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PHYLOGENETIC RELATIONS AND HISTORICAL BIOGEOGRAPHY OF FORDIA AND IMBRALYX (PAPILIONACEAE: MILLETTIEAE)

ANNE M. SCHOT

Rijksherbarium / Hortus Botanicus, Leiden, The Netherlands

SUMMARY

Cladistic analyses are performed on morphological and anatomical data of *Fordia* and *Imbralyx*. It is shown that both genera should be unified. Biogeographical analysis is performed and vicariance events are presented as results of speciation events due to climatic changes in the Pleistocene. The necessary new combinations for the species in *Fordia* and a key to all species have been presented in a separate paper (Dasuki & Schot, 1991, this issue).

INTRODUCTION

The genus *Fordia* Hemsley has recently been revised by Buijsen (1988). Cladistic analysis led to unresolved polytomies, resulting in the conclusion that more characters were needed. This study was set up to retry the analysis of *Fordia* in combination with the genus *Imbralyx* Geesink. The phylogenetic analysis will be followed by a biogeographical analysis. If a plausible areagram will be found, it will increase the credibility of the taxon cladogram.

Van Welzen (1989) showed that for a phylogenetic analysis the parsimony method renders the best results and for a biogeographic analysis the component compatibility method. The cladistic analysis was therefore run with the computer program 'HENNIG86' (Farris, 1988) and the biogeographical analysis with the program 'CAFCA' (Zandee, 1988).

Fordia consisted of the eight species (with two subspecies) described by Buijsen (1988), namely *F. brachybotrys*, *F. cauliflora* (type), *F. johorensis*, *F. lanceolata*, *F. ophirensis*, *F. pauciflora*, *F. splendidissima* subsp. *splendidissima*, *F. splendidissima* subsp. *rheophytica, and F. stipularis*. The two subspecies of *F. splendidissima* are separated into two species, *F. splendidissima* and *F. rheophytica* (Dasuki & Schot, 1991). Geesink (1984: 95) raised Dunn's section *'Albiflorae'* from *Millettia* (Dunn, 1912: 189–191) to generic rank, calling it *Imbralyx* after the imbricate calyx. It consists of *Imbralyx albiflorus* (type), *Millettia leptobotrya*, *M. nivea*, *M. unifoliata* (no new combinations had been made) and *Fordia* species *F. incredibilis* and *F. ngii* (excluded by Buijsen, 1988). A new species was separated from *Imbralyx albiflorus*, deviating by its large persistent bracteoles (*'bracteolata'*). The descriptions of former *Imbralyx* species, left by Dasuki as an (unpublished) manuscript, have been included and renamed under *Fordia* in a separate paper (Dasuki & Schot, 1991, this issue). Where distinction between the two groups is needed, I will refer to '*Fordia* s.s.' when meaning the former eight species and to '*Imbralyx*' when meaning the group of seven species with imbricate calices.

MORPHOLOGY

Leaves — The leaves are spirally arranged, pulvinate, and mostly imparipinnate. Simple leaves can occasionally be found in the upper part of *F. albiflora* and *F. brachybotrys*; *F. unifoliata* and *F. spec. b* have consistently unifoliolate leaves which entirely lack a rachis.

The leaflets are opposite or sometimes subopposite. The margin is always entire. Terminal leaflets are usually larger than lateral ones. Base cuneate to obtuse, some slightly oblique and apex mostly acuminate to caudate or caudate to cuspidate. Only *F. rheophytica*, a rheophyte, lacks a distinct tip.

The blades of the leaflets are symmetric and variable in shape, also within a species. A constant range from elliptic, ovate, and obovate to narrowly elliptic, narrowly ovate, and narrowly obovate is found. In *F. rheophytica* the shape of the leaflets ranges from linear ovate to linear elliptic.

The leaflets are sericeous to sparsely hairy. The lower surface is usually more densely hairy than the upper surface, sometimes the hairs on the upper surface are found only on the nerves. Often they are glabrescent. *Fordia unifoliata* and *F. johorensis* have completely glabrous leaflets. The number of leaflets per leaf varies, but has mostly a constant range within a species. Although overlap is possible, together with other differing characters, the number of leaflets is useful for identification.

The nervation on the lower surface of the leaflets is always distinctly prominent. *Fordia johorensis* and *'Imbralyx'* are characterized by a raised nervation remarkably similar on both sides. In other species nervation on the upper surface is inconspicuous or variable. *Fordia splendidissima* exhibits in this character the full variability; some specimens have even been mistaken for *F. johorensis* on account of their distinct nervation on the upper side (cf. Whitmore, 1972).

Stipellae are usually caducous but persistent in *F. lanceolata*, *F. cauliflora*, and *F. pauciflora*. Stipule persistence varies, sometimes even within a specimen, except in *F. stipularis* which is characterized by its long and mostly persistent stipules.

Inflorescence — The flowers can be arranged in raminascent, caulinascent, (supra-) axillary or terminal pseudoracemes or panicles. Intermediate forms are also possible. *Fordia pauciflora* has its flowers clustered directly on the trunk; *F. incredibilis* and the very similar *F. spec. a* have their pseudoracemes clustered on warty knobs on the trunk. Some specimens of *F. splendidissima* seem to have also clustered pseudoracemes on knobs, but these are much smaller.

The brachyblasts can be short wart-like to thick or slender cylindric. Usually the higher placed brachyblasts are shorter. Brachyblast length and the number of the flowers on the brachyblast proved to be useful discriminating characters.

The bracts to the inflorescence are caducous. The bracts to the brachyblasts can be caducous or persistent; they are often persistent in flowering specimens and have dropped in fruiting specimens.

Flowers — The length of the flowers varies from 6 to 20 mm. The petals are recorded to be white, pink, or purple. Bracteoles are persistent or caducous, situated on the top of the pedicel, mostly small, narrowly triangular. *Fordia bracteolata* is characterized by large triangular bracteoles.

The calyx is campanulate, the lobes are sparsely hairy on the inside and densely or sparsely hairy on the outside. *'Imbralyx'* has a densely hairy calyx with four obtuse or acute calyx lobes (the upper one two-topped) which are distinctly imbricate in the buds, giving these a spindle-shaped appearance. '*Fordia* s.s.' has a sparsely hairy and truncate or subtruncate calyx (slightly lobed in *F. johorensis*).

Shape and size of the petals show no noticeable variation, the standard being ± orbicular and the wing and keel obovate to falcate. The keel blades are partly connate along the lower margin and equal to or slightly shorter than the wing blades. The standard can be sericeous outside, wing and keel can have basal and apical hairy parts. Standard basal callosities, standard lateral auricles, wing upper auricles, and wing and keel pockets can be present or absent.

The disc is mostly indistinct; if distinct it can be free or adnate to the wall of the hypanthium.

The ovary is laterally flattened, densely sericeous, and contains 2(–4) or 2–7 ovules. The style is glabrous and curves upwards. The stamens are monadelphous, the vexillary one partly connate to the others, forming two distinct basal fenestrae. The free parts of the filaments alternate in length, becoming longer on the lower side.

Pods and seeds — The pods are flattened with thickened margins, woody, beaked, tardily dehiscent, unwinged, sparsely hairy in '*Fordia* s.s.' and soft velvety in '*Imbralyx*'. The seeds are only known from some species and had little variation. They are lens-shaped to reniform and dark to reddish brown.

LEAF ANATOMY

Material used (from L unless stated otherwise):

Fordia albiflora: Malaya: *KEP-FRI 8640, 14082*; *King's coll. 5993*; *KL 1678* – *F. brachybotrys:* Borneo: *Endert 2907; S 13790; SAN 29356* – *F. bracteolata:* Malaya: *Hamid 10465* (K); *KEP-FRI 2991* – *F. cauliflora:* Hongkong Bot. Gardens: *Hu 6700A* (K) – *F. incredibilis:* Malaya: *SF 37025* – *F. johorensis:* Malaya: *J.C. 1627* – *F. lanceolata:* Malaya: *KEP-FRI 11278* – *F. leptobotrys:* China, Yunnan: *Bons d'Anty s.n.* (P) (received 28 July 1898, possibly a duplicate of *Bons d'Anty 244* or *251*, K); *Henry 12792* (K) – *F. ngii:* Malaya: *Lewis 135*; *SF 32042* – *F. nivea:* Sumatra: *Forbes 2915*; *TBF (Roos & Franken) 1836* – *F. ophirensis:* Malaya: *KEP-FRI 19219* – *F. pauciflora:* Malaya: *Ridley 14679* (K) – *F. rheophytica:* Borneo: *Chew Wee Lek 1070* – *F. splendidissima:* Borneo: *Amdjah 150*; *Enggoh 10177*; *Geesink 9345*; *van Niel 4595*; *S 8434, 19095*; *SAN 41399*. Sumatra, Anambas: *van Steenis 889* – *F. stipularis:* Sumatra: *Forbes 2948* – *F. unifoliata:* Malaya: *KEP-FRI 3069, 3103* – *F. spec. a:* Malaya: *KEP-FRI 7798* – *F. spec. b:* Borneo: *Wiriadinata 3320.*

Possible outgroups:

Millettia pulchra: Hongkong: *Ford 503* (K); *Shiu Ying Hu 13681* (K) – *M. sericea:* Malaya: *Hardial 670* – *M. xylocarpa:* Thailand: *Santisuk 674* – *M. pendula:* Thailand: *Put 1126.*

And: *Burkill 6381* (K), Malaya, supposedly *M. caerulea* but more likely *F. albiflora.* These two species are often confused (cf. Craib, 1928: 388).

One leaflet per specimen was rehydrated by boiling in water. Transverse sections were made of the basal part, the central midrib and the margin. Some sections were bleached with household bleach and subsequently stained with Astrablue, others were left unstained. All were mounted in glycerin jelly.

Cuticular macerations were obtained by incubating overnight at 60° C in a mixture of hydrogen peroxide and acitic acid and staining with Sudan IV (see also Van Welzen, 1989: 19).

Polarized light was used to score for occurrence of crystals and sclerified secondary cell walls (e.g. xylem cells, sclerenchyma cells).

Leaf anatomical characters

Epidermis — The anticlinal walls of the epidermal cells are slightly to strongly undulated, often most distinctly so on the adaxial surface (cf. figs. 1–3, 11). *Fordia lanceolata, F. rheophytica* and *F. spec. b* have almost straight anticlinal walls on both abaxial and adaxial sides of the leaflet. The undulation of the anticlinal walls is less around hair bases and over the veins (fig. 10). *Fordia incredibilis* and *F. spec. a* have thicker anticlinal walls than other species (cf. fig. 10, 11).

The abaxial epidermis is lowly papillate in *F. splendidissima, F. brachybotrys, F. rheophytica, F. spec. b,* and *F. stipularis* (figs. 1, 9) and domed in *F. ngii* and *F. nivea* (figs. 3, 8). The other specimens studied have flat outer periclinal walls (e.g. figs. 2, 7).

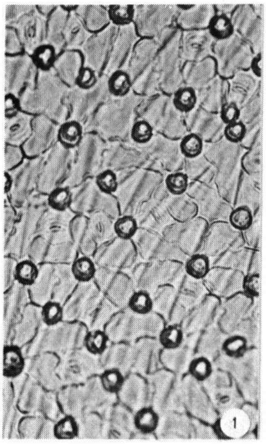
Stomata — All studied specimens have paracytic stomata. They are scattered without specific orientation over the abaxial lamina of the leaflet (figs. 1–3). *Fordia lanceolata* and *F. johorensis* have in addition a very low frequency of cyclocytic stomata on the adaxial surface in the midrib area (fig. 11). The stomata can be in level with the leaf surface (fig. 8, arrow) or slightly sunken in transverse view (fig. 13, arrow).

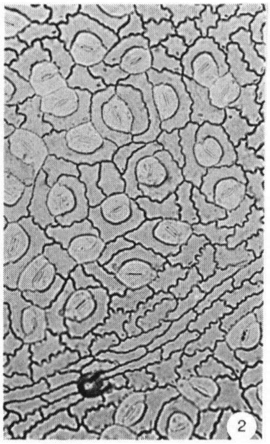
Vascular system — The vascular system of the midrib in *Fordia* is usually approximately cylindrical. At the basal end of the leaflet the vascular system starts cylindrically (fig. 4) but breaks and flattens in more central parts of the leaflet (fig. 5). *Fordia pauciflora* has an arc-shaped vascular bundle at the basal end of the leaflet (fig. 6).

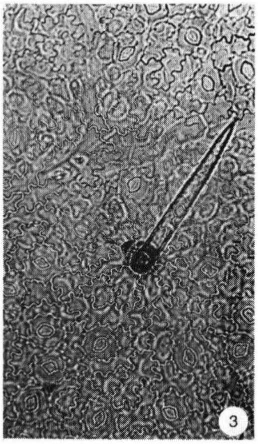
The vascular bundle is surrounded by a sclerenchyma sheath. This sheath varies in thickness between evenly thickened on all sides (fig. 4) to slightly to distinctly extended on the adaxial side (fig. 5).

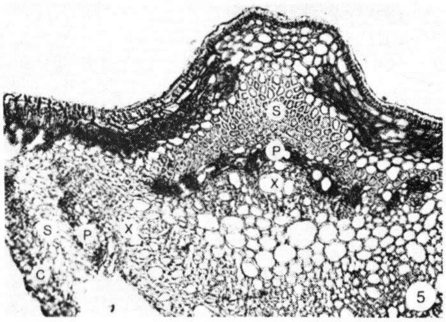
The secondary and tertiairy veins all have vertically transcurrent collateral bundles (figs. 7–9).

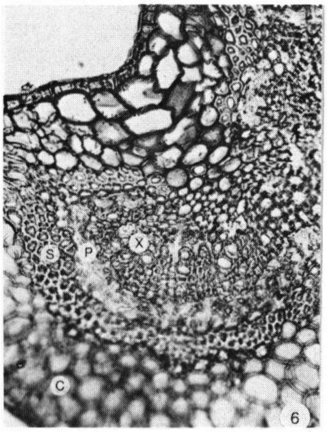
Mesophyll structure — Two major patterns in mesophyll structure are found. They can, as Keijner (unpubl.) also noted, best be described by presence or absence of conspicuous large cells in the spongy tissue. Presence is often correlated with two adaxial and one abaxial layer of short palisade parenchyma cells (figs. 7, 8). Sometimes, however, only one of the adaxial layers is distinct. *Fordia lanceolata, F. pauciflora, F. johorensis,* and *'Imbralyx'* are characterized by large spongy cells. The cell walls are slightly thickened. When the spongy tissue is very lacunar the palisade cells are more elongated and mostly in one distinct adaxial layer (fig. 9), but sometimes in two. This is found in *F. brachybotrys, F. rheophytica, F. splendidissima, F. spec. b, F. ophirensis, F. stipularis,* and *F. cauliflora.*





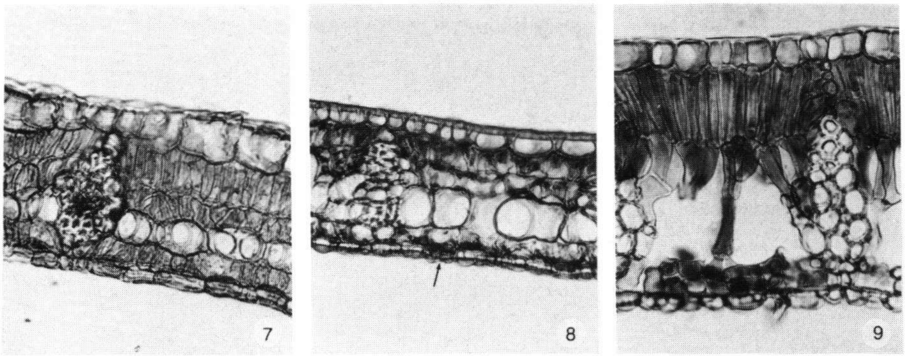






Figs. 1–6. – 1. *Fordia splendidissima*. Paracytic stomata, papillate and densely hairy abaxial side, × 190. – 2. *F. bracteolata*. Paracytic stomata and basal cell of broken non-glandular hair, flat abaxial side, × 190. – 3. *F. ngii*. Paracytic stomata, domed abaxial side, × 190. – 4. *F. splendidissima*. Cylindrical vascular system of midrib, basal section, × 30. – 5. *F. splendidissima*. Vascular system of midrib, section halfway lamina, × 78. – 6. *F. pauciflora*. Arc-shaped vascular system of midrib, basal section, × 100. – X = xylem; P = phloem; S = sclerenchyma; C = cortical region.

Hairs — According to literature both non-glandular hairs and glandular hairs can be present (Solereder, 1899). The non-glandular hairs are the common uniseriate type found in the Papilionaceae with a short basal cell and an elongated top cell (Metcalfe & Chalk, 1950). They are fairly thick-walled and dark orange/brown in *'Imbralyx'*, *F. lanceolata*, and *F. pauciflora* (fig. 12). Longer and silvery, more thin-



Figs. 7–9. – 7. *Fordia leptobotrys*. Mesophyll state 2: compact with 2 adaxial and 1 abaxial palisade layer and spongy tissue with conspicuous large cells, transcurrent vein. – 8. *F. nivea*. Mesophyll state 2: idem but less compact; epidermis domed. Note stoma in transverse view (arrow). – 9. *F. splendidissima*. Mesophyll state 4: 1 distinct palisade layer, spongy tissue very loose, transcurrent vein, epidermis lowly papillate. All × 190.

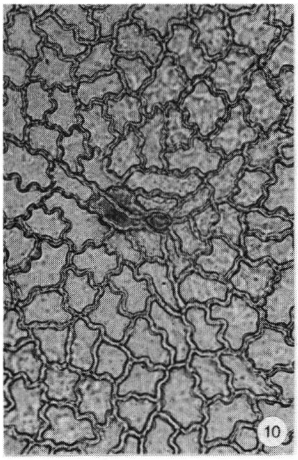
walled non-glandular hairs are present in *F. brachybotrys*, *F. rheophytica*, *F. splendidissima*, *F. stipularis*, *F. cauliflora*, and *F. ophirensis* (fig. 13).

Glandular hairs were not seen. The frequency of hairs varied considerably. It could be measured in all specimens, because the basal cells remain visible even in glabrescent leaflets.

Crystals — Both rhomboidal and rod-like crystals have been found in *Fordia*. Rhomboidal crystals are the most common. They occur in all specimens in the bundle sheath cells of the midrib and the secondary veins (figs. 10, 18). Often the minor veins have crystalliferous bundle sheaths as well. Rhomboidal crystals may also be found scattered in the cortical region and in the palisade layers of the mesophyll. Small birefringent granules are present in the adaxial epidermis of *F. bracteolata* (fig. 15).

Rod-like and irregularly shaped crystals are less frequent. They are present in the palisade layers of most *F. splendidissima* specimens, *F. rheophytica*, *F. brachybotrys* specimens, *F. cauliflora*, *F. stipularis*, and *F. spec. b* (fig. 14).

Figs. 10–18. – 10. *Fordia incredibilis*. Thick anticlinal walls and base of hair (glandular or non-glandular!). Note declining undulation around hair base, × 195. – 11. *F. johorensis*. Cyclocytic stoma near adaxial midrib, rhomboidal crystals under epidermis of midrib, × 195. – 12. *F. pauciflora*. Non-glandular hair in adaxial epidermis, × 530. – 13. *F. splendidissima*. Non-glandular hair in abaxial epidermis. Note stoma in transverse view (arrow), × 530. – 14. *F. splendidissima*. Rod-like crystals in palisade layer, × 530. – 15. *F. bracteolata*. Birefringent granules in adaxial epidermis, × 530. – 16. *F. splendidissima*. Tannin idioblasts and idioblastic sclereids in phloem and cortical region (basal section), × 80. – 17. *F. albiflora*. Tannin idioblasts in spongy layer, × 195. – 18. *F. splendidissima*. Secretory canal in cortical region and rhomboidal crystals under epidermis (basal section), × 195. – R = rhomboidal crystal; I = rod-like crystal; BG = birefringent granules; TI = tannin idioblast; IS = idioblastic sclereid; SC = secretory canal.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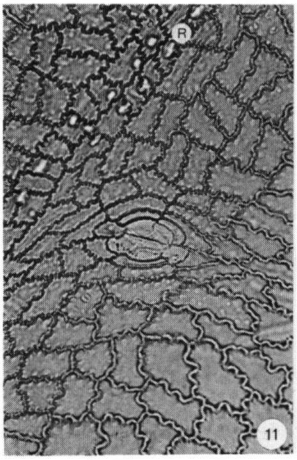
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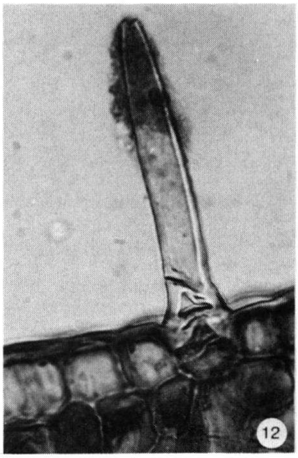
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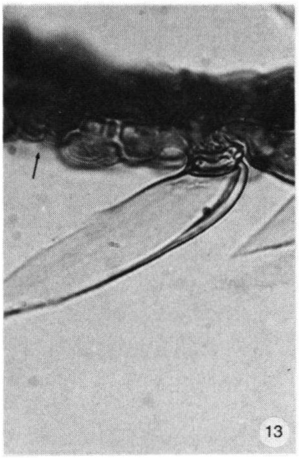
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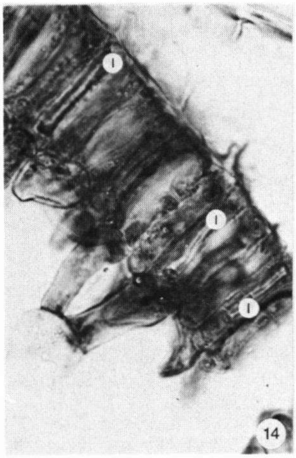
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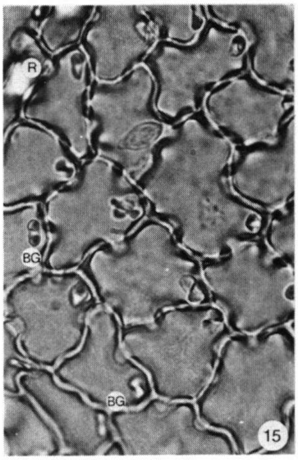
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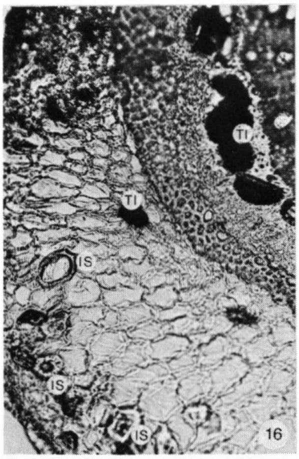
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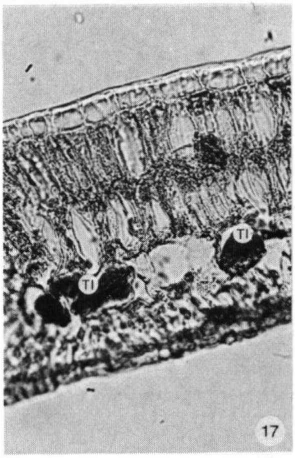
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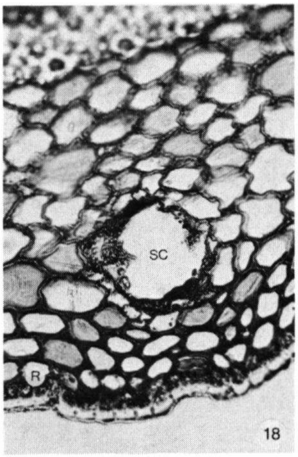
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Table 1a. Character states used for morphological analysis. Characters marked '+' were ordered, characters marked '–' unordered. It is a special feature of HENNIG86 to start numbering at 0.

– 0. Leaves
1 = compound
2 = simple

– 1. Maximum length leaf rachis
1 = < 29 cm
2 = > 30 cm

– 2. Minimum length leaf rachis
1 = < 10 cm
2 = > 10 cm

– 3. Maximum length pulvinus
1 = < 10 mm
2 = > 10 mm

– 4. Number of leaflets
1 = 1–7
2 = 7–20
3 = 7–> 20
4 = > 20

– 5. Stipellae
1 = present
2 = absent

– 6. Midrib on upper surface
1 = sunken or flat
2 = raised
3 = raised in a furrow

– 7. Secondary nerves on upper surface
1 = prominent
2 = flat

– 8 Intersecondary nerves on upper surface
1 = distinct
2 = variable
3 = indistinct

– 9. Lower surface leaflets
1 = sericeous
2 = sparsely hairy
3 = glabrous to sericeous
4 = glabrous

+ 10. Inflorescence
1 = axillary to terminal
2 = axillary to raminascent
3 = raminascent to caulinascent

+ 11. Flowers
1 = in panicles or pseudoracemes
2 = in pseudoracemes only
3 = directly on trunk

– 12. Warty knob of inflorescence on trunk
1 = absent
2 = present

– 13. Brachyblast
1 = absent
2 = 1–7 mm
3 = 1–20 mm
4 = 7–20 mm

– 14. Number of flowers on brachyblast
1 = 1–10
2 = 1–20
3 = 10–20
4 = > 20

– 15. Bracteoles
1 = persistent
2 = caducous

– 16. Spindle-shaped flowerbuds
1 = absent
2 = present

– 17. Calyx lobes
1 = acute
2 = obtuse
3 = subtruncate

– 18. Imbricate calyx
1 = absent
2 = present

– 19. Calyx
1 = densely sericeous
2 = sparsely sericeous

– 20. Standard basal callosities
1 = absent
2 = present

– 21. Standard lateral auricles
1 = absent
2 = small
3 = distinct

– 22. Wing lower auricle
1 = absent
2 = present

– 23. Wing lateral pocket
1 = absent
2 = present

– 24. Keel lateral pocket
1 = absent
2 = present

– 25. Petals hairy
1 = wing, keel, and standard
2 = only standard
3 = petals glabrous

- 26. Disc
  1 = inconspicuous
  2 = distinct (free or adnate)
- 27. Number of ovules
  1 = 2–7
  2 = 2
- 28. Mature pods
  1 = not velvety
  2 = velvety
- 29. Flowers recorded to be
  1 = pink to purple
  2 = pink to white
  3 = white
- 30. Leaflets
  1 = never longer than 10 cm
  2 = never longer than 20 cm
  3 = never longer than 30 cm
  4 = longer than 30 cm

Table 1b. Data matrix for morphological characters.

Species / Characters	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Millettia pulchra	1	1	1	1	3	1	1	2	3	1	1	1	1	2	1	1
Fordia albiflora	1	1	1	1	1	2	2	1	2	4	1	1	1	4	3	2
brachybotrys	1	2	1	2	1	2	3	2	2	1	2	1	1	3	2	2
bracteolata	1	1	2	1	1	2	2	1	1	4	1	1	1	1	1	1
cauliflora	1	2	2	1	4	1	1	2	2	1	3	2	1	2	3	2
incredibilis	1	2	2	2	2	2	2	2	2	2	3	2	2	2	3	2
johorensis	1	1	2	1	2	2	2	1	3	4	3	2	1	4	3	2
lanceolata	1	2	2	1	2	1	2	1	1	2	2	2	1	2	1	2
leptobotrys	1	1	2	1	2	2	2	1	1	3	1	2	1	4	3	2
ngii	1	1	1	1	1	2	2	1	2	2	2	2	1	2	1	2
nivea	1	1	2	1	2	2	2	1	2	2	2	2	1	2	1	2
ophirensis	1	2	2	1	3	2	1	2	3	2	1	2	1	2	2	2
pauciflora	1	2	2	1	2	1	1	2	3	2	3	3	1	2	1	2
splendidissima	1	2	1	2	2	2	3	2	2	3	2	2	1	2	1	2
rheophytica	1	1	1	2	2	2	3	2	2	1	2	2	1	2	1	2
stipularis	1	2	2	2	2	2	3	2	1	1	2	2	1	2	1	2
unifoliata	2	1	1	1	1	2	2	1	1	4	1	2	1	4	1	2
spec. a	1	2	2	1	2	2	2	2	2	2	3	2	2	4	4	2

Species / Characters	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Millettia pulchra	1	1	1	1	1	3	2	1	2	1	1	1	1	1	1
Fordia albiflora	2	1	2	1	2	3	2	2	2	3	?	1	2	3	3
brachybotrys	1	3	1	2	1	1	2	1	1	1	1	2	1	2	4
bracteolata	2	1	2	1	2	3	2	2	2	3	?	1	2	3	3
cauliflora	1	3	1	2	1	1	1	1	1	1	2	2	1	1	2
incredibilis	2	2	2	1	1	2	1	1	2	3	1	1	2	1	3
johorensis	1	3	1	2	1	1	2	1	1	3	2	2	1	3	1
lanceolata	1	3	1	2	1	1	2	1	1	1	2	2	1	3	3
leptobotrys	2	2	2	1	1	2	2	1	2	3	?	1	2	3	3
ngii	2	2	2	1	1	2	2	1	1	3	1	2	2	3	2
nivea	2	2	2	1	1	2	1	1	1	3	1	1	2	3	2
ophirensis	1	3	1	2	1	1	?	1	1	?	?	2	1	3	2
pauciflora	1	3	1	2	1	1	2	1	1	2	2	2	1	3	3
splendidissima	1	3	1	2	1	1	2	1	1	1	1	2	1	2	4
rheophytica	1	3	1	2	1	1	2	1	1	1	1	2	1	1	2
stipularis	1	3	1	2	1	1	?	1	1	?	?	2	1	1	2
unifoliata	2	1	2	1	2	3	1	2	2	3	?	1	2	3	2
spec. a	2	2	2	1	1	1	2	1	1	3	1	1	2	1	2

Idioblasts — Special cells containing a dark substance could be seen in most specimens studied. Solereder (1899) mentioned these cells as 'Gerbstoffschläuchen', Metcalfe & Chalk (1950) simply as 'cells with tanniniferous contents'. They are said to be common within the Papilionaceae, but references to these cells in *Millettia* and *Fordia* are, strangely enough, few. As in the material studied the tannin occurred mostly in single cells, the term 'tannin idioblasts' was preferred for these cells.

Tannin idioblasts occur mostly in the phloem and pith of the vascular bundle, sometimes extending to the cortical region of the midrib (fig. 16). Occurrence of tannin cells in the spongy layer is also possible (fig. 17). *Fordia leptobotrys* and *F. lanceolata* lack tannin idioblasts entirely. *Fordia pauciflora* has only tannin cells in the spongy layers. Occurrence of tannin idioblasts in the xylem of the midrib was seen irregularly in *F. johorensis*, *F. rheophytica*, *F. stipularis*, and some of the *F. splendidissima* specimens.

Idioblastic sclereids occurred in many species in the cortical region of the midrib (fig. 16). Sometimes an erratic one was seen in the pith and/or phloem of some specimens of *F. splendidissima*.

Secretory canals were observed only in most specimens of *F. splendidissima* and in *F. rheophytica* (fig. 18).

CLADISTIC ANALYSIS

Morphological analysis

A data matrix of the morphological characters (table 1a) was first scored according to the descriptions given by Buijsen (1988) and Dasuki's descriptions of *'Imbralyx'*. When a character state could not be defined it was scored as missing, e.g. the flower characters in *F. ophirensis* and *F. stipularis*. Otherwise controversial characters were also noted as '?': e.g. the disc in *F. leptobotrys* is inconspicuous and adnate in *F. unifoliata* according to our observations but vice versa according to Dunn (1912). In some species several missing characters were assumed to be the same as in resembling species. So *F. spec. a* is assumed to have velvety pods as the rest of *'Imbralyx'* and *F. stipularis* and *F. ophirensis* are assumed to have non-imbricate calices, absence of standard basal callosities and standard lateral auricles like '*Fordia* s.s.'.

According to Geesink's assumptions of the evolution of the inflorescences within the tribe Millettiae (Geesink, 1984: 8), a pseudoraceme is considered to be derived from a true panicle. Considering this, inflorescence characters were entered as ordered. Under this command a change from e.g. state 1 (axillary or terminal panicle) to a caulinascent pseudoraceme (state 3) via an intermediate state 2 (axillary or raminascent in the axil of the leafscar) takes two steps. In an unordered character state 3 can be reached from state 1 in one step.

Polarity of all character states is automatically set due to the neccessity to choose an outgroup in HENNIG86. The primitive state is the state present in the outgroup. *Millettia pulchra* was chosen as outgroup, as in Buijsen (1988), because of its similarity in pods to '*Fordia* s.s.'.

The data matrix (table 1b) was run with HENNIG86, using the command 'mhennig' followed by 'bb*'. The characters marked with '+' in table 1a are ordered (10 and 11). This resulted in three equally parsimonious trees (length 101, consistency index

Table 2. Characters, number of character states, steps, and consistency index for the characters in the morphological analysis (fig. 19).

Characters	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Character states	2	2	2	2	4	2	3	2	3	4	3	3	2	4	4	2
Steps	1	4	5	2	5	3	2	2	7	6	5	4	1	5	8	2
Consist. index	1.0	.25	.20	.50	.60	.33	1.0	.50	.28	.50	.40	.50	1.0	.60	.37	.50

Characters	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Character states	2	3	2	2	2	3	2	2	2	3	2	2	2	3	4
Steps	1	3	1	2	1	4	4	1	3	2	2	3	1	4	7
Consist. index	1.0	.66	1.0	.50	1.0	.50	.25	1.0	.33	1.0	.50	.33	1.0	.50	.42

0.48 and retention index 0.67), differing only in the three taxon statement for *F. albiflora*, *F. bracteolata*, and *F. unifoliata*. Of these the one with *F. albiflora* and *F. bracteolata* as sister species (fig. 19) was chosen because they share character 11 state 1 (panicle). This was considered a more powerful character than the often changing characters 8 or 14 (table 2).

Nine characters are placed in the cladogram without the assumption of homoplasious events (table 2, consistency index 1.00). They are synapomorphies for: *'Imbralyx'* (16, 18 and 28); *F. albiflora*, *F. bracteolata*, and *F. unifoliata* (20 and 23); *F. incredibilis* and *F. spec. a* (12); *F. brachybotrys*, *F. stipularis*, *F. rheophytica*, and *F. splendidissima* (6 state 3); *'Imbralyx'*, *F. johorensis*, and *F. lanceolata* (6 state 2); *'Imbralyx'* and *F. johorensis* (25). This last one, hairiness of petals, is only a synapomorphy if *F. stipularis* and *F. ophirensis*, only known in fruit, have hairy petals. The autapomorphy 'only standard hairy' (25 state 2) for *F. pauciflora* holds under the same assumption. Character 0 is an autapomorphy for *F. unifoliata*.

Some characters have a consistency index of 0.50 or lower (table 2). These are characters that show parallel developments (2, 22, 30) or reversals (5, 27) or repeated 'switching' on/off (8, 14). Characters like these are probably connected with ecological factors, as size (1, 2, 13, 14, 30) or flower structure, that can be dependent on the pollinator (22, 24).

The most striking feature in the tree is, of course, the fact that with *'Imbralyx'* strongly set at the end of one branch (three synapomorphies and a couple of reversals) '*Fordia* s.s.' is shown as a paraphyletic group. This seems unexpected at first sight, because in some ways *'Imbralyx'* looks more primitive than '*Fordia* s.s.' especially in the inflorescence. As shown in the cladogram, many reversals occur within *'Imbralyx'* (10, 19, 21, 26, 27), thus the seemingly primitive characters of *'Imbralyx'* must be seen as derived, as e.g. the panicle, the many-ovuled ovary and the sericeous, distinctly toothed calyx.

Yet, *F. ngii* and *F. incredibilis* have earlier been placed in *Fordia* and *F. ngii* is easily confused with *F. nivea*. The two 'groups' must be closely related. *Fordia johorensis* is intermediate between the two.

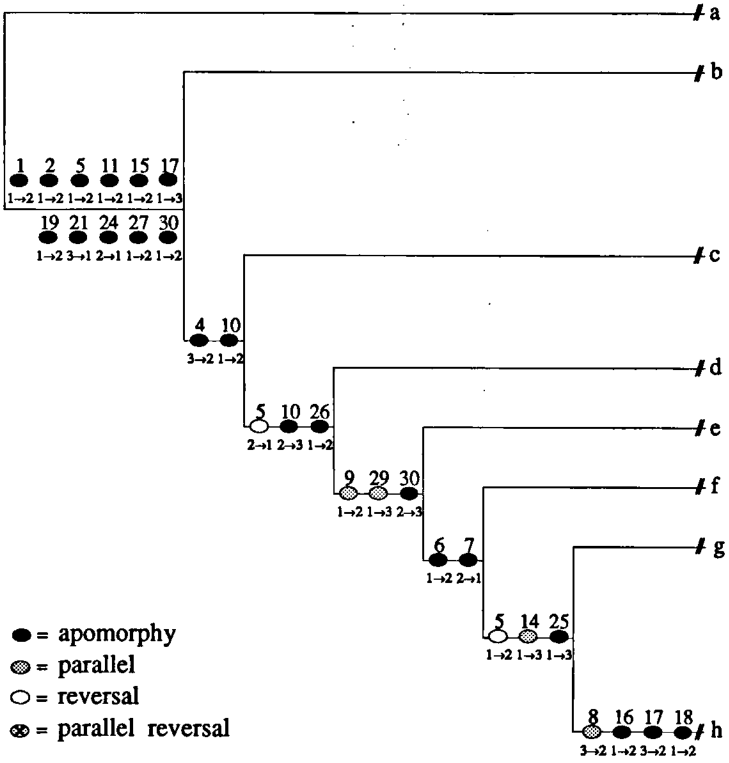

Fig. 19. Cladogram showing the result of the combined analysis (length 101, CI 0.48).

*Anatomical analysis**

Before combining *'Imbralyx'* with *Fordia* I thought it necessary to find confirmation in extra characters and therefore the leaf anatomy of *Fordia* and some *Millettia* specimens was studied.

Many of the anatomical characters show much infraspecific variation and are not directly useable for cladistic analysis. Thus, the differences between specimens of

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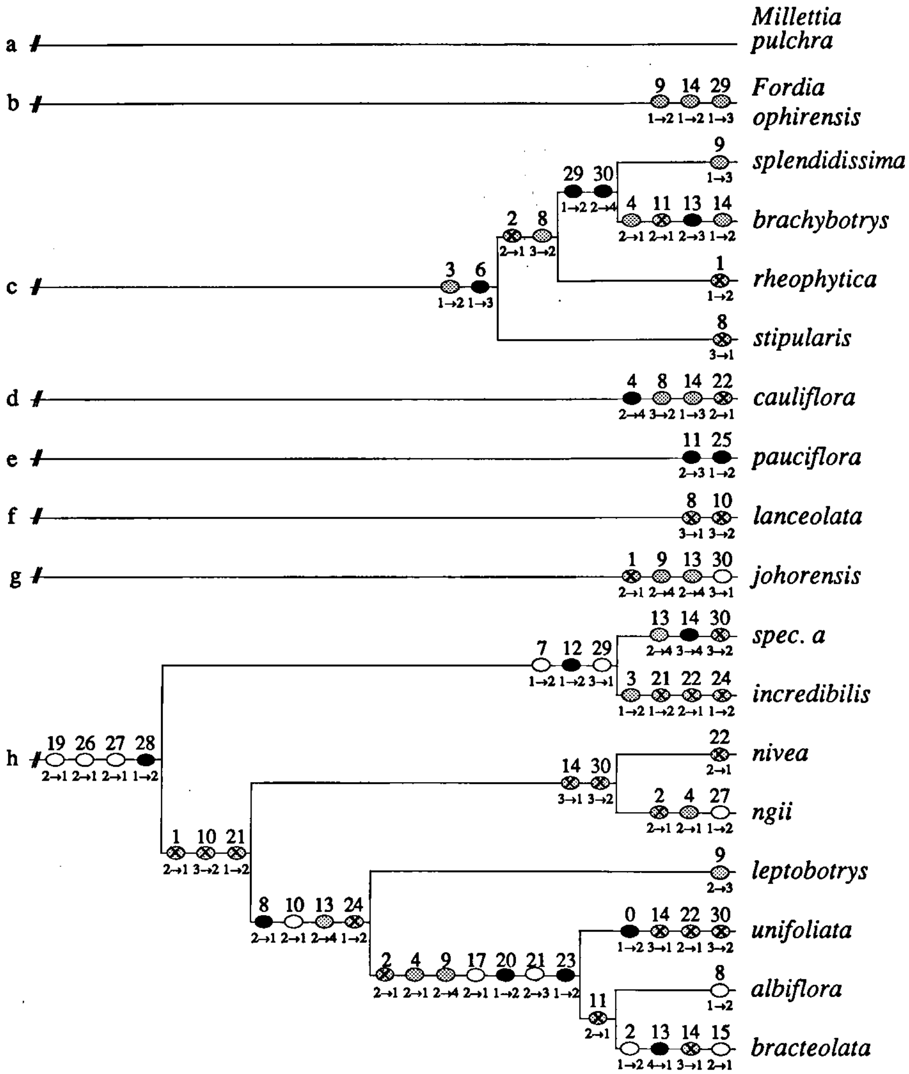
* From here the recently collected specimen *Wiriadinata 3320* is included in further analyses as *Fordia spec. b*. It resembles *F. splendidissima*, but has larger, unifoliolate leaves.



the same species had to be smoothed in some way. I solved this sometimes by 'formulating away' the variation, e.g. for tannin idioblasts in the midrib section the same state is scored for occurrence in the cortical region or not (table 3a, character 34). Other characters had to be left out, e.g. crystals in the mesophyll. Further characters that showed infraspecific variation were scored according to the state found in the majority of the specimens of a species: e.g. in *F. albiflora* adaxial stomata are scored as absent, despite presence in *KL 1678*. *Fordia splendidissima* is scored to have no idioblastic sclereids (though present in *Enggoh 10177* and *van Niel 4595*), to have tannin occurring throughout the vascular bundle (though seen only in the xylem

Table 3a. Character states used for the complete analysis.

Characters 0–5 as in table 1a

Characters 6 is more detailed than in table 1a:

6. Midrib on upper surface
  1 = sunken to flat
  2 = flat to raised
  3 = distinctly raised
  4 = raised in a furrow

Characters 7 & 8 as in table 1a

Characters 9 is new:

9. Tertiary venation
  1 = indistinct
  2 = distinct

Based on anatomical information character 9 (table 1a) is changed to:

10. Upper surface leaflets
  1 = glabrous
  2 = venation sparsely hairy
  3 = venation sericeous
  4 = almost glabrous
  5 = sparsely hairy

11. Lower surface leaflets
  1 = glabrous
  2 = almost glabrous
  3 = sparsely hairy
  4 = sericeous
  5 = densely sericeous
  6 = sparsely to densely sericeous

Character 12 is also new:

12. Hairs
  1 = absent
  2 = thick-walled, coloured
  3 = thin-walled, silvery
  4 = some thick and coloured, most thin and silvery
  5 = long, curled

Characters 13–33 correspond to characters 10–30 of the morphological matrix

34. Tannin idioblasts
  1 = absent
  2 = present only in phloem
  3 = present only in pith
  4 = present in more places

35. Tannin idioblasts in spongy layer
  1 = absent
  2 = present

36. Idioblastic sclereids in cortical region
  1 = absent
  2 = present

37. Secretory canal(s) in cortical region
  1 = absent
  2 = present

38. Vascular system in midrib at base
  1 = cylindrical
  2 = arc-shaped

39. Mesophyll structure
  1 = large cells in spongy tissue and 2 distinct palisade layers
  2 = large cells in spongy tissue and 1 distinct palisade layer
  3 = spongy layer with inconspicuous cells and 1 distinct palisade layer
  4 = spongy layer with inconspicuous cells and 2 distinct palisadxe layers

40. Birefringent granules in adaxial epidermis
  1 = absent
  2 = present

41. Abaxial epidermis
  1 = flat
  2 = lowly papillate
  3 = domed

42. Stomata on adaxial surface
  1 = absent
  2 = present

43. Undulation of anticlinal walls of abaxial epidermis
  1 = straight to slightly curved
  2 = curved
  3 = sinuous

44. Character 43, but for adaxial epidermis

Table 3b. Data matrix for morphological and anatomical characters.
(*M.* = *Millettia*; *F.* = *Fordia*)

Species / Character	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
M. pulchra	1	1	1	1	3	1	1	2	3	1	5	4	5	1	1	1	2	1	1	1	1	1	1
F. albiflora	1	1	1	1	1	2	3	1	2	2	5	3	2	1	1	1	4	3	2	2	1	2	1
brachybotrys	1	2	1	2	1	2	3	2	2	1	3	4	3	2	1	1	3	2	2	1	3	1	2
bracteolata	1	1	1	1	1	2	3	1	1	2	4	3	2	1	1	1	1	1	1	2	1	2	1
cauliflora	1	2	2	1	4	1	2	2	2	1	2	4	3	3	2	1	2	3	2	1	3	1	2
incredibilis	1	2	2	2	2	2	3	2	2	2	4	3	2	3	2	2	2	3	2	2	2	2	1
johorensis	1	1	2	1	2	2	1	1	3	2	1	1	1	3	2	1	4	3	2	1	3	1	2
lanceolata	1	2	2	1	2	1	3	1	1	1	1	3	3	2	2	1	2	1	2	1	3	1	2
leptobotrys	1	1	2	1	2	2	3	1	1	2	5	3	2	1	2	1	4	3	2	2	2	2	1
ngii	1	1	1	1	1	2	3	1	2	2	5	3	2	2	2	1	2	1	2	2	2	2	1
nivea	1	1	2	1	2	2	3	1	2	2	5	3	2	2	2	1	2	1	2	2	2	2	1
ophirensis	1	2	2	1	3	2	1	2	3	1	2	3	2	1	2	1	2	2	2	1	3	1	2
pauciflora	1	2	2	1	2	1	1	2	3	2	4	2	2	3	3	1	2	1	2	1	3	1	2
rheophytica	1	1	1	2	2	2	3	2	2	1	3	5	3	2	2	1	2	1	2	1	3	1	2
splendidissima	1	2	1	2	2	2	2	2	2	1	3	6	4	2	2	1	2	1	2	1	3	1	2
stipularis	1	2	2	2	2	2	3	2	1	1	3	4	4	2	2	1	2	1	2	1	3	1	2
unifoliata	2	1	1	1	1	2	3	1	1	2	1	1	1	1	2	1	4	1	2	2	1	2	1
spec. a	1	2	2	1	2	2	3	2	2	2	4	3	2	3	2	2	4	4	2	2	2	2	1
spec. b	2	1	1	1	1	1	4	2	3	1	3	5	3	3	2	1	2	1	2	1	3	1	2

Species / Character	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
M. pulchra	1	3	2	1	2	1	1	1	1	1	1	4	1	1	1	1	4	1	2	1	1	1
F. albiflora	2	3	2	2	2	3	?	1	2	3	3	4	2	2	1	1	1	1	1	1	3	3
brachybotrys	1	1	2	1	1	1	1	2	1	2	4	2	1	2	1	1	3	1	2	1	2	2
bracteolata	2	3	2	2	2	3	?	1	2	3	3	4	2	2	1	1	1	2	1	1	3	3
cauliflora	1	1	1	1	1	1	2	2	1	1	2	4	1	1	1	1	3	1	2	1	3	3
incredibilis	1	2	1	1	2	3	1	1	2	1	3	4	2	2	1	1	2	1	1	1	3	3
johorensis	1	1	2	1	1	3	2	2	1	3	1	2	1	2	1	1	1	1	1	2	3	3
lanceolata	1	1	2	1	1	1	2	2	1	3	3	1	1	1	1	1	1	1	1	2	1	1
leptobotrys	1	2	2	1	2	3	?	1	2	3	3	1	1	2	1	1	1	1	1	1	2	2
ngii	1	2	2	1	1	3	1	2	2	3	2	2	1	2	1	1	1	1	3	1	3	3
nivea	1	2	1	1	1	3	1	1	2	3	2	2	1	2	1	1	1	1	3	1	3	3
ophirensis	1	1	?	1	1	?	?	2	1	3	2	3	1	1	1	1	3	1	3	1	3	3
pauciflora	1	1	2	1	1	2	2	2	1	3	3	1	2	1	1	2	2	1	1	1	3	3
rheophytica	1	1	2	1	1	1	1	2	1	1	2	4	1	1	2	1	4	1	2	1	1	1
splendidissima	1	1	2	1	1	1	1	2	1	2	4	4	1	1	2	1	3	1	2	1	1	2
stipularis	1	1	?	1	1	?	?	2	1	1	2	4	1	1	1	1	3	1	2	1	1	3
unifoliata	2	3	1	2	2	3	?	1	2	3	2	4	2	2	1	1	2	1	1	1	3	3
spec. a	1	1	2	1	1	3	1	1	2	1	2	4	2	2	1	1	2	1	1	1	3	3
spec. b	1	1	2	1	1	1	1	2	1	3	4	2	1	1	1	1	3	1	2	1	1	1

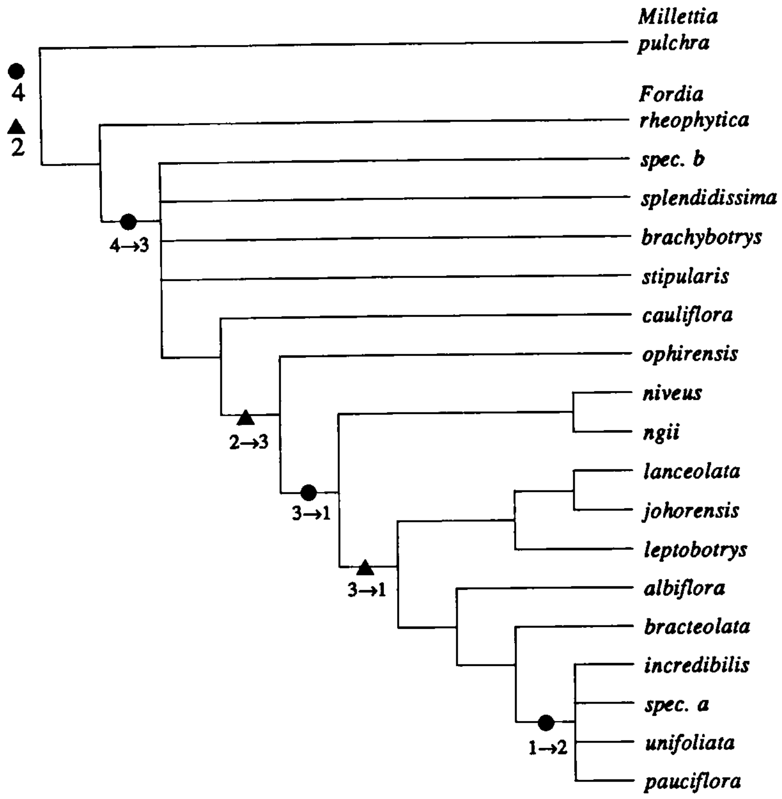


Fig. 20. Cladogram based only on anatomical characters (length 43, CI 0.62). ● = mesophyll state (character 39), ▲ = abaxial epidermis (character 43).

of *Amdjah 150*), and to have secretory canals (not found in *Amdjah 150* and *van Niel 4595*).

The anatomical characters thus defined were added to the morphological data matrix (table 3a). The former characters 6 and 9 had to be changed according to more detailed information found in the leaf anatomy studies. They were reformulated in characters 6 respectively 10 and 11. Characters 9 and 12 are new.

Before running this combined data matrix (table 3b), a preliminary analysis was made in HENNIG86 with mhennig and bb* on only the anatomical data (characters 10, 11, 34–45). *Millettia pulchra* acted as outgroup.

Forty-six trees were found with length 43, CI (consistency index) 0.62 and RI (retention index) 0.75. Automatic iterative character weighting left 12 trees, of which six, however, united *F. unifoliata* and *F. pauciflora* in a terminal branch based on the absence (!) of character 11 state 3. The other six trees differed in the sequence

Table 4. Characters, number of character states, steps, and consistency index for the characters in the morphological analysis (fig. 21).

Characters	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Character states	2	2	2	2	4	2	4	2	3	2	5	6	5	3	3	2
Steps	2	3	4	3	7	4	7	3	9	1	8	6	7	9	4	1
Consist. index	.50	.33	.25	.33	.42	.25	.42	.33	.22	1.0	.50	.83	.57	.22	.50	1.0

Characters	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Character states	4	4	2	2	3	2	2	2	3	2	2	2	3	2	2	2
Steps	5	8	2	1	3	1	2	1	4	4	1	3	2	2	3	1
Consist. index	.60	.37	.50	1.0	.66	1.0	.50	1.0	.50	.25	1.0	.33	1.0	.50	.33	1.0

Characters	32	33	34	35	36	37	38	39	40	41	42	43	44
Character states	3	4	4	2	2	2	2	4	2	3	2	3	3
Steps	4	8	7	2	2	2	1	6	1	3	2	4	4
Consist. index	.50	.37	.42	.50	.50	.50	1.0	.50	1.0	.66	.50	.50	.50

of *F. brachybotrys*, *F. splendidissima*, and *F. stipularis*. Figure 20 shows these species in a polytomy. None the less, approximately the same two groups can be found here as in the morphological tree. The most primitive species are the Bornean species (*F. brachybotrys*, *F. rheophytica*, *F. splendidissima*, *F. spec. b*), *F. stipularis*, and *F. cauliflora*. The second group unites *'Imbralyx'* with *F. johorensis*, *F. lanceolata*, and *F. pauciflora*. *Fordia ophirensis* holds an intermediate position. The tree is mainly based on mesophyll structure (char. 39) and presence of papillae on the abaxial epidermis (char. 43).

Complete cladistic analysis

The complete data matrix (table 3b) was run with mhennig and bb*, with the same characters ordered as in the morphological analysis (char. 13 and 14). This resulted in 111 trees (length 165, CI 0.47 and RI 0.63), but after automatic iterative character weighting only two trees remained with length 471 (= 167 without weighting), CI 0.61 (= 0.46 without weighting) and RI 0.81. They differ in the position of *F. bracteolata* as sister species to either *F. albiflora* or to *F. unifoliata*. For reasons already stated in the macromorphological analysis, the tree with *F. bracteolata* and *F. albiflora* as sister species is preferred (fig. 21). The tree corroborates in most aspects the macromorphological one (cf. fig. 19 and fig. 21).

Ten out of the 45 characters used have a maximum CI (table 4). These are approximately the same characters as those in the morphological analysis. Character 0 (leaves compound) now shows a parallel caused by the inclusion of the unifoliolate *F. spec. b*. Character 6 is no longer a synapomorphy as the *F. lanceolata*, *F. johorensis* and *'Imbralyx'* group no longer exists. Character 9 proves a new synapomorphy for *F. johorensis* together with *'Imbralyx'*. Other morphological characters do not change much in consistency index in the new tree (cf. tables 2, 4).

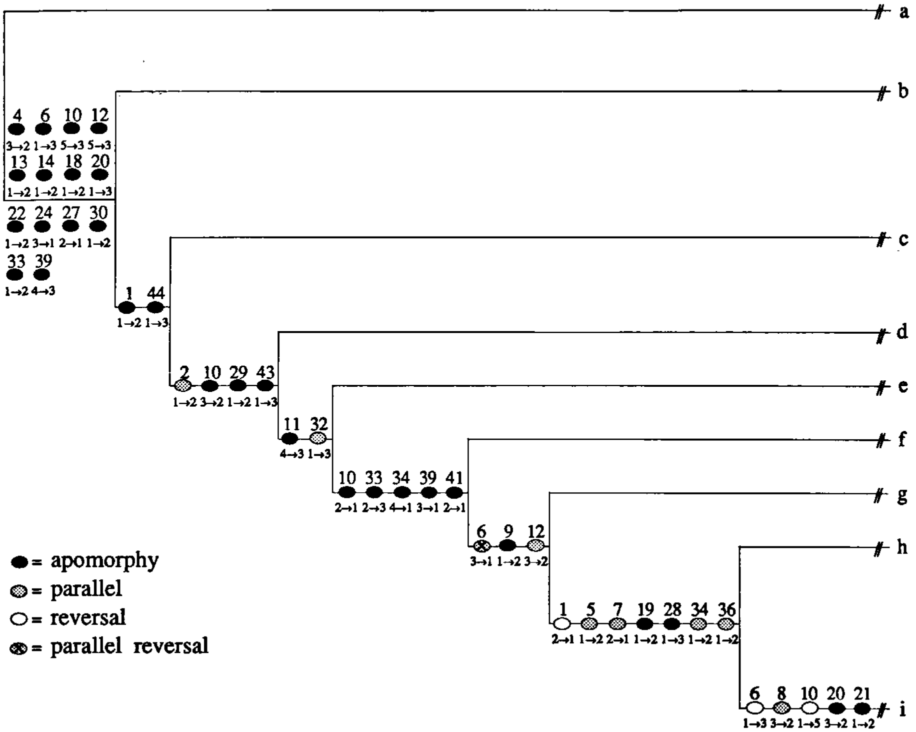
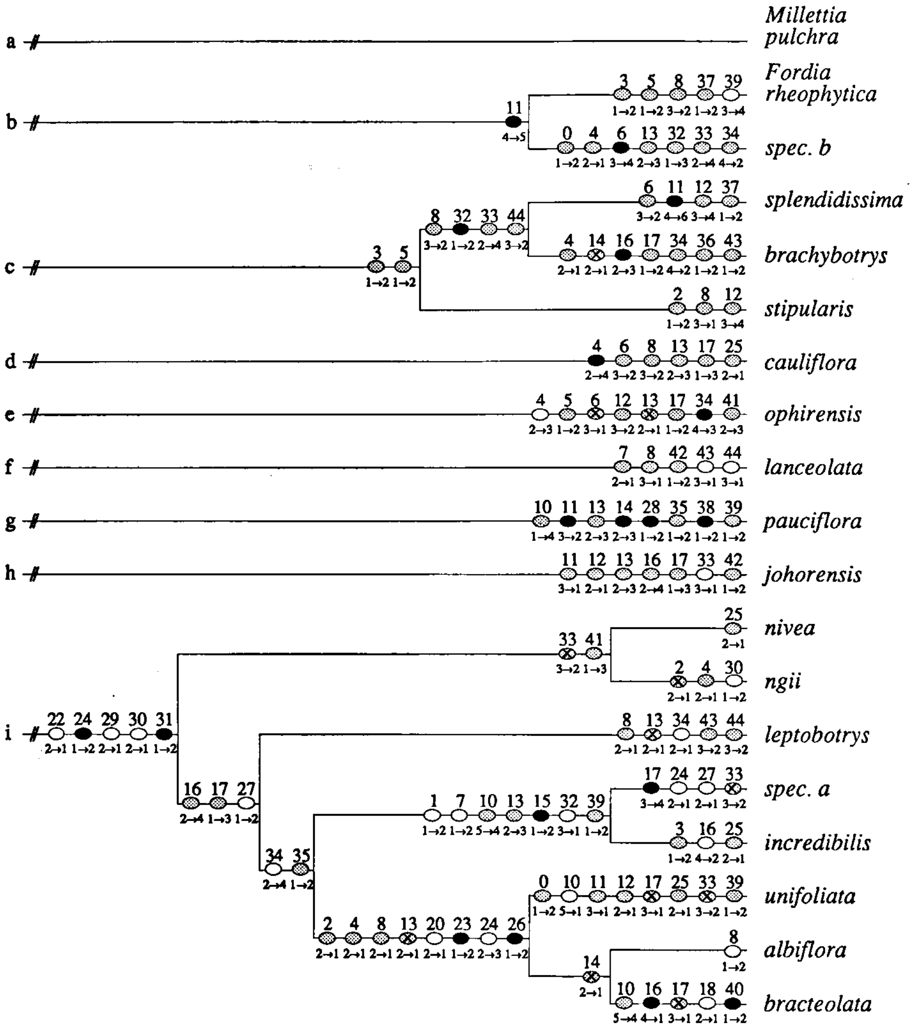


Fig. 21. Cladogram showing the result of the combined analysis (length 167, CI 0.48).

Of the anatomical characters (34–44) only character 34 (tannin idioblasts) has a consistency index below 0.50. The presence of a dark coloured substance can be caused by the drying of the specimen for herbarium collections. It was not always easy to see whether the tannin really occurred in idioblasts. Character 38 (arc-shaped bundle at base) and character 40 (birefringent granules) are autapomorphies for *F. pauciflora* and *F. bracteolata*, respectively. Most other characters can be explained by only one parallel.

It has often been remarked that the taxonomic value of many epidermal characters (e.g. undulation, presence of papillae etc.) is very doubtful (Jansen & Baas, 1973; Den Hartog-Van ter Tholen & Baas, 1978). This is mostly the result of the large



infraspecific and infraspecimen variation. In the present analysis, however, these characters have a CI of 0.50 or more. This can be a side effect of scoring the most frequently occurring character state. When most variation is discarded in the scoring for the data matrix, small external effects are lost.

Other characters are expected to show parallels as e.g. the development of adaxial stomata. This can be an effect of habitat or of random genetic variation. According to Stirton (pers. comm.) the occurrence of amphistomaty (stomata on abaxial side and adaxial nerves) is derived from hypostomaty (only on abaxial side). It is often correlated with temperate and drier regions, e.g. coastal or disturbed forests. These parallelisms can therefore be explained by ecological factors. The discarded amphistomaty of *F. albiflora, KL 1678* and the fact that Keijner (unpubl.) found stomata on the adaxial side of the leaflet in *F. bracteolata* (as *Millettia albiflora*) which I failed to locate, can also be environmental adaptations with no bearing to phylogenetic reconstruction. Stirton (pers. comm.) mentioned that amphistomaty can vary with organ, age and species, that it is sometimes correlated with anomocytic stomata and may be useful in cladistic analysis. The research conducted here has been too small to record this variation fully and it is possible that more of the studied species have, in fact, adaxial stomata somewhere on the leaflets.

In order to find specific patterns in the characters mentioned above many more leaflets per species and per specimen should be analysed.

CONCLUSION AND DISCUSSION

It is my conclusion that *'Imbralyx'* and *'Fordia* s.s.' must be placed in the same genus. As *Fordia* is the oldest of the two, it will be preserved over *'Imbralyx'*. Calling the branch with the Bornean species *Fordia* and the rest *Imbralyx* is not possible as the type species, *F. cauliflora,* is situated on the *'Imbralyx'* branch. The only way to change this would be, I think, to use an outgroup that is more close to *'Imbralyx'*, but no better candidates than *M. pulchra* for the outgroup position have yet been found. In the present situation the only possible solution is lumping the two genera.

The other deviating fact from the nomenclature as defined by Buijsen (1988) is the separation of the subspecies of *F. splendidissima.* To maintain the credibility of the cladogram, *F. rheophytica* is regarded as a separate species. The formal renaming of this rheophyte to *F. rheophytica* (formerly *F. splendidissima* subsp. *rheophytica*),will be found in the paper by Dasuki & Schot (1991, this issue).

Another solution would be to reduce also the status of *F. brachybotrys* and *F. stipularis* into the *F. splendidissima*-complex. As this would only further obscure the relations in this complex, I prefer to re-establish the rheophyte. The differences between the two species are mostly caused by adaptations to the rheophytic habitat, however. But this makes distinguishing easier. For instance, *F. brachybotrys* is much sooner confused with *F. splendidissima* than the rheophyte is. Intermediate specimens are found between the two subspecies but also between *F. splendidissima* and *F. brachybotrys*, and might be found between *F. splendidissima* and *F. stipularis* if the latter was better known. In fact, the *F. splendidissima* as a whole shows such a wide variation that it might even be possible to distinguish more, but less distinct varieties. The rheophyte is about as distinct as *F. brachybotrys* or *F. stipularis* and deserves a separate name, at least as long as relationships within the Bornean complex remain as obscure as they are now.

The successive weighting procedure in HENNIG86 is meant to provide groups on more reliable characters without making prior decisions on weighting (Farris, 1988). The weights are calculated by scaling the product of CI and RI as given in 'best fits' between 0 and 10. Unique synapomorphic characters (CI 1.0) thus obtain the highest weight (10); characters that need more than the necessary steps to explain their distribution get lower values. A new tree is then calculated, in which each step is as long as the weight assigned to the character. Characters with weight 10 use 20 steps instead of 2 without prior weighting. The result is that trees with most characters with high CI- and RI-values have the fewest number of steps. The total length of the tree becomes longer, of course. The statistics given are artefacts, and it is possible that, after counting the true number of steps (with equal weights for the characters), the new tree is not the most parsimonious one.

So character weighting in the combined analysis produced a tree with length 167 vs. 165 in the 111 trees before character weighting. More steps were mostly needed for those characters with a low CI- and RI-value in the first analysis. The number of (syn)apomorphies was maximized, e.g. characters 9, 28 and 42 did not always have a maximum CI in the first 111 trees.

The fact that the remaining tree after character weighting is not the most parsimonious one, does not change the conclusion that *'Imbralyx'* should be lumped in *Fordia*. All 111 trees with length 165 still gave *'Imbralyx'* at the end of a branch containing the Malayan species of '*Fordia* s.s.'. This is not unexpected because the strength of a tree is dependent on its synapomorphies. The group *'Imbralyx'* has at least three synapomorphies and a couple of reversals (fig. 21) and *'Imbralyx'* with *F. johorensis* has two synapomorphies (char. 9, 28). The three Bornean species with *F. stipularis* have the most primitive character states resulting in all cases in a cladogram with these species on the lower branches and the rest with *'Imbralyx'* at the higher branches.

This lumping violates the weak distinction between *Fordia* and the genus *Millettia*. The distinghuishing characters that have until now been used to separate *Fordia* from *Millettia*, viz. two ovules, raminascent or caulinascent pseudoracemes, and the capacity to flower and germinate in the dark understorey of evergreen forests (Geesink, 1984: 94), can no longer be maintained. Indeed, extension of *Fordia* with *'Imbralyx'* characters makes it very difficult to find notable differences with some groups of the heterogeneous *Millettia*. Separation from sections with e.g. big flowers or one-seeded fruits or climbers is still evident.

Difficulties arise when the species *Millettia acutiflora* or *M. pierrei* have to be distinguished as non-*Fordia*. Both tree species have small white flowers, axillary pseudoracemes, imbricate calyces, flat woody beaked pods, 3 or 4 ovules, leaflets sparsely hairy with prominent nervation on both sides and cuspidate apices and more characters that suggest partly '*Fordia* s.s.' and partly *'Imbralyx'*. Gagnepain (1913), who first described them, placed *M. pierrei* close to the 'Albiflorae' and *M. acutiflora* with *M. eberhardtii* (which I have not seen). Craib (1928: 387) on the other hand, allies *M. acutiflora* with *M. pubinervis* and *M. brandisiana*. This is not likely because these species belong to the *M. xylocarpa*-complex which has flat pods with lenticels and pulvinate inflorescences that lack in *M. acutiflora*.

Other groups that resemble *Fordia* are the *M. pulchra*/*M. extensa* relatives. *Millettia extensa* differs in having thicker-walled pods, but many have small flowers with structures similar to both the Bornean group and the *'Imbralyx'* group of *Fordia*. The group around *M. pulchra* (here used as outgroup) has similarity in pods (flat, woody, beaked) but differs in number, shape and hairiness of leaflets. Probably these three groups (*xylocarpa, extensa, pulchra*) represent closely related genera but it will need a full revision of *Millettia* to understand which species can possibly be transferred to *Fordia*.

Despite the possibility that the phylogenetic tree of *Fordia* is incomplete, a biogeographical analysis is feasible. Even if some species should be inserted into the clado-

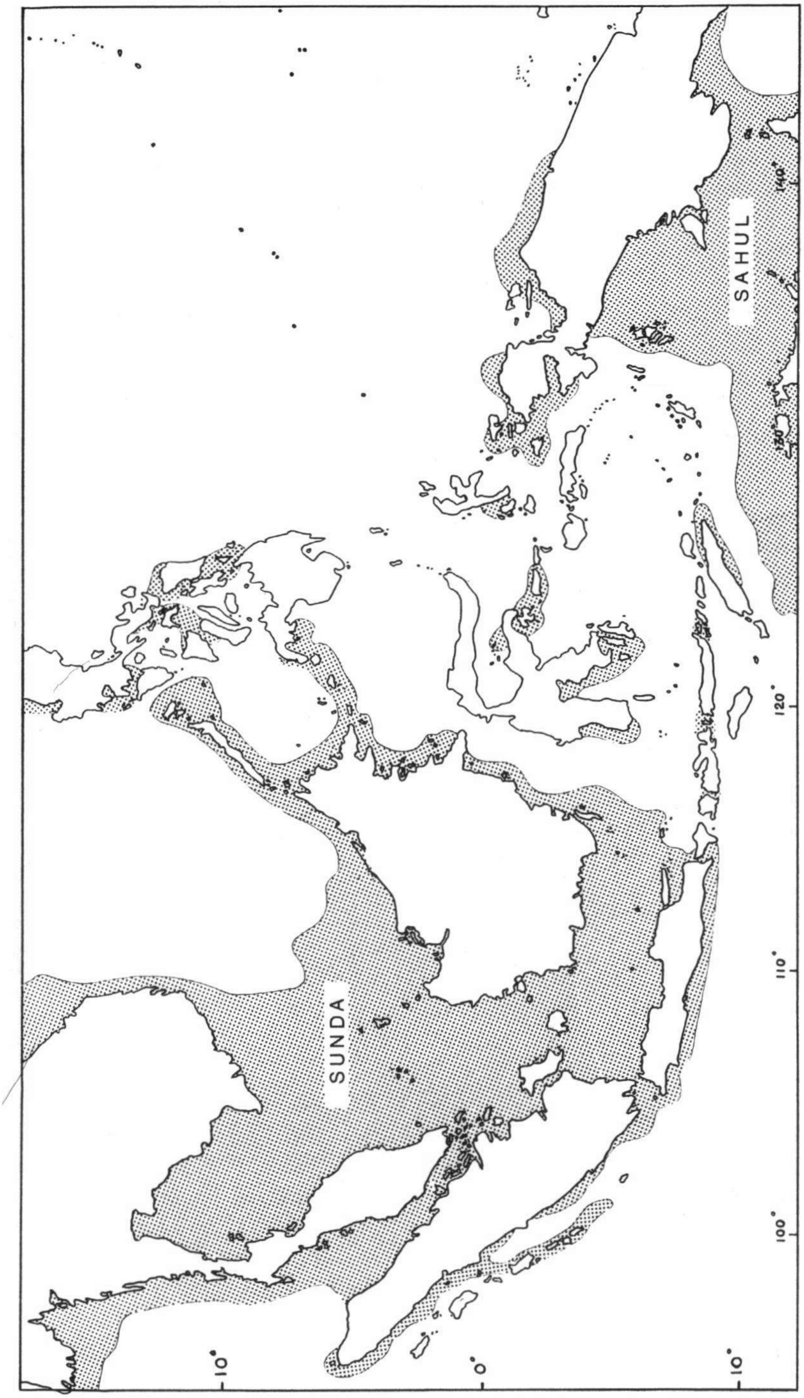


Fig. 22. Map showing the Sunda and Sahul shelves. Dashed areas have low sea levels and become dry when a sea level drop occurs. Drawn after Morley & Flenley (1987).

gram, the relations for the species that now constitute the tree will not change. More information will probably not disrupt the distinction between the two groups: Borneo and Malaya. Insertion of e.g. *M. acutiflora* and/or *M. pierei* into the cladogram will only complete the picture. They are both in character and in distribution (Indo-China, Laos, Burma, Thailand) in between the Malayan species and the two Chinese ones.

BIOGEOGRAPHICAL ANALYSIS

Summarized biogeographical history of Malesia

The geological history of the Indonesian archipelago is a very complex one. The area has an active tectonic history. Starting with the breakup of the supercontinent Pangea approximately 180 My BP the southern part, Gondwana, rifted into parts about 140 My BP (Weijermars, 1989). A part of Southeast Asia had a Gondwanic origin (Audley-Charles, 1987). Iran, Tibet, Burma with Malaya, and part of Indo-China are microcontinents that started drifting at the same time as India did. The islands Borneo, Sumatra, Java, and part of Sulawesi followed later on, sometimes fragmented. Ollier (1985) extends these microcontinents with Chinese terranes.

The collision of the Eurasian and the Australian continent is thought to have taken place approximately 15–10 My BP. The active tectonic movements on the ridges of the microcontinents resulted in the extension of land masses and uplifting of East Indonesia. There have been no major changes since. New pathways were provided for diffusion of flora and fauna. The Indonesian islands have acted as stepping stones for plants dispersing both ways between Asia and Australia. It is also assumed that new land masses originated in those times but they are now lost again (Audley-Charles, 1987).

By the end of the Tertiary the sea level started lowering as the result of tectonic events like the reduction of oceanfloor, followed by the glaciation of Antarctica (Morley & Flenley, 1987). Later these effects were accentuated periodically by the climatic cooling in the Pleistocene. The accumulation of ice in the glacial times brought about an eustatic drop in sea level. The Sunda and Sahul shelves, which are only about 100 m below the present sea level, became land and provided further pathways for species diffusion (Biswas, 1973; Verstappen, 1980). Malesia was then characterized by two extended shallow areas. These were separated by a sea too deep to become dry, consequently Sunda and Sahul stayed isolated like the scattered islands in this deep sea (fig. 22).

An extended savanna vegetation occurred on these shelves while continental conditions prevailed (e.g. Climap, 1976; Geyh et al., 1979). The lower limit of the mountain flora, following the drop in temperature, was lowered. Tropical rain forests declined but did not disappear, as they where buffered by the dry shelves. The forests in Malaya, Borneo, and Sumatra were surrounded by savanna areas and monsoon forests which kept evergreen conditions from desiccation. The reduction in rain forest was not so severe that distinct refugia occurred. When the warming climate caused the sea level to rise again, the savanna and monsoon vegetations were flooded (Meijer, 1982).

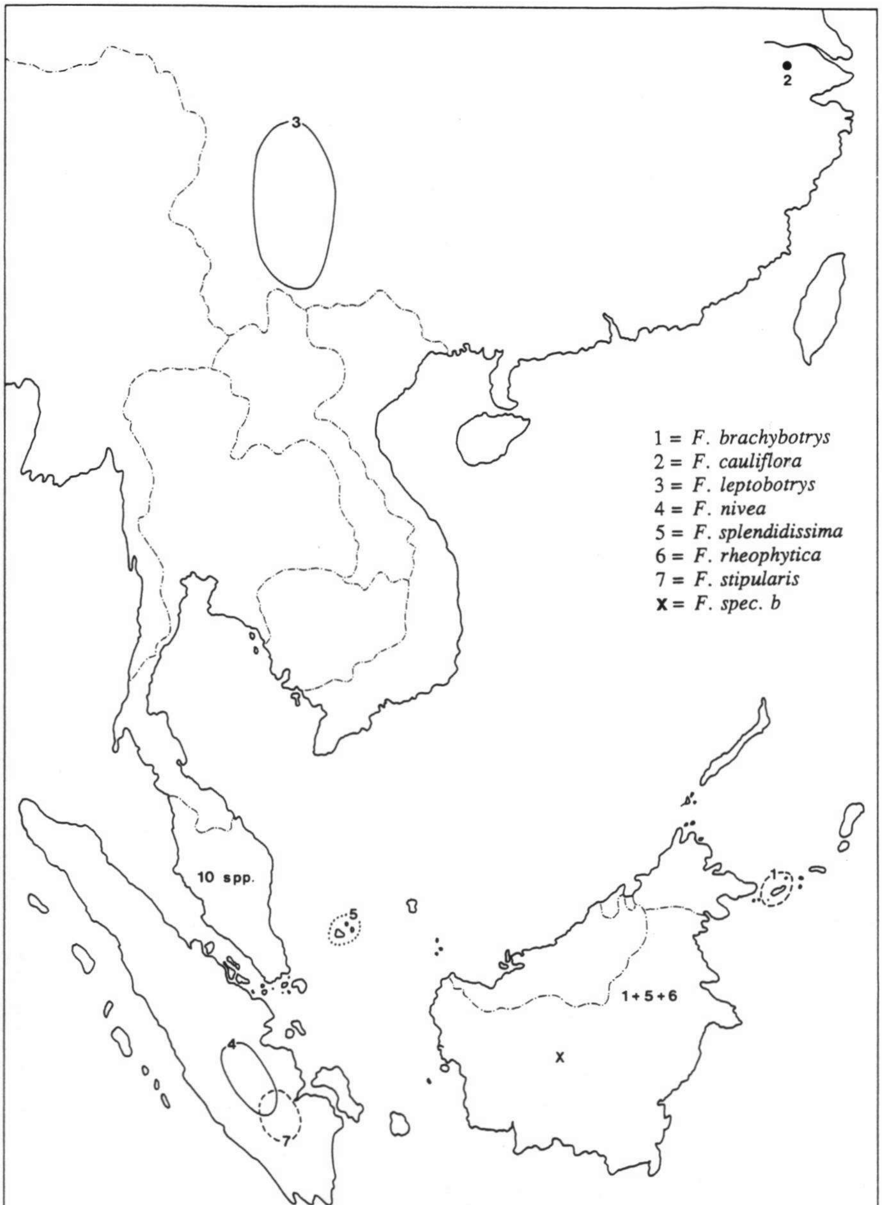


Fig. 23a. Distribution of *Fordia*. See for a detailed map of the distribution in Malaya figure 23b.

The first Leguminosae records in Africa date from late Cretaceous times, when Pangea had already fallen apart. The colonization of Europe and Asia by Papilionaceae became possible after the closing of Tethys approximately 17 My BP. When the climate started cooling in the Pliocene, which continued throughout the Pleistocene, the new conditions resulted in rapid radiation (Raven & Polhill, 1981).

The origin of *Fordia* is to be expected in these times of rapid climatic change and dispersal. This implies that the distribution does not show effects of tectonic movements. It is also possible that modern climatic factors are the main cause of the present-day distribution. But presuming that the distribution of *Fordia* is caused by vicariance and if *Fordia* originated on the mainland as the Chinese outgroup *Millettia pulchra* suggests, it is expected that the areagram shows a diffusion from the mainland via the dry South China Sea. Pleistocene lower sea levels provided continental connections for the colonization of the islands on the Sunda shelf followed by subsequent speciation.

Distribution and delimitation of areas

Fordia shows a Sunda-distribution. Two species are found in South China, three on Borneo, two on Sumatra (fig. 23a), and the remaining ten in Malaya (fig. 23b), of wich *F. pauciflora* extends to southern Peninsular Thailand.

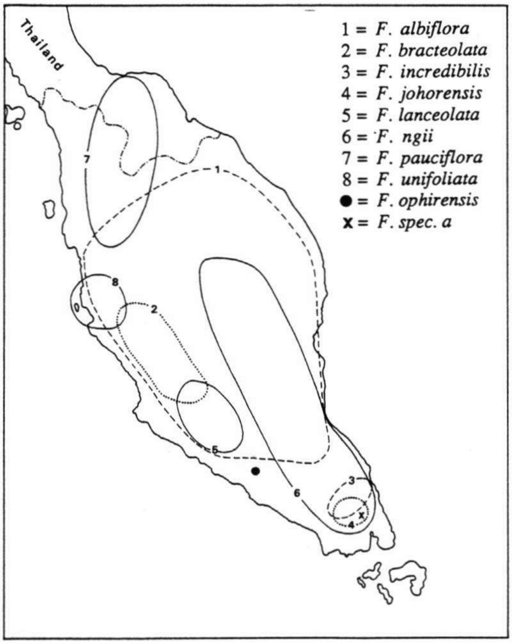


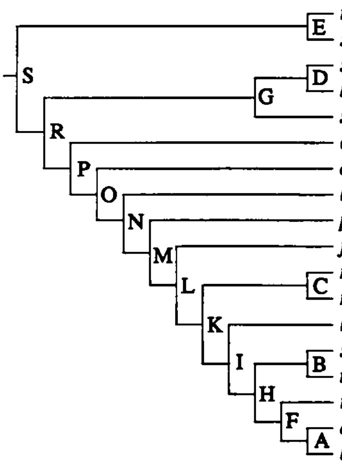
Fig. 23b. Distribution of *Fordia* in Malaya.

As seen from the distribution maps some areas are well separated. The two Chinese provinces Kwantung (*F. cauliflora*) and Yunnan (*F. leptobotrys*) are areas of endemism. Sumatra with its two species (*F. nivea* and *F. stipularis*) cannot be separated as the distributions show overlap. For Borneo the same is true: the distributions overlap. No difference in a southern and a northern part is seen. The Sulu Archipelago (some *F. brachybotrys*) was reckoned to Borneo.

The Anambas (a province of Sumatra, with one *F. splendidissima* specimen), were taken as a separate area. Their position in the middle of the South China Sea makes it difficult to include it in any of the surrounding islands.

Table 5. Distribution matrix for *Fordia* and its ancestors.

Cladogram



Species	no.	Area 1	2	3	4	5	6	7	8
rheophytica	13	0	0	0	1	0	0	0	0
spec. b	18	0	0	0	1	0	0	0	0
splendidissima	14	0	0	0	1	1	0	0	0
brachybotrys	2	0	0	0	1	0	0	0	0
stipularis	15	0	0	1	0	0	0	0	0
cauliflora	4	1	0	0	0	0	0	0	0
ophirensis	11	0	0	0	0	0	1	0	0
lanceolata	7	0	0	0	0	0	0	1	0
pauciflora	12	0	0	0	0	0	0	1	1
johorensis	6	0	0	0	0	0	1	0	0
nivea	10	0	0	1	0	0	0	0	0
ngii	9	0	0	0	0	0	1	1	0
leptobotrys	8	0	1	0	0	0	0	0	0
spec. a	17	0	0	0	0	0	1	0	0
incredibilis	5	0	0	0	0	0	1	0	0
unifoliata	16	0	0	0	0	0	0	1	0
albiflora	1	0	0	0	0	0	1	1	0
bracteolata	3	0	0	0	0	0	0	1	0
Ancestor A	19	0	0	0	0	0	1	1	0
Ancestor B	20	0	0	0	0	0	1	0	0
Ancestor C	21	0	0	1	0	0	1	1	0
Ancestor D	22	0	0	0	1	1	0	0	0
Ancestor E	23	0	0	0	1	0	0	0	0
Ancestor F	24	0	0	0	0	0	1	1	0
Ancestor G	25	0	0	1	1	1	0	0	0
Ancestor H	26	0	0	0	0	0	1	1	0
Ancestor I	27	0	1	0	0	0	1	1	0
Ancestor K	28	0	1	1	0	0	1	1	0
Ancestor L	29	0	1	1	0	0	1	1	0
Ancestor M	30	0	1	1	0	0	1	1	1
Ancestor N	31	0	1	1	0	0	1	1	1
Ancestor O	32	0	1	1	0	0	1	1	1
Ancestor P	33	1	1	1	0	0	1	1	1
Ancestor R	34	1	1	1	1	1	1	1	1
Ancestor S	35	1	1	1	1	1	1	1	1

Malaya was split into three areas: South Malaya, containing the province Johore with its many endemic species; Central Malaya, containing the provinces Selangor, Perak, Pahang, Kelantan, Terenganu, and Negeri Sembilan, also has some endemic species; North Malaya with Peninsular Thailand contains only *F. pauciflora*, which is also found in Perak.

Eight areas are distinguished:

1. Kwantung
2. Yunnan
3. Sumatra
4. Borneo + Sulu Archipelago
5. Anambas
6. South Malaya
7. Central Malaya
8. Peninsular Thailand + North Malaya

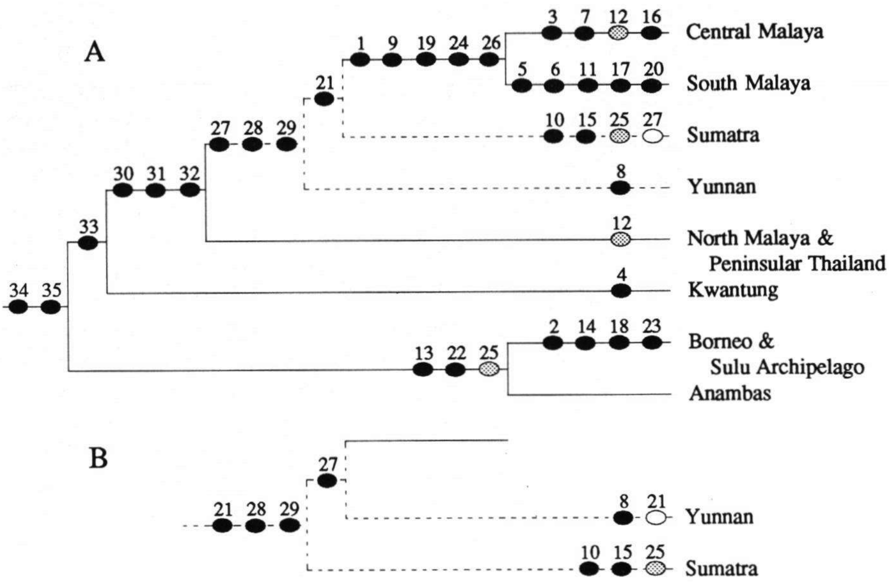


Fig. 24. Areagrams of Fordia; A & B show the two alternative ways in dashed lines. Both areagrams have 3 homoplasious events, 36 steps, and CI 0.971. ● = apomorphy; ◍ = parallel; ○ = reversal.

Areagram

The distribution matrix for *Fordia* and its ancestors (table 5) was analysed in the program CAFCA under assumption 0 (Zandee & Roos, 1987; Zandee, 1988). Furthermore, the distribution of the ancestors is presumed to be the sum of the distributions of all the descendants. No outgroup area was defined (i.e., *Millettia pulchra* was not included in the biogeographic analysis).

Two equally parsimonious areagrams were found, each with 3 homoplasious events, 36 steps, redundancy index 0.459, and consistency index 0.917 (fig. 24). The two areagrams differ only in either Sumatra or the Chinese province Yunnan as sister area to South and Central Malaya (fig. 24: A, B). This difference is caused by species 21 and 27, respectively the ancestor of *F. ngii*/*F. nivea* and the ancestor of the *F. leptobotrys–F. albiflora*-group. If Sumatra is in reality the sister area of Malaya this implies that species 27 became extinct or never occurred on this island. If, on the other hand, Yunnan is the real sister area to Malaya it implies extinction or primitive absence of species 21 in China. It is impossible at this stage to make an argued choice between these possibilities.

The other two homoplasious events are parallels to be explained by dispersal: *F. pauciflora* (12) dispersed to South Peninsular Thailand and the ancestor of the *F. splendidissima*/*F. brachybotrys*/*F. stipularis*-group dispersed to Sumatra. This ancestor evolved into *F. stipularis* on Sumatra and into the *F. splendidissima*-complex on Borneo. The coexistence of ancestor 25 with two of its descendants (22 and 13) is a consequence of the fact that the Anambas have no endemic species of their own.

Generalized areagram

In a proper biogeographic analysis more cladograms of different groups of species should show congruent distribution patterns. The genera that can be compared to *Fordia* on account of their distributions have often not been cladistically analysed. The few revised genera that were considered, *Pyrrosia* (Polypodiaceae), *Matapa* (Lepidoptera), and *Xanthophytum* (Rubiaceae) proved not te be very useful. They have a wide distribution (India to Australia), therefore only monophyletic subgroups in the appropriate area could be compared. From *Pyrrosia* the '*P. costata*-group', the '*P. lingua*-group' and the '*P. angustata*-group' (Hovenkamp, 1986: 116) were tried. For *Xanthophytum* the groups consisting of: *X. capitatum / setorum / olivareum / borneense / fruticulosum / ferrugineum*, and *X. kwangtungense / attopevense / polyanthum / balansae / nitens / papuarum / grandiflorum / magnisepalum* (Axelius, 1990: 489) were chosen. *Matapa* consists of 8 mostly widespread species (De Jong, 1983: 260).

When using such small groups together with the larger *Fordia*, the information content of the generalized areagram is mostly stated according to the cladogram with most data: *Fordia*. So, after running a general analysis, the same two areagrams were found as before, with exactly the same choice which area to use as sister area to Malaya. Another cause of difficulties can be the different ages of the origin of the compared groups. The much older family of e.g. Polypodiaceae probably has a Gondwanic distribution and may show effects of a different stage in the geological history.

Some genera that seem to fit better in view with their distributions and age are for instance the Papilionoid *Spatholobus* or the Orchids *Anya* and *Tainia* which are still under revision. Therefore, the areagram was left as it is, for the time being.

DISCUSSION

Both areagrams show in their root the same splitting events (fig. 24). At first, Borneo and the Anambas are separated from the rest of the Malay Archipelago. This can be explained easily. During the glacial maxima the savanna of the Sunda shelf was intersected by rivers. One of the major river systems ran in between Malaya and Borneo (Morley & Flenley, 1987: fig. 5.5; Verstappen, 1980: fig. 3). The warming up of the climate and the correlated rise in sea level had their first effects on these major rivers. They grew wider and started to become barriers against geneflow. The isolated specimens left on Borneo and on the Anambas became new species. The second splitting event was the separation of the Anambas from Borneo.

After further warming up, the climatic differences in the seasonal area became accentuated. In the decreased rain forests in Malaya these changes were not so severe (Meijer, 1982) but there were effects in the northern areas. First Kwantung reacted to the change with speciation into *F. cauliflora*. The two other, now seasonal, areas Peninsular Thailand and Yunnan, followed by the emergence of *F. leptobotrys* (Yunnan) and whatever survived in Thailand developed into a yet unknown seasonal *Fordia*. The presence of *F. pauciflora* is a dispersal or an extinction according to the areagram.

Further flooding eventually separated Sumatra from Malaya and afterwards species differentiation in Malaya completed the picture. In this case areagram A (fig. 24) is the most acceptable one.

It is also possible that the separation of Sumatra and Malaya became distinct before climatic change led to speciation in Yunnan as suggested by areagram B (fig. 24). The extinction of ancestor 21 of *F. ngii* and *F. nivea* is not unlikely, if it could not adapt to the change in climate. On account of the climatic history outlined above the first solution seems more acceptable. However, the absence of ancestor 27 (*F. leptobotrys* onwards) is more difficult to explain. It might not have survived the warming up of the climate on Sumatra while its descendants on Malaya did.

But there is more. It has long been known that global cooling occurred more than once during the Pleistocene. It is likely that the Sunda (and Sahul) shelf emerged two or three times (Biswas, 1973; Verstappen 1980). The distribution of *Fordia* today can equally well be caused by more than one wave of dispersal. In a former cold period *Fordia* could have reached only Malaya. After a warming up and a speciation in a second period the Malayan ancestor (21) diffused to Sumatra but a second ancestor (27), starting in Yunnan, did not get that far. The absence of this species in Sumatra is then a primitive one. It could also explain that the *F. leptobotrys–F. albiflora* group is more different from the primitive '*Fordia* s.s.' than e.g. the *F. ngii/F. nivea*-group.

But why is there no effect of this second wave in Borneo? Malaya is geologically very stable, but Borneo is still tectonically very active and unstable (Ashton, 1972). For the species on this island this instability resulted in the fact that no easily recognizable species did develop. Only species complexes are found (see also Van Welzen, 1989: 50). The variation within *F. splendidissima* is so wide that it could consist of more species, but the clines are so gradual, that delimitation is impossible. The colonization of the Anambas and/or the diffusion of ancestor 25 to Sumatra and its speciation to *F. stipularis* might have taken place later. These dispersals could have been the effects of the later ice age in Borneo.

The geologically more stable conditions in Malaya provide a better basis for speciation. Here, many closely related, well defined species occur. If the Bornean extremes were species, their number would be roughly the same as in Malaya, indicating a correlation in the age of isolation.

All this is speculation, but it explains the present-day distribution of *Fordia* fairly satisfactorily. Most species originated as the result of dispersal followed by speciation during changing climates in the Pleistocene. No other effects of the biogeographical history can be seen, but this is as expected from the supposed recent origin of *Fordia*. The three homoplasious events in the cladogram are possibly caused by two different diffusion events. Although the hypothesis fits nicely together, more areagrams of other genera are badly needed.

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