulted in 324 equally most parsimonious cladograms (length 316, c.i. = 0.52, h.i. = 0.48, r.i. = 0.69, r.c. = 0.36). The consensus of these 324 cladograms is shown in Figure 4.5. There are not as many clades resolved as in the results of the assumption 0 analysis. It is remarkable that the Borneo clade is nearly totally collapsed into polytomy.

The strict consensus tree (Fig. 4.5a) shows only resolved clades for:

1) Part of the *continental SE Asia group*: India as sister to W Burma/E India and Indochina; the rest of the group is a polytomy with the other areas mentioned above (the assumption 0 analysis).
2) The *Isthmus of Kra group* (S Thailand, Penang/Kedah) together with Yunnan/N Thailand.
3) The *Malay Peninsula group*: W Malaya, E Malaya, Singapore, W Java and SE Sumatra.
4) The complete *Borneo group* (but including the Nicobar Islands) has collapsed into a polytomy with the Malay Peninsula clade.

The aforementioned groups 1 & 2 and 3 & 4 are placed as a polytomy to the sister areas N Philippines and S Philippines, and the areas N Sumatra, Sumatra coast, Palawan and Sulawesi.

The 50% majority rule consensus tree is better resolved for the continental SE Asia group (Fig. 4.5b). The clades with 100% support are—naturally—the same as the clades for the strict consensus tree. The tree shows two major groupings:

1) A *continental SE Asia group* of India, W Burma/E India, Indochina, with as sister the group of S Thailand, Penang /Kedah, Yunnan /N Thailand, and the Andaman Islands. Kerala and Mergui/Tenasserim are both connected to the base of these clades. The place of the Andaman Islands, Kerala, and Mergui/Tenasserim is not certain.
2) The *Malay Peninsula group*: W Malaya, E Malaya, Singapore, W Java and SE Sumatra, in polytomy with the collapsed Borneo clade and the Nicobar Islands. The Philippines are added to the base of the group mentioned under 2. The unresolved clade of N Sumatra, Sumatra coast, Palawan, and Sulawesi, at the base of the cladogram, with W Nepal at its very base. This last group was also at the base in the PAUP area cladogram under assumption 0, and probably remains uninformative. W Nepal is basal to all other clades.

Figure 4.6. Generalised area cladogram
obtained by analysis of the area-taxon
matrix of *Butea, Fordia, Genianthus,
Meizotropis, Spatholobus*, and *Xan-
thophytum* with CAFCA, under assump-
tion 0 (missing areas coded as 0 in the
datamatrix).

Analysis with CAFCA under as-
sumption 0 leads to 37 cliques, out
of which one is chosen by the mini-
mal number of state changes (see
Fig. 4.6; 450 steps, c.i. = 0.37, r.c.
= 0.19; for comparison with the oth-
er results, length is 447 steps when
calculated by PAUP). Here we see
some of the already known groups
again, with some slight changes:

1) The groups in *Borneo* (Meratus,
   SW Borneo, Semitau, NE Bor-
   neo, CE Borneo, Sarawak/C
   Borneo and NW Borneo), in-
   cluding the S Philippines at the
   base of the clade.

2) The *Malay Peninsula–Sumatra
   group* (W Malaya, E Malaya,
   Singapore, SE Sumatra, and in addition to the PAUP cladograms Yunnan/N Thai-
   land at the base of Singapore) and the *Isthmus of Kra group* (S Thailand and
   Penang/Kedah), with Indochina at the base of these two groups, forming one
   clade.

3) The *continental areas in SE Asia*, i.e. Kerala, India, W Burma/E India, Mergui/
   Tenasserim, the Andaman Islands, together with W Java and the N Philippines are
   collapsed into one polytomy at the same level as the base of the two former groups
   together.
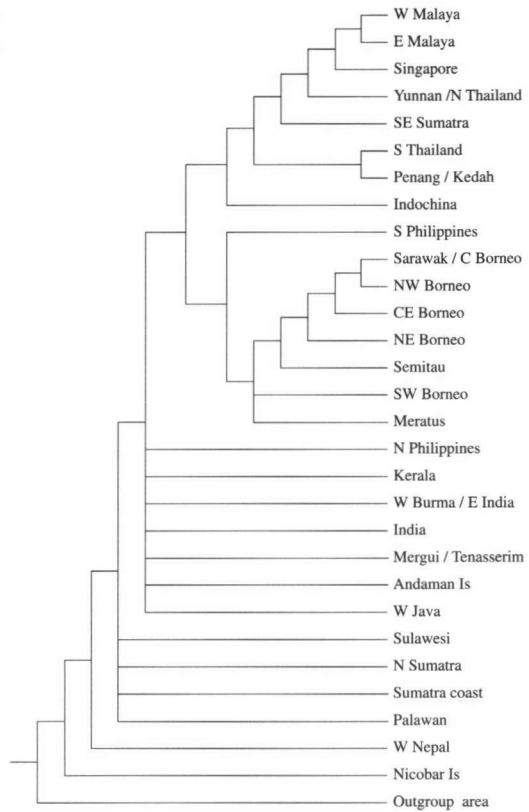
To the base of this, the configuration is the same as in the PAUP analysis under as-
sumption 0: the unresolved clade of Palawan, Sumatra coast, N Sumatra and Sulawesi;
at the base W Nepal; and then the Nicobar Islands at the very base.

Analysis with CAFCA under assumption 1 resulted in 1 most parsimonious tree out of
133 cliques found (length 417, c.i. = 0.396, r.i. = 0.68, r.c. = 0.48; Fig. 4.7). Now a
slightly different cladogram is the result. Some groups are the same as in the cladogram
obtained by the analysis under assumption 0:

Figure 4.7. Generalised area clado-gram obtained by analysis of the area-taxon matrix of *Butea, Fordia, Genianthus, Meizotropis, Spatholobus*, and *Xanthophytum* with CAFCA, under assumption 1 (missing areas coded as '?' in the datamatrix.

1) The *Borneo group* (including also the S Philippines).
2) The *Isthmus of Kra–Malay Peninsula group* with Indochina at the base, but without Yunnan / N Thailand. Here, however, not as sister group to the Borneo one, but between the Borneo group and the rest.
3) The *continental SE Asia group* is more resolved than in the tree obtained with the CAFCA analysis under assumption 0 (W Burma / E India, Yunnan / N Thailand, India, W Nepal the Nicobar Islands, and Kerala). All other basally placed areas in the assumption 0 cladogram (Mergui / Tenasserim, the Andaman Islands, N Sumatra, Sumatra coast, W Java, Palawan, N Philippines, and Sulawesi) are now in a polytomy at the base of the continental SE Asia group.
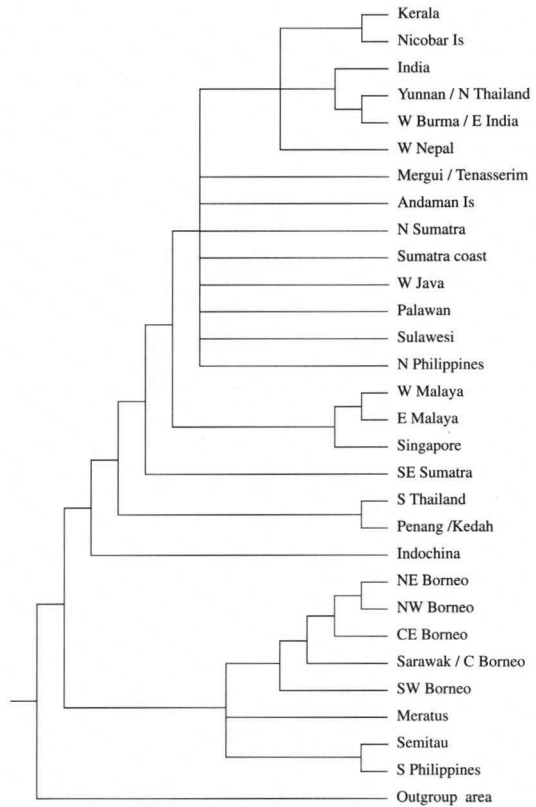
EVALUATION OF THE RESULTS

The results described above show that there are parts in all the obtained area cladograms that have similar topologies: a continental SE Asia group (unresolved under analysis with CAFCA), a Borneo group (in CAFCA including the S Philippines as well), an Isthmus of Kra group and a Malay Peninsula–SE Sumatra group (in CAFCA these last groups together with Indochina at the base). The area cladograms obtained by analysis with PAUP are the best resolved ones. As suggested in Sosef (1994) the clades in the cladogram found by PAUP were checked on the absence of taxa. Fortunately, the problem inherent in BPA analysis (Van Welzen, 1989, 1992), the definition of groups of areas on the absence of taxa, did not occur here. Sosef indicates that it is better to use BPA (PAUP) than CCA (CAFCA) in case of many extinction or dispersal events. Probably this is the reason for the better resolution of the PAUP cladogram compared to the one obtained by CAFCA under assumption 0. The better resolution of the cladogram,

however, cannot be the only selection criterion. Comparison with geological informa-
tion is another possibility to discriminate between the four possibilities presented above,
although one has to be careful for circular reasoning in case of setting up a historical
biogeographical hypothesis.

In contrast to the other area cladograms, the place of the unresolved areas in the
CAFCA assumption 1 area cladogram is near the top of the tree instead of near the
base. The continental SE Asia group plus the unresolved part of the tree are placed in
such a way that the group of the Malay Peninsula–SE Sumatra–Indochina becomes a
paraphyletic base of this part of the tree; the Borneo group forms the other part of the
tree. It is possible that this result is mainly due to the fact that those areas, with a lot of
missing data, all received a '?', which is translated in these areas as present (a '1') in
connection to species occurring in the continental part of SE Asia.

The following areas are not very informative due to a lack of species occurrences,
and probably for that reason appear low at the base of the cladogram: Sulawesi, the
Nicobar Islands, W Nepal, N Sumatra, Sumatra coast, Palawan.

On the Nicobar Islands only one endemic species, *Genianthus nicobarensis*, is pres-
ent. This single species, however, is outnumbered by the other species in the clade to
define a node in the area cladogram, and the area is placed basal in the area cladogram.
The place of the Nicobar Islands in the assumption 1 area cladograms must be artificial
as well: in the PAUP area cladogram it is placed within the group consisting of the
areas in Borneo and the Malay Peninsula, where one would expect it to be considering
the distribution of its closest relatives. Under CAFCA, however, it is placed as sister to
Kerala. This is probably another artefact of the analysis under assumption 1.

For West Nepal the situation is different: this area is probably placed at this basal
position due to the place of the species occurring in this area; the species present in this
area (*Butea monosperma, Meizotropis buteiformis, M. pellita*, and *Spatholobus par-
viflorus*) are all basal in the phylogenetic cladogram.

COMPARISON WITH THE GEOLOGICAL INFORMATION

It is not possible to construct a cladogram-like structure of the geological information
(Chapter 3), because in the geological history of Southeast Asia the areas did not split
up, but accumulated in SE Asia from the Gondwanaland margin. In the case of divid-
ing areas (vicariance events), it is possible to construct a geological 'cladogram' in
which the branches represent the geographical entities. The splitting up in this case,
however, took place at the Gondwanaland margin, after which rifting occurred. The
continental fragments rifted in different eras towards what is now SE Asia, and welded
together into one large area (China/Indochina etc.) or some smaller parts (Sumatra,
Borneo) within the SE Asian area. Below, these splitting and welding events are sum-
marised; the different continental fragments and sutures are shown in Figure 3.5.

Before the Eocene no reliable fossils are known for the Leguminosae, and one can-
not expect to see vicariance events before that time in this study. Only since Miocene
times have fossils been found that can be attributed to specific genera within the Legu-
minosae. This is probably the reason why the areas of distribution on the continent and

Indochina (e.g., area 4, 5, and 6 in Fig. 4.3) 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 developed.

Before the Eocene most of the SE Asian region was already present, but tectonic movement was still going on. The Tethys Ocean was subducting below the SE Asian margin that formed a volcanic arc from Lhasa, W Burma, Sumatra and part of Java to W Sulawesi, where the arc extended northwards. In the Early Eocene India started to collide with Asia. From the Oligocene to the mid-Miocene the South China Sea opened, and rifting from the Chinese continental margin towards the south took place. The Andaman Sea Basin and Thai Basin opened, and the Malay Peninsula rotated. Several changes took place in Borneo. In the Palaeocene large parts of Borneo were not yet uplifted, but an extensive landmass south and southeast of what is now Sarawak and Sabah was present, up to what is now W Sulawesi. Sarawak and Sabah were part of the Rajang Basin, facing the Pacific Ocean. The Crocker range represents an accretionary complex and deltas were present receiving sediment from the uplifted parts of Borneo as well as from the Indochinese part of the Sunda shelf. In Late Oligocene times, large parts of Borneo were inundated during a marine transgression phase. The Makassar Strait opened in the Late Eocene/Oligocene resulting in the separation of W Sulawesi. The rest of Sulawesi arrived at the end of the Oligocene. The Meratus mountains were uplifted rapidly in the Late Miocene-Pliocene. In the Miocene the Philippines were formed.

Until the mid-Miocene there were several periods of lower sea level. In the Late Oligocene, the sea level was as low as 250 m below the present one, thus the Sundaland plateau was for the largest part above sea level (see Fig. 3.4). 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 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, see also Chapter 3) this is 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).

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 that is obtained by analysis with PAUP assumption 0 is between the *continental SE Asia group* (inclusive 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 (see also Table 3.1). It is clear from the reconstructions of Rangin et al. (1990b), that during high sea level there was a separation between the Malay Peninsula and Indochina. It is im-

possible 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 specula- tive, however, because on the Andaman Islands only the widespread, but continental, species *Spatholobus acuminatus* is found. It would be better (for future research) to add a genus to the analyses with one or more endemics on the Andaman Islands.

All area cladograms, except the one obtained by PAUP assumption 1, are resolved for the areas in *Borneo*. In the area cladogram obtained by PAUP assumption 0 (Fig. 4.4a), 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 Creta- ceous. This part of Borneo is probably uplifted in the same period as the Meratus (Hutchison, 1992). The next area, NE Borneo, was, according to Hutchison (1992), 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 up to the Late Miocene-Pliocene, and were probably submerged during some of the sea level rises. The first four splits (in both assumption 0 general area cladograms) may indi- cate these uplift events and the related changes in climatological/ecological factors. The other parts of Borneo in these times consisted of the large Rajang Basin and the Crocker Range (Sarawak/C Borneo and NW Borneo). The last split in the Borneo group (PAUP assumption 0) is formed by the central parts of Borneo: Sarawak/C Bor- neo 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).

The *Malay Peninsula* group is another group that can be found in most area cladograms. W Malaya and E Malaya form in most cases the top of this clade together with Singapore. SE Sumatra is at the base. In the PAUP area cladograms W Java is basal in the same clade, and the N and S Philippines are connected to the base as well. In the area cladograms obtained by CAFCA, W Java and the N Philippines form part of the polytomy with the unresolved SE Asian areas; the S Philippines are placed basal to the Borneo group. There is no difference between the area cladograms in the sister relationship between the E Malaya part of the Indochina block and the W Malaya part of the Sibumasu block; these have a sister relation to each other in the area cladogram together with Singapore. 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 distri- bution areas may of course be due to ecological or climatological factors as well: the area around Singapore and SE Sumatra are both lowland areas. The E and W Malaya parts of the Malay Peninsula consist largely of the 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 the moun-

tains 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 in colour of Rangin et al. (1990b) indicate that during certain periods of high sea level, between the Middle Eocene and the Pliocene, there were emergent areas in Borneo, the Malay Peninsula, large parts of Sumatra, and West Java (Fig. 3.4). Other parts are shown as submerged, although based on continental crust, e. g., the areas 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 PAUP assumption 0 analysis this clade is in polytomy to the continental SE Asian areas and the Andaman Islands. In the CAFCA analyses the same clade is found at the base of the Malay/Sumatra group (with Indochina). They form the region around the *Isthmus of Kra*, which was easily inundated during periods of high sea level (Fig. 3.4). Floristically this is the place where the distribution of the species from everwet and seasonal areas overlap. The Malay Peninsula group as indicated by the PAUP assumption 0 area cladogram, which also included WJava at the base of the group, fits this reconstruction best. It is probable that the area around the Isthmus of Kra was later invaded, an assumption supported by the fact that 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). In this view, the place of the Isthmus of Kra clade basally to the continental SE Asia areas is the best explanation, as is found in the area cladogram obtained by PAUP assumption 0.

The fact that the N and S Philippines are placed closely to each other favours the PAUP assumption 0 area cladogram. The place of the Philippines as close to Borneo as it is to West Java (and the rest of the Malay/Sumatra clade) perhaps indicates that Borneo had its own history, separate from the Philippines.

On the basis of the best resolved tree and the geological comparisons I give preference to the PAUP assumption 0 area cladogram, especially because of the relations within the Malay/Sumatra group (no intruding continental areas), the resolved part of the continental SE Asia group, the place of the Isthmus of Kra clade.

RECONSTRUCTING THE HISTORY OF SPATHOLOBUS

As shown above, the differences between the PAUP and CAFCA analyses are mainly in the unresolved part of the area cladogram, where either the continental SE Asian areas (CAFCA) or the Borneo areas (PAUP assumption 1) are unresolved. In order to reconstruct the possible history of speciation within *Spatholobus*, the phylogeny of the genus *Spatholobus* and allies (Fig. 4.1) is optimised on the generalised area clado-

Figure 4.8. Generalised area cladogram obtained by analysis with PAUP of the area-taxon matrix of *Butea, Fordia, Genianthus, Meizotropis, Spatholobus,* and *Xanthophytum,* under assumption 0 (= missing areas coded as 0 in the datamatrix). Species of *Butea, Meizotropus,* and *Spatholobus* are superimposed on the area cladogram. ● = present; x = absent.
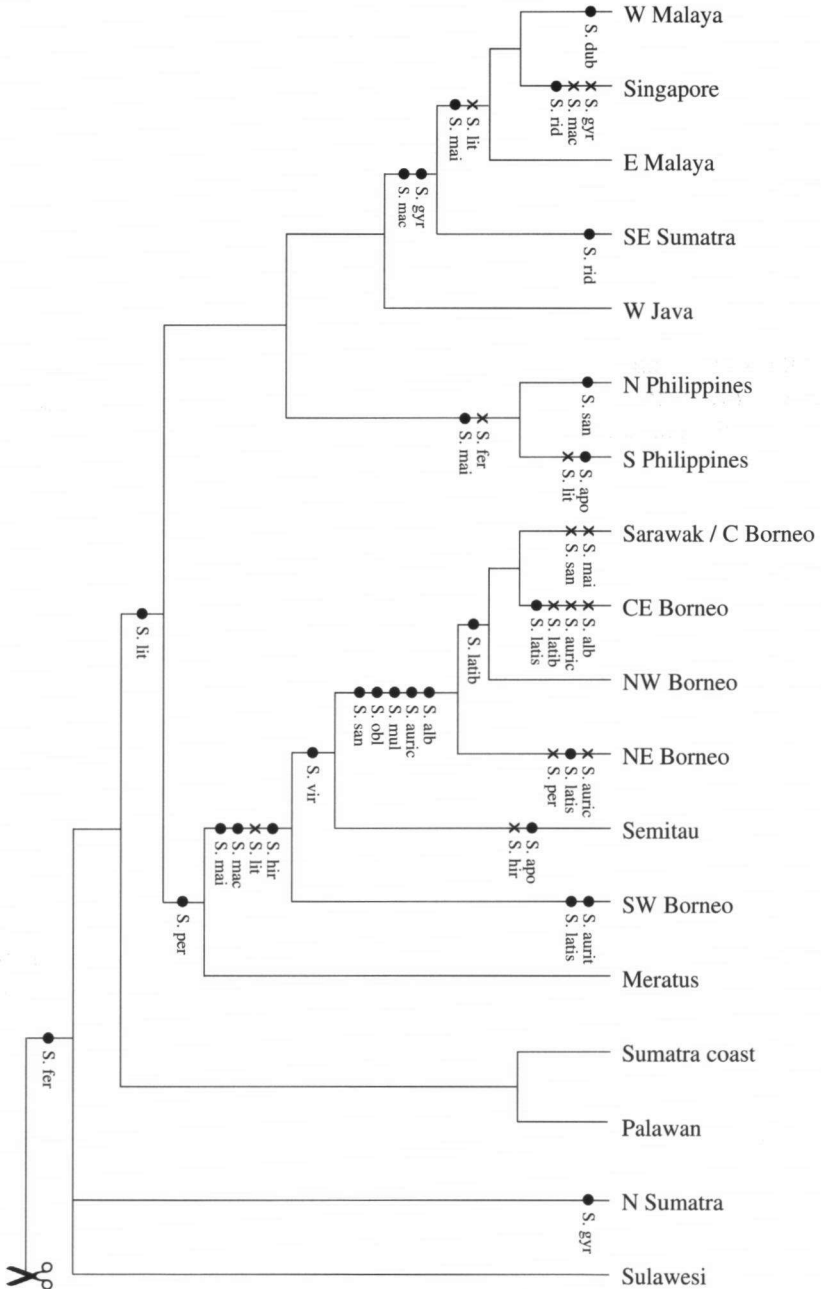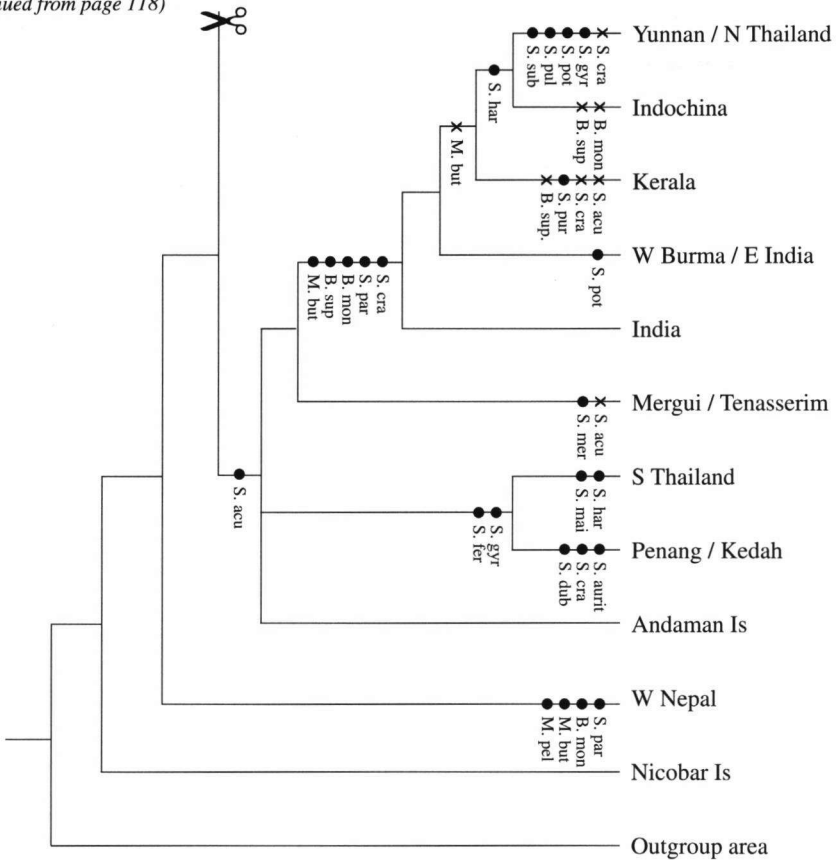
gram that is the result of the biogeographical analysis with PAUP under assumption 0 (Fig. 4.8). The speciation events indicated by the cladogram of *Spatholobus* will be used to relate the general area cladogram to the phylogenetic history of the genus as reconstructed in the *Spatholobus* cladogram. It is assumed that the phylogenetic clado-gram and the general area cladogram correctly reflect the history of speciation of the genus and the historical relation of the areas respectively.

Below, the implications of the optimisation on the area cladograms is described. The most representative parts of the cladogram of *Spatholobus* and corresponding parts of the area cladogram will illustrate this. When in the text an ancestor (A) is men-tioned, a number (in parentheses) is given indicating its place in the cladogram (Fig. 4.1a). The basal – for the greater part polytomous – areas, however, are mostly ex-cluded, i.e., N Sumatra, the west coast of Sumatra, Palawan, W Nepal, the Nicobar Is-lands and Palawan.

In all area cladograms *Spatholobus* (and also *Butea* and *Meizotropis*) is absent from the Nicobar Islands; in the PAUP assumption 0 area cladogram this is considered to be a primitive absence, in the other area cladograms the option of extinction is also open.

The second area that splits off in the area cladogram is W Nepal. Of the genus *Spatholobus*, only *S. parviflorus* occurs here. If this presence is due to dispersal from, e. g., India, the rest of *Spatholobus* can be assumed to be originally present (i.e., the ancestral area of the genus) in all four area groups (continental SE Asia, Malay Peninsula/ SE Sumatra, Isthmus of Kra and Borneo).

The areas at the base of the Sundaland clade (N Sumatra, the SW coast of Sumatra, Palawan and Sulawesi) are inhabited by only one species of *Spatholobus*, the widespread *S. ferrugineus*. The closely allied *S. gyrocarpus* occurs also in N Sumatra, but not in the other three areas mentioned.

The ancestor of *Butea* and *Meizotropis* (A45) is present on the continent of SE Asia, but not in Indochina or Mergui/Tenasserim (Fig. 4.9). It is also found in W Nepal with its area placed low in the cladogram. It is possible that W Nepal split off early, and that the other species never reached this region because the area became isolated by the extreme climatic circumstances. *Meizotropis* (A44) has a more restricted distribution than *Butea*, and probably originated in India and W Burma/E India (in fact the actual area will be even more restricted, but these are the areas delimited for this analysis).

The ancestor of *Spatholobus* (A47) is optimised in the area cladograms as occurring in the whole area, except the Nicobar Islands (Fig. 4.9). The most basal splits, however, are the ones of *S. parviflorus*, and those of the genera *Butea* and *Meizotropis*, all occurring only on the SE Asian continent. Because all later clades have ancestors optimised as occurring one way or another in both the SE Asian areas and the areas southwards and including the Isthmus of Kra, the ancestors of these first splits (*S. parviflorus, Butea* and *Meizotropis*) are optimised as occurring in the whole area as well. In this option, the parts of Borneo and the Malay Peninsula became isolated later, providing opportunities for geographical differentiation in these isolated areas. It is, however, not necessary that the first ancestor occurred in the whole area. It is easily possible that the limits of the area were those of the present distribution of *S. parviflorus*,
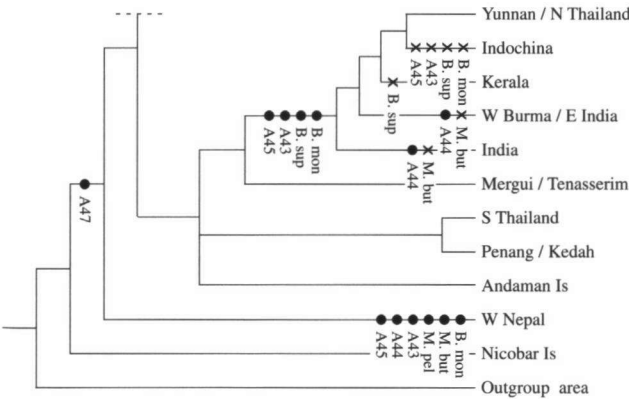
Figure 4.9. Part of the area cladogram (PAUP, assumption 0) showing *Butea, Meizotropis* and the ancestor node of *Spatholobus* (A47). ● = present; x = absent.
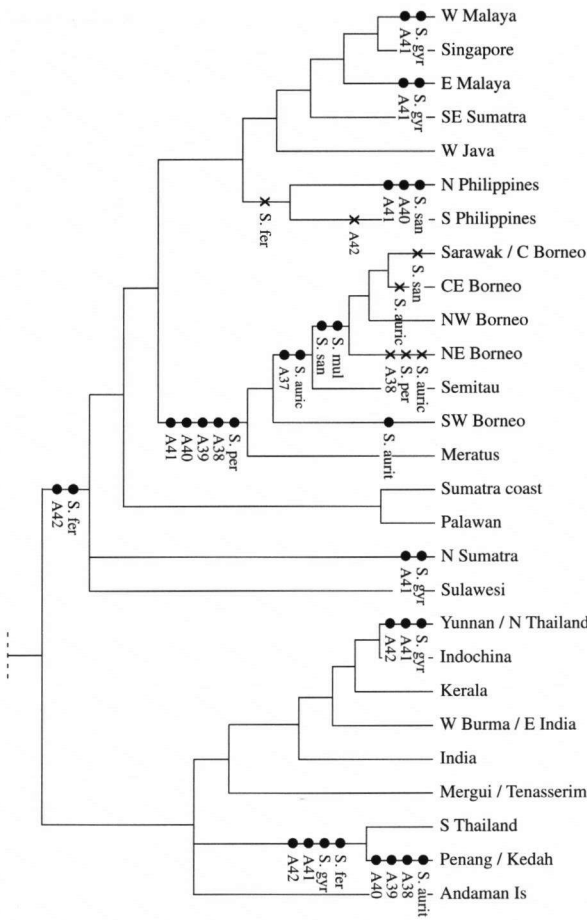
Figure 4.10. Area cladogram showing the *Spatholobus fer-rugineus*-clade. ● = present; x = absent.

and that at a certain time the genus *Spatholobus* dispersed over the whole area, when the circumstances were favourable (e.g., low sea level during Late Oligocene). If one would wish to date the ancestor of the group much earlier, the group could have had a distribution including SW Borneo, because in Early Eocene times there was an emerged land mass connecting the SE Asian continent to what is now SW Borneo. In Middle Eocene times, the high sea level already separated Borneo from Sumatra and the Malay Peninsula.

The ancestor of the *S. ferrugineus*-clade (A42), the second split in the cladogram, can be found in all of the Borneo areas, the Malay Peninsula/SE Sumatra areas (including W Java), the Isthmus of Kra, and Yunnan/N Thailand (Fig. 4.10). In the CAFCA results Yunnan/N Thailand is incorporated in the Malay Peninsula/SE Sumatra group of areas, whereas the analysis with PAUP resulted in combining Yunnan/N Thailand with the continental SE Asia areas, and in the Malay Peninsula/SE Sumatra group including W Java (instead of sending it into polytomy). If the total of extant areas is

indeed reflecting the ancestor area, it will be most parsimonious to assume that both
W Java and Yunnan/Thailand belong to the Malay Peninsula/SE Sumatra group of
areas. If, however, part of the area has been reached by one or more (ancestor) species
in later times by dispersal, it is very well possible that, e.g.,Yunnan/Thailand is part of
the continental SE Asia group of areas instead of the Malay Peninsula/SE Sumatra
area group. However, the fact that the ancestor of the *S. ferrugineus*-clade is present in
the area Yunnan/Thailand, is due to the presence of only one specimen of *S. gyrocarpus*,
a species that occurs otherwise only south of the Isthmus of Kra. This could be ex-
plained by an occasional dispersal of this species to the north in more recent times. In
the latter case the result of PAUP reflects the history better than the result of CAFCA.
On the other hand, if dispersal from the ancestral area into W Java took place, it is
possible that the CAFCA area cladogram gives a better solution. The ancestor of the
S. ferrugineus-group is shown otherwise absent from the continental SE Asia areas
and present in the whole of the areas from the Isthmus of Kra southwards. This indi-
cates that rather early in the history of this group there has been a vicariance event
between the continent of SE Asia and the other parts of its distribution area. It is pos-
sible that after a period of isolation, i.e. high sea levels (Late Eocene/Early Oligocene,
mid-Miocene, Pliocene), speciation took place. In the palaeogeodynamic maps of
Rangin et al. (1990b) it is obvious that during all periods of higher sea level the Isth-
mus of Kra region was inundated, thus leaving a smaller or larger gap between the
Malesian region and the continent of SE Asia (Fig. 3.4). The *S. ferrugineus*-group,
however, either never reached the S Philippines, or it went extinct later. In the CAFCA
area cladogram the N Philippines are not included in the Borneo-Malay Peninsula
groups, but are placed lower in the area cladogram, and in polytomy. It is possible that
the occurrence of *S. sanguineus* in the N Philippines (the only species in the *S. ferru-
gineus*-group occurring here) is due to dispersal in later times. In this case the *S. fer-
rugineus*-group is primitively absent from the Philippines, and may even have been
present in the area before the Philippines arrived. This would imply at least a Middle
to Late Miocene age for the ancestor of the *S. ferrugineus*-group. It is also possible that
the ancestor never reached the Philippines, although these islands were already present
in the region. However, it is hard to believe that such a widespread species as *S. fer-
rugineus* did not disperse over, e.g., the whole island of Java, or from Palawan into the
Philippines. It is more satisfactory in this case to invoke climatological or ecological
factors to explain the absence of *S. ferrugineus* than to explain it by 'primitive' ab-
sence (because it could not reach the Philippines). The Philippines, and also the more
eastern and central parts of Java have a relatively dry climate, compared to the everwet
rain forest climate (e.g. of Borneo). It is possible that the ancestor of *S. ferrugineus*
became extinct in the Philippines, and that the later developed *S. sanguineus* is better
adapted to drier circumstances, although it is occurring in the wet parts of Borneo as
well. *Spatholobus gyrocarpus* developed, as second species in this clade, on the Malay
Peninsula and N Sumatra. The barrier between Borneo on the one side and the Malay
Peninsula and Sumatra on the other was probably too large to bridge. *Spatholobus
gyrocarpus* occurs in the higher parts of the Malay Peninsula, an area that was continu-
ous with the higher parts of N Sumatra during periods of low sea level. *Spatholobus*

gyrocarpus is absent from the lower parts of the Malay Peninsula (towards Johore and Singapore) and from SE Sumatra. *Spatholobus sanguineus,* on the other hand, probably developed on the northern and central part of Borneo. These are parts that later accreted to the older parts of SW Borneo, Meratus and Semitau. According to Hutchison (1992) these older parts formed a single landmass continuous with W Sulawesi and the Java Sea in the Tertiary. In Early Miocene times the accreted sediments of Sarawak and the Crocker Formation were compressed and uplifted. The younger parts were uplifted in the Late Miocene-Pliocene after having been filled with sediments. This is also the case for *S. sanguineus,* which occurs in areas that contain the higher parts of – in this case – Borneo and the northern Philippines. It is not evident from the specimen labels, however, that the species themselves occur only in higher altitudes; on the contrary, the only indication of altitude for *S. gyrocarpus* is up to 160 m above sea level; for *S. sanguineus* the altitude is indicated from low altitudes up to 1000 m. The fact that *S. sanguineus* is found on the northern Philippines indicates either a vicariance between Borneo and the Philippines (a more recent dispersal event), or a primitive presence of the clade in the Philippines. In the latter case *S. sanguineus* is a remnant of a once larger distribution of the *S. ferrugineus*-clade. Consequently, the ancestor of the *S. ferrugineus*-clade was already present in the area in Late (or even Middle) Miocene times, and *S. sanguineus* developed in the newly accreted and uplifted areas in the northwest of Borneo and the Philippines, which came within reach especially after a lowering of the sea level in the Late Miocene. The Philippine group of *S. sanguineus* has already been separate from the Borneo part of the species for a considerable period of time, indicated by slight morphological differences, e.g., the flowers of the Philippine specimens are larger than those of Borneo, which have very small flowers. *Spatholobus auricomus* and *S. multiflorus,* two other species with small flowers within the *S. ferrugineus*-clade, also developed on the northern half of Borneo (Sarawak/C Borneo, CE Borneo, NW Borneo, and NE Borneo). In addition to the northeastern parts of Borneo, *S. auricomus* also occurs in the Semitau area, which is close to Sarawak. This species does not occur in the eastern part of the northern half of Borneo (CE Borneo and NE Borneo), and only in the southernmost part of the NW Borneo. *Spatholobus multiflorus* occurs in the complementary parts. It is probable that the mountainous area of C Borneo is the natural delimitation of *S. auricomus* and *S. multiflorus.* Both species do not occur in the parts with the highest altitudes. The ancestor probably occurred in the whole area, and the two species developed on either side of the central mountain part. It is, however, difficult to give an indication of timing for this last event. Sarawak and the Crocker Formation were uplifted in the Early Miocene, and these mountains were probably already in existence before the ancestor of the species came into the region. The parts south of the mountains were inundated during the Late Oligocene. The high sea level that isolated the Meratus from the rest of Borneo during the Pliocene may also have played a role in the differentiation of these two species. The other split at the end of the *S. ferrugineus*-clade is that of *S. persicinus* and *S. auritus. Spatholobus persicinus* occurs in the whole of Borneo, but *S. auritus* is found only in SW Borneo and in Penang/Kedah. Apart from *S. ferrugineus* itself, *S. auritus* is the only species that occurs both in Borneo and on the Asian mainland. The species is not
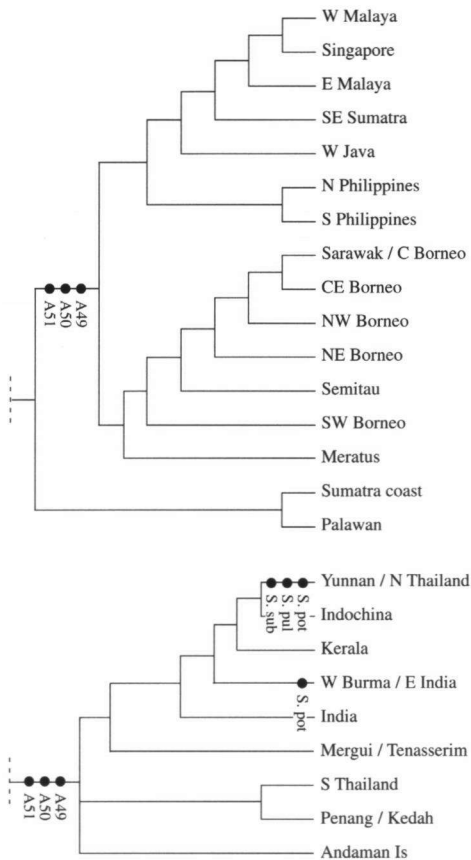
Figure 4.11. Area cladogram showing the species *Spatholobus pottingeri*, *S. pulcher* and *S. suberectus*.

very common, and except for one (sterile) specimen in Borneo there are indications that it is in fact endemic in Penang. The occurrence of *S. auritus* in Borneo suggests that it is either a relict of a more widespread distribution, or a dispersal event, or an identification error (the specimen is sterile).

The next split off in the *Spatholobus* cladogram is that of *S. pottingeri*, occurring in Yunnan/Thailand and W Burma/E India (Fig. 4.11). This species probably came into existence at the periphery of the ancestral area of *Spatholobus*. The Yunnan/N Thailand area remains present in the ancestral areas of the next two splits (A50, A51). The first split is that of *S. pulcher*, an endemic occurring in the higher parts of the area Yunnan/N Thailand. After a period of being more or less isolated, the area probably became occupied by the ancestor of *S. pulcher*. In the Pliocene, tropical montane forest was present in the area (Guo, 1993). *Spatholobus pulcher* grows between altitudes of 1325 and 1525 m. The second species, *S. suberectus*, is found also at high altitudes (1250–2500 m) in evergreen forest. It is possible that by a climatic change this area became isolated, and that the ancestor of *S. suberectus*, occurring at the periphery of the whole area of *Spatholobus* on the continent, became adapted to living at high altitudes.
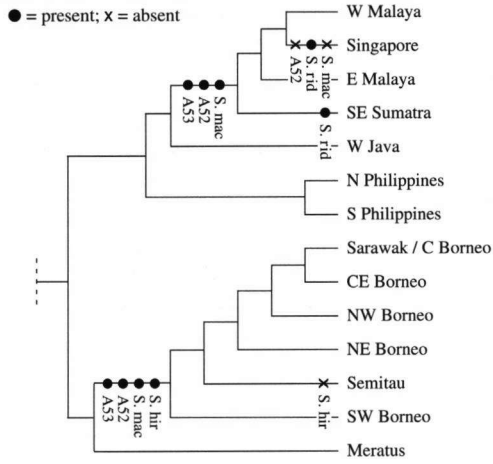
Figure 4.12. Area cladogram showing the *Spatholobus macropterus*-clade.

The next clade, that of *S. macropterus*, is present in the whole Sundaland area, except W Java, the Philippines, and the Meratus area on Borneo (Fig. 4.12). It is likely to assume a primitive absence in these areas. The first split off from its ancestor (A53) is *S. ridleyi*, occurring only in the south of the Malay Peninsula (Singapore area) and SE Sumatra. *Spatholobus hirsutus* is present on the whole island of Borneo except for the Meratus. As far as information on the labels allows, *S. hirsutus* is present at low altitudes. *Spatholobus macropterus*, which occurs nearly in the whole area of the clade, is found up to 1700 m.
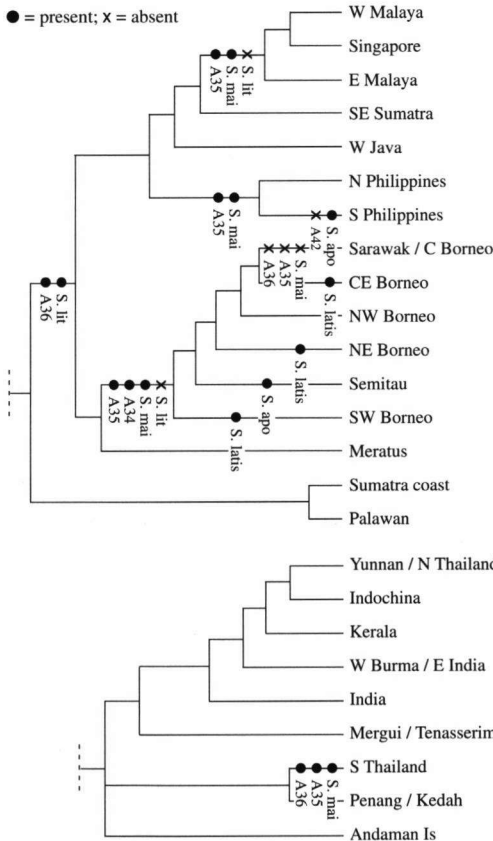
The next species to split off from the ancestor is *S. oblongifolius*. This species occurs in the northern, more recent accreted parts of Borneo.

The ancestor of the *S. maingayi*-clade (A36), the next split in the cladogram, is present in the Sundaland areas (Fig. 4.13). The ancestor of the whole genus (A56) is assumed to be still present in the whole area. Ancestor 36 occurs in the whole region south of the Isthmus of Kra, including S Thailand. The first species that developed is *S. littoralis*, which occurs in a rather restricted area: the Meratus in Borneo, SE Sumatra, W Java, and the northern Philippines. It is best to assume that the species was restricted to these parts and thus primitively absent from the other parts. The next species splitting off

Figure 4.13. Area cladogram showing the *Spatholobus maingayi*-clade.

● = present; x = absent

```
                              ●●● W Malaya
                        S. dub A58 Singapore
                             A59
                              — E Malaya
                              — SE Sumatra
                              — W Java
                              — N Philippines
                              — S Philippines
                              ● Sarawak / C Borneo
                        S. latib CE Borneo
                              — NW Borneo
                        S. latib NE Borneo
                   ●●●● S. vir Semitau
                   A57 A58 A59
                              — SW Borneo
                              — Meratus
                              ●● Yunnan / N Thailand
                        S. har A59 Indochina
                              — Kerala
                              — W Burma / E India
                              — India
                              — Mergui / Tenasserim
                              ● S Thailand
                        S. har Penang / Kedah
                   ●●● S. dub A58 A59 Andaman Is
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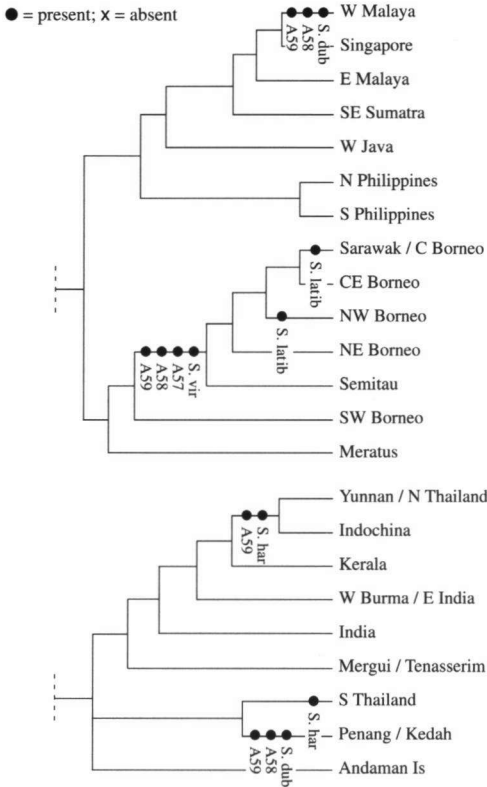
Figure 4.14. Area cladogram showing the *Spatholobus harmandii*-clade.

in this clade is *S. maingayi*, which is more widespread than *S. littoralis*, and except for W Java reflects the area of ancestor 36. *Spatholobus apoensis* and *S. latistipulus* occur in part of the area of *S. maingayi*: *S. latistipulus* only in Borneo (SW Borneo, NE Borneo, CE Borneo), and *S. apoensis* in the southern Philippines and the Semitau. This last species has a disjunct distribution, which is perhaps due to extinction.

The ancestor to the rest of *Spatholobus* (A60) does not occur in the oldest parts of Borneo and the Malay Peninsula, except for W Malaya. The ancestor of the *S. harmandii*-clade (A59) is present in both Yunnan / N Thailand and Indochina, the Isthmus of Kra region, W Malaya and the northern part of Borneo (Fig. 4.14). The first species in this clade, *S. harmandii*, is restricted to the area north of S Thailand. It is most likely that a vicariance event took place which isolated the ancestor of *S. harmandii* from the rest. If this event was a sea level rise, the Isthmus of Kra will have been inundated, and the occurrence of *S. harmandii* in S Thailand can then be explained by dispersal from the north. Obviously this species is adapted to a drier climate, as indicated by the thick leaflets, and was (and is) prevented from dispersing further south by the wet climate. The species south of the Isthmus of Kra survived in rather restricted

● = present; x = absent

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                              — Sarawak / C Borneo
                        S. alb x x x CE Borneo
                        A63 A64 NW Borneo
                   ●●● S. alb A63 A64 NE Borneo
                              — Semitau
                              — SW Borneo
                              — Meratus
                   x x x Yunnan / N Thailand
                   S. cra A61 A62 Indochina
                   x●x● Kerala
                   S. acu S. cra S. pur A64 W Burma / E India
                   ●●● S. acu A62 India
                   S. cra A61
                   x●x S. acu A64 Mergui / Tenasserim
                        S. mer S Thailand
                   ●●● S. acu A64 A63 Penang / Kedah
                   A64
                   S. cra A61 A62 Andaman Is
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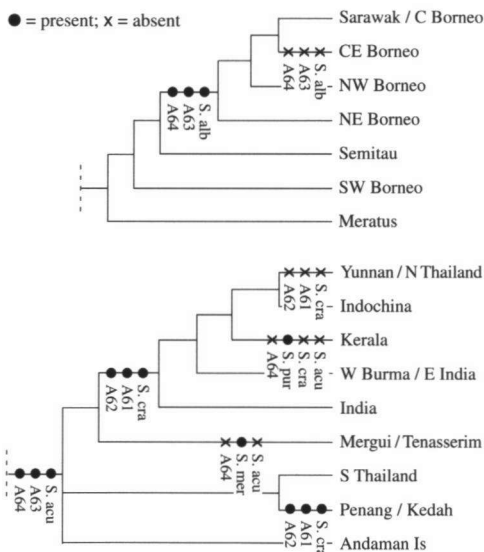
Figure 4.15. Area cladogram showing the clades of *Spatholobus acuminatus* and *S. classifolius*.

areas: W Malaya/Penang/Kedah and the northern parts of Borneo (Fig. 4.22). In West Malaya, *S. dubius* is present in only the part close to Penang/Kedah, and is nearly endemic. The presence of this species is in fact a relict of the larger ancestral area from Yunnan in the north over the south of Thailand into the Malay Peninsula and further to Borneo. In the Malay Peninsula no species of the *S. harmandii*-clade are found, and it is most parsimonious to assume that in these areas the ancestor went extinct, and survived only in Borneo and the Penang and surrounding areas. On Borneo two species occur: one up to 350 m altitude, *S. viridis*, and the other, *S. latibractea*, in a more restricted area at higher altitudes (1300 m).

The ancestor of the remaining part of *Spatholobus* (A63) is optimised in the area cladogram as occurring in the whole SE Asian region, and in the north and western parts of Borneo. Ancestor 64 occurs in a less restricted region than ancestor 62 (Fig. 4.15). Ancestor 64 gave rise to two species occurring in completely different areas: *S. albus* in the northern part of Borneo except for CE Borneo, and *S. acuminatus* in the area north of and including the Isthmus of Kra. This last species is (primitively) absent from Kerala and the Mergui/Tenasserim. Probably this split is as much the result of the differences in climate as that of isolation during high sea level. The area in which ancestor 62 occurred is, except for Yunnan/N Thailand and S Thailand, the whole of the continental SE Asia area. The first speciation, resulting in *S. merguensis*, took place in the Mergui archipelago that was separated first; then Kerala was split off (became isolated) resulting in *S. purpureus*. This last event was perhaps due to the remaining everwet climate, whereas in large areas of continental SE Asia the climate became drier. The remaining areas form the distribution area of *S. crassifolius* that is widespread in the rest of continental SE Asia.

During the whole development of the genus *Spatholobus* there must have been several events during which the Malay Peninsula/Sumatra or the Borneo region were isolated from the mainland of SE Asia. Events that could be held responsible for such an isolation can be found in the sea level changes followed by a change in humidity and probably temperature. Timing is very speculative, however, because there have been a considerable amount of sea level changes during all periods.

SUMMARY OF THE RELATIONS OF SPATHOLOBUS THROUGH SPACE AND TIME

It is rather speculative to superimpose older (= older than Pleistocene) geological events 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, i.e. changes in sea levels, have occurred several times during geological history. The best possible way to reconstruct fragments of the history of *Spatholobus*, with the available area cladograms and the present knowledge of geology, is to assume that a taxon has to come from somewhere in the first place (distribution of the ancestor) and then find explanations on the deviations from this area. Later events, e.g. Pleistocene ice ages, can 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. However, as not all species will react on separation with speciation (non-adaptive radiation), some of these disjunct patterns will remain.

The generalised area cladograms indicate a vicariance event between the areas on the continent of SE Asia and the areas south of the Isthmus of Kra. It is probable that this indicates one of the sea-level rises in the Late Eocene, the mid-Miocene, or the Pliocene. During all sea-level rises the areas between Borneo, Sumatra and the Malay Peninsula were inundated. The Isthmus of Kra region was also frequently inundated. In this area no endemics of the groups under study occur, only species that dispersed from either north or south towards this region. The area forms an overlap between continental SE Asia and the West Malesian areas.

In the area south of the Isthmus of Kra two separate groups of areas can be recognised: Borneo and the Malay Peninsula/SE Sumatra. There is a relation between SE Sumatra and W Java on one hand, and SE Sumatra and E Malaya on the other. West Java has long been part of the continental margin under which the Indian Plate subducted; SE Sumatra and E Malaya were part of the continental fragment that included Indochina as well. West Malaya, the region round Singapore, and E Malaya form one part. This is, however, not reflecting the older geological pattern of a separate Sibumasu and Indochina/E Malaya that welded in the Triassic. In Borneo the geological entities are recognisable in part in the distribution areas of the species; the oldest parts are the ones split off first, and the younger parts in the north are inhabited usually by the younger species. The uplift in the Late Miocene-Pliocene of parts of Borneo, e.g., Semitau and the Meratus, is probably reflected in the first splits.

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 were usually inundated (= Sunda plateau) (Fig. 4.16). On the continent *S. parviflorus* (or rather its ancestor) 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 Borneo (the oldest parts of Borneo) (Fig. 4.17). 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. 4.18). During later periods of lower sea level, the whole area was inhabited by the predecessor of *S. ferrugineus*, 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. 4.19). On Borneo, but only in the north, a small-flowered species developed, later splitting into two species due to the separation by a mountainous area: *S. auricomus* and *S. multiflorus*.

In the meantime speciation events occurred on the SE Asian continent as well (Fig. 4.19). The first split on the continent is that of *S. pottingeri.*, immediately after the splitting off of the *S. ferrugineus*-clade. *Spatholobus pottingeri*, developed at the margin of the total area of *Spatholobus*, became adapted to higher altitudes and is found in
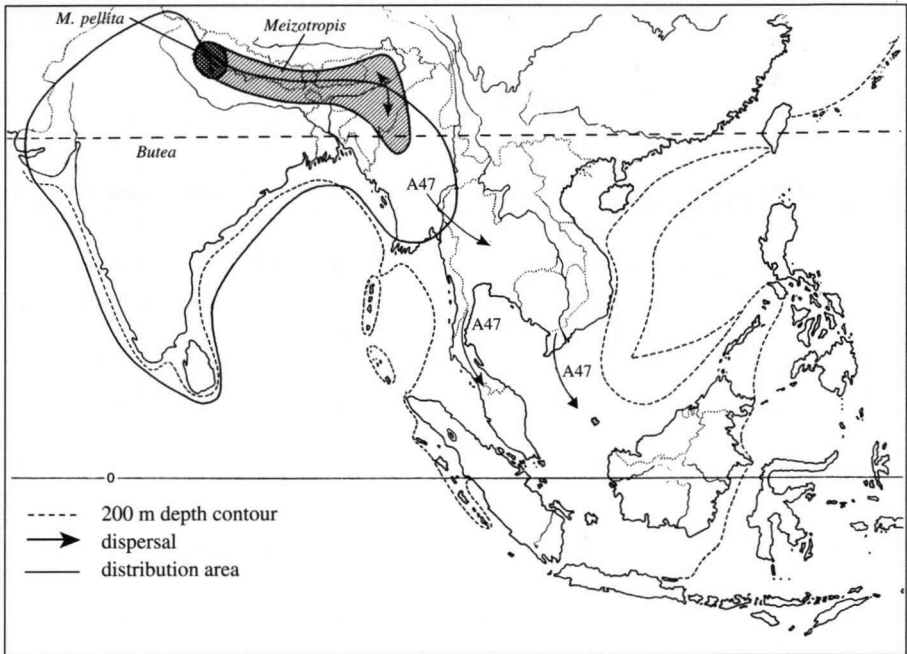
Figure 4.16. Hypothetical distributions of the ancestors of *Butea, Meizotropis* and *Spatholobus*. Dispersal of ancestor 47 (*Spatholobus*) into the Malay Archipelago.
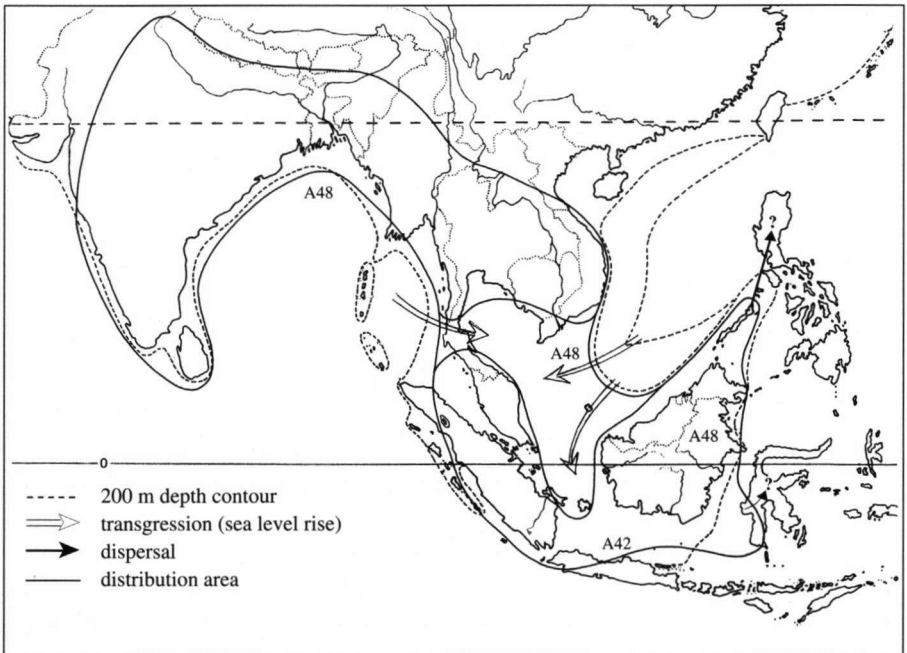
Figure 4.17. After a sea level rise part of the ancestor 48 became isolated and developed into the ancestor of the *Spatholobus ferrugineus*-clade (A42).
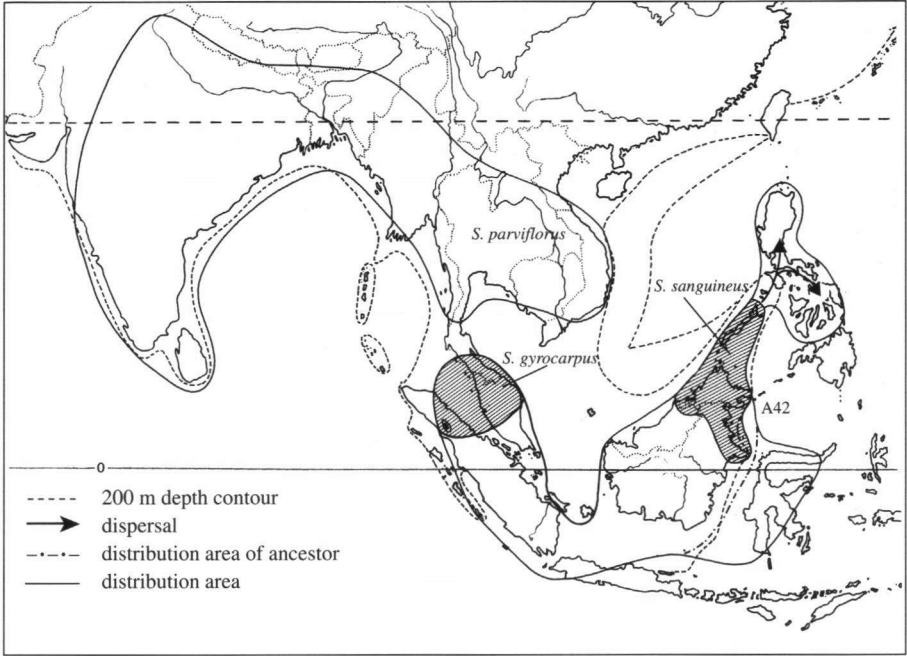
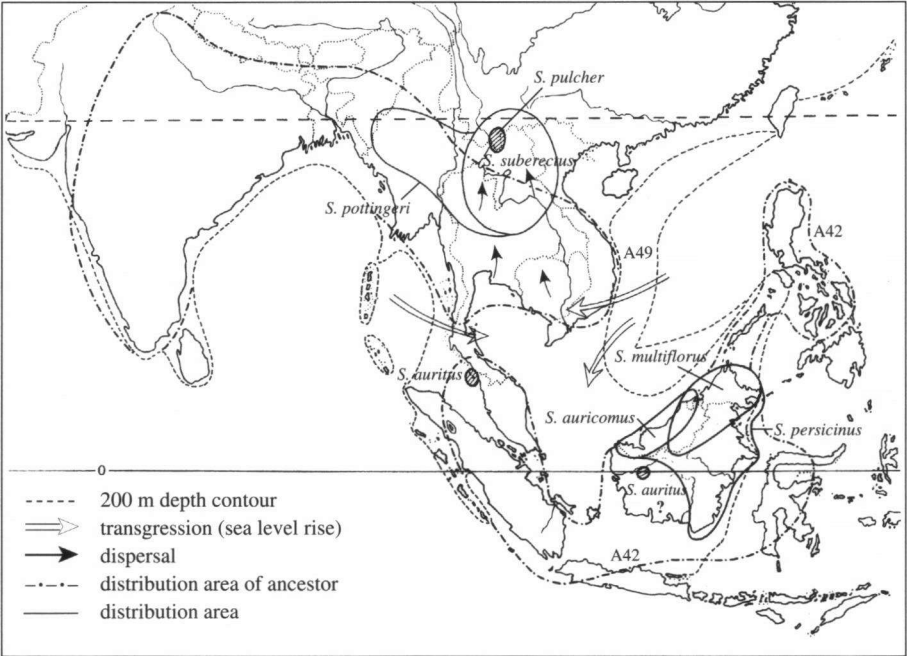Figure 4.18. In isolated parts of the area *Spatholobus gyrocarpus* and *S. sanguineus* are speciated.

Figure 4.19. Further speciation in the *Spatholobus ferrugineus*-clade, and speciation on the continent.

the lower mountains of Yunnan/N Thailand and W Burma/E India. Once again, a speciation event on the continent has occurred, probably at the same time as the Sunda plateau became inundated (Pliocene). The climate on the continent was during this time more humid, and a tropical montane forest was present in the northern parts as well. The ancestor of the rest of *Spatholobus* (A50) probably dispersed further north, and in response to lower temperatures and a drier climate, two species developed after each other in the higher mountains of Yunnan/N Thailand, *S. pulcher* and *S. suberectus*.

The rest of *Spatholobus* (A54) remained present in the whole area, implying the option of renewed invasions from the continent into the West Malesian archipelago (Fig. 4.20). The next clade was present in the whole Sundaland area, but parts of it became isolated during high sea level (probably in the Pliocene), when not only Borneo, Sumatra and the Malay Peninsula became isolated, but the Meratus area as well. In the area in between these areas the high sea level caused large parts to inundate, and the ancestor in this area only survived in the Malay Peninsula/Sumatra and Borneo (without Meratus) and Palawan. Later, in the lower parts of the Malay Peninsula (Singapore area) and SE Sumatra, *S. ridleyi* became a separate species, and in the lower parts of Borneo *S. hirsutus* also had speciated. The remaining part of the ancestor differentiated into *S. macropterus*. Later another species, *S. oblongifolius*, managed to split off and stay in the northern part of Borneo.

After a period of low sea level another intrusion into the Sundaland area was possible. Ancestor 36 developed south of the Isthmus of Kra (Fig. 4.21). The first species that split off here is *S. littoralis*, with a rather restricted area, probably in drier parts. The second, *S. maingayi*, had a larger area, probably the same as its ancestor. The other two species differentiated in part of this area: *S. latistipulus* in SW Borneo, NE Borneo, CE Borneo, and *S. apoensis* disjunct on the Semitau and the southern Philippines.

Again, a period of relatively low sea level caused a spreading of species over a larger area. Here the same has happened as earlier in the *S. macropterus*-clade. North of the Isthmus of Kra, *S. harmandii* developed into a species adapted to drier circumstances, while south, in Penang, *S. dubius* remained as a relict of a once larger distribution, which was probably disrupted by a rising sea level (Fig. 4.22). On the northern part of Borneo two species are present, one at lower altitudes (*S. viridis*), the other in a more restricted area at higher altitudes (*S. latibractea*).

Ancestor 57 occurred in the whole SE Asian area and the northern and western parts of Borneo. Here a split between the small clade of *S. acuminatus* and the equally small rest of *Spatholobus* (A62) occurred (Fig. 4.23). The clade of *S. acuminatus* consists of only two species: *S. acuminatus* on the continent, and also on the Andaman Islands (dispersal), and *S. albus*, which occurs only on the northern part of Borneo. The ancestor of the *S. acuminatus*-clade (A64) invaded Borneo in a late stage. After an isolation event (high sea level) *S. albus* speciated on Borneo, but this species does not pass the mountain barrier of Central Borneo.

The rest of *Spatholobus* (A62) eventually became divided into three species: *S. merguensis* split off in the Mergui area; *S. purpureus* occurred later in another remote part of the area, in Kerala; the rest speciated as *S. crassifolius* in all not too northern parts (Fig. 4.23).
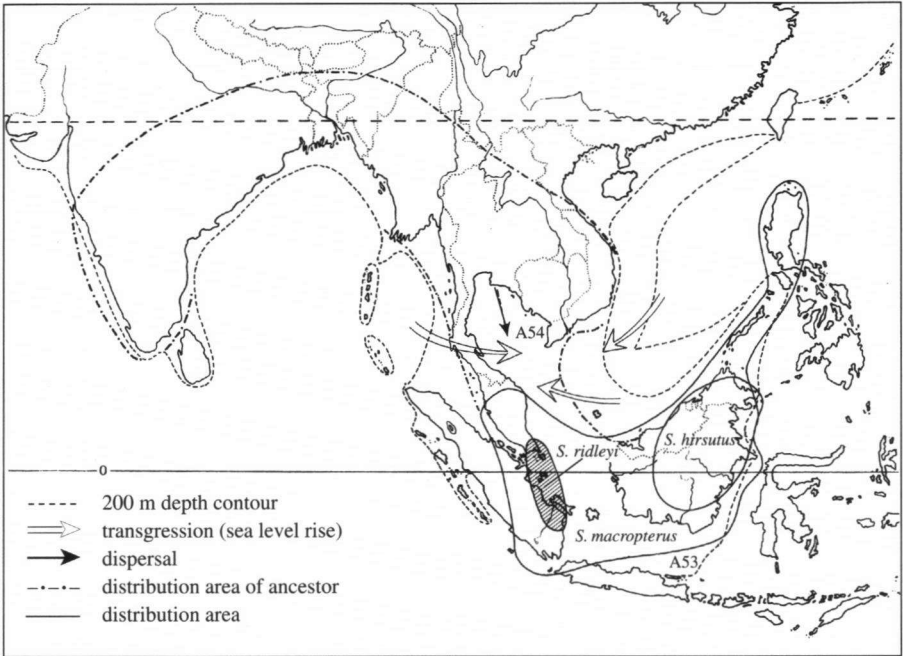
Figure 4.20. After invasion of ancestor 54 into the Malay Archipelago, once again a sea level rise. In the isolated part development of a new clade (A53).
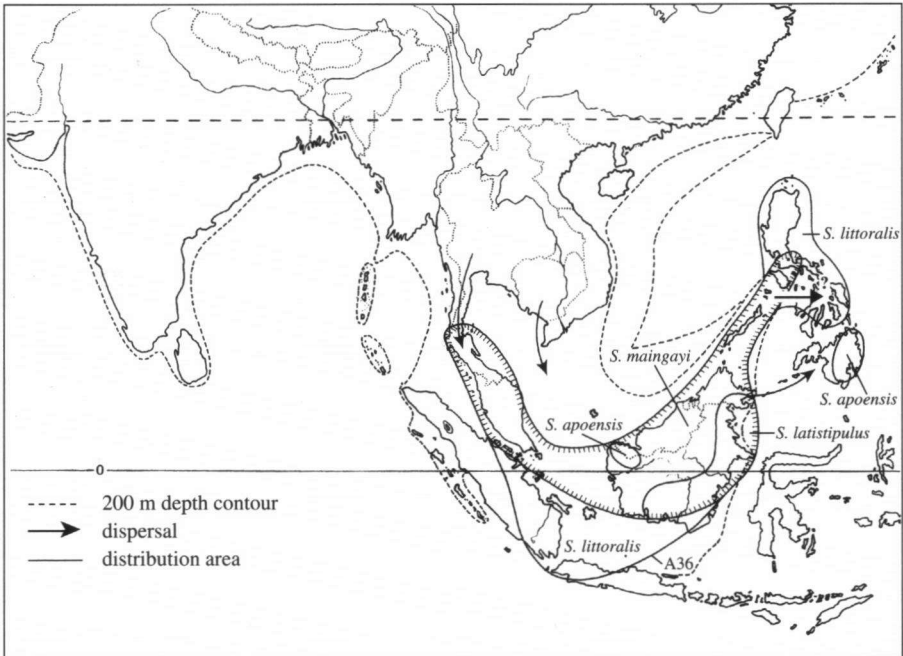

Figure 4.21. Development of the *Spatholobus maingayi*-clade after another intrusion into the Malay Archipelago.
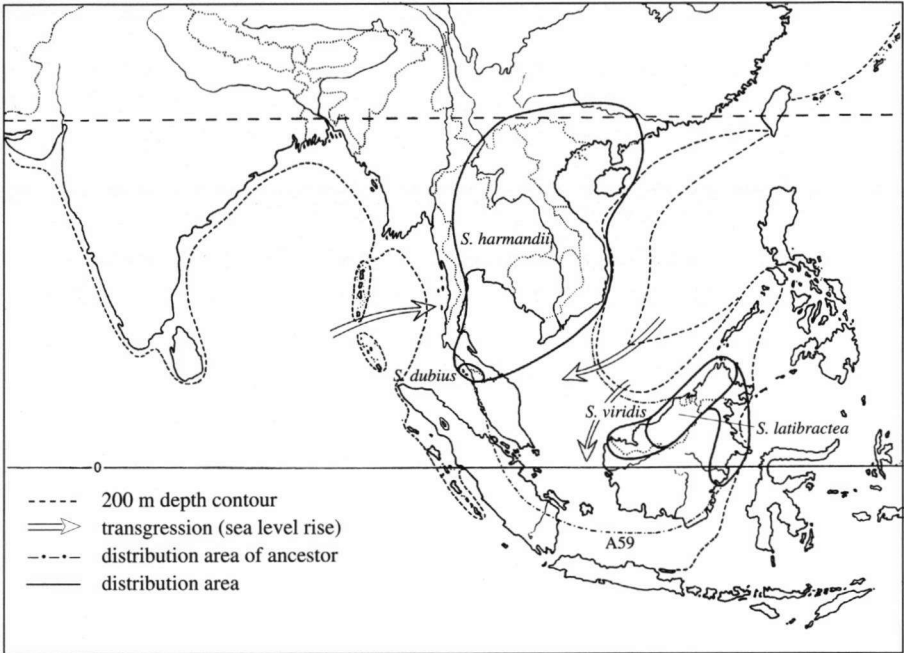
Figure 4.22. The ancestor of the *Spatholobus harmandii*-clade (A59), which spread out over the Malay Archipelago, gets isolated and speciates.
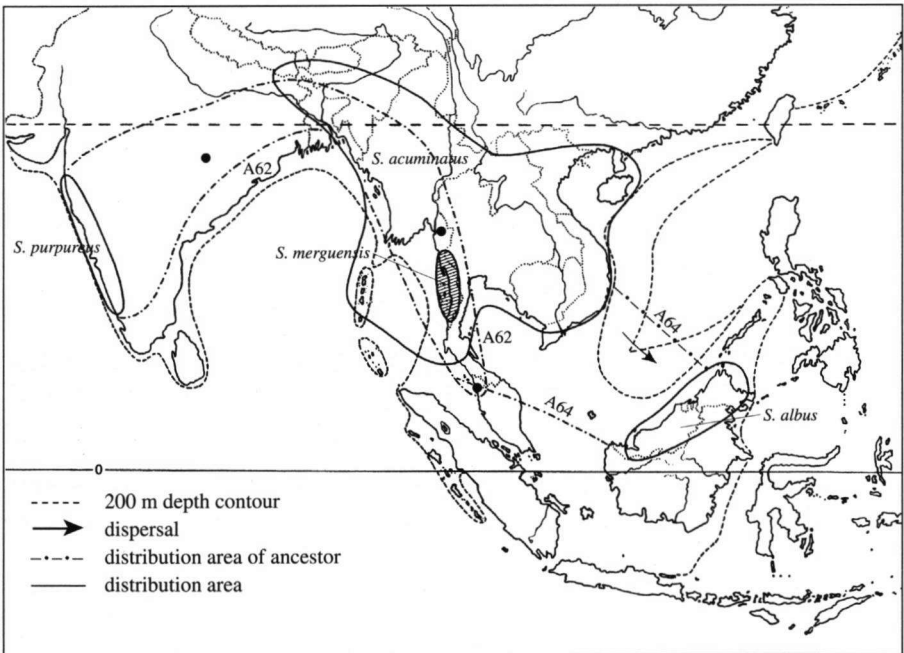

Figure 4.23. Distribution of the species and ancestors of the clades of *Spatholobus acuminatus* (A64) and *S. crassifolius* (A62).

CONCLUSIONS

Evident from the history of *Spatholobus* is that there have been many events that have led to isolation of parts of the Sundaland plateau from the Asian continent. The most obvious events are the 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 Van der Kaars and Dam (1994), describing a rather recent but long period (135,000 years) on Java, are helpful.

Spatholobus probably originated on the continent of SE Asia, together with the genera *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 arose. 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.

As far as the biogeographical analysis is concerned: this study shows that it is preferable to use more than one method of analysis. To avoid clades that are supported by only absences, it is better to use CAFCA. However, in order to make sure that all extinction events and primitive absences are also incorporated PAUP (or other parsimony procedures) is a better option. Checking the results of PAUP analyses on clades formed on absence of areas is very easy with the help of MacClade (Maddison & Maddison, 1992).

It is not enough that an area contains an endemic species, the endemic should have relations with taxa in 'related' areas as well. If there are not enough relations, this species with its distribution area – although endemic – will stand on its own and will not be very informative. Similarly it is not necessary to use only distribution areas that are areas of endemism; areas containing overlapping widespread species can be informative as well. It all depends on how informative their relatives are.

Another problem is timing. In a large area it is very well possible that more than one species develops at the same time out of the same (widespread) ancestor. For example, an ancestor occurring in the entire area from Indochina to Borneo, may develop species in each of the peripheral parts of the area: e.g., the north of Indochina and the northern part of Borneo. If this happens to be a sympatric speciation pattern, the species continuing the line of the ancestor may be present in the same area as well, or after some time may re-invade the area. This last species may in turn again be split up in other species. In this way it is evident that we recognise a split in the phylogenetic cladogram, but not in the area cladogram. It is possible that two species are placed as most related to each other because they are in fact the first split-offs from the ancestor; these two species are present in areas only related to each other by the ancestor 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.

Some areas are not very informative due to a lack of species in the area. It would be worthwhile to expand the analysis with groups occurring in the same region, but with

more representatives in India, E India and W Burma, Sumatra, Sulawesi, Palawan and the Philippines. In an expanded analysis, it is expected that more information can be obtained on these areas. The groups added should preferably be of about the same geological age, and in this case not older than the Eocene. It is possible that more ancient groups will reflect a different pattern; the results will be mixed and end up in an uninformative area cladogram. Some groups that can be added are the orchid genera *Ania*, *Tainia* and *Mischobulbum* (Turner, 1992a, b), the leguminous genus *Kunstleria* (Ridder-Numan & Kornet, 1994) that has been used as an outgroup in the phylogenetic analysis in the present study, and the genus *Exacum* (Gentianaceae; Klackenberg, 1985).

On the other hand it would be worthwhile to extend the analysis 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 option worthwhile to take into account 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 postulations 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 not dependent on 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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