
PHYLOGENETIC CONSIDERATIONS OF EUPHORBIACEAE TRIBE ALEURITIDEAE¹

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ABSTRACT

A phylogenetic analysis based on morphological characters of Euphorbiaceae tribe Aleuritideae was performed, examining the monophyly of subtribe Aleuritinae and its delimitation into three genera. The subtribe was supported as monophyletic and its current classification justified. Differences between the genera, though small, are based on apomorphies, and the genera are monophyletic. Within subtribe Aleuritinae, *Aleurites* (2 species) is sister to both monotypic *Reutealis* and *Vernicia* (3 species). Monophyly was not confirmed for tribe Aleuritideae. One of the selected outgroups for Aleuritideae (*Paracroton*, formerly *Fahrenheitia*) appeared within the ingroup in the most parsimonious cladograms. For the other subtribes, monophyly was tentatively supported for only subtribe Garciinae (monogeneric), Crotonogyninae (3 genera), and Neoboutoninae (2 genera). The largest subtribe, Grosserinae (7 genera), is probably paraphyletic, because *Domohinea* (recently placed in synonymy of *Tannodia* by Radcliffe-Smith) and *Tannodia* group with subtribe Aleuritinae.

Nowadays subtribe Aleuritinae comprises three small genera: *Aleurites* (2 species), *Reutealis* (1 species), and *Vernicia* (3 species). Müller (1866) had formerly united the three genera within a broader *Aleurites*. Airy Shaw (1967) subdivided *Aleurites* s.l. because of three new genera, *Deutzianthus*, *Loerzingia*, and *Tapoides*, thought to be closely related to *Aleurites* s.l. Recently, *Tapoides* was placed in subtribe Grosserinae (tribe Aleuritideae) by Webster (1994b). He considered *Deutzianthus* (with *Loerzingia* as synonym) to belong to tribe Jatrophae and not tribe Aleuritideae.

Revision of subtribe Aleuritinae for *Flora Malesiana* suggests differences between the genera to be narrow and reticulate. It is therefore reasonable to ask whether this taxonomic division is justified and whether the split genera and subtribe Aleuritinae are monophyletic. The phylogenetic analysis herein for all genera of tribe Aleuritideae (Table 1) will address these questions.

For tribe Aleuritideae, the four subtribes Garciinae, Grosserinae, Crotonogyninae, and Neoboutoninae show various degrees of homogeneity (see Table 1 for classification). American subtribe Garciinae is monogeneric and almost by definition homogenous; however, the two species of *Garcia* differ considerably in the stamen number (29 versus 63 to 160). The two genera of subtribe Neoboutoninae share the absence of petals and leaves

with small glandular hairs; however, they differ in leaf venation, presence of a caruncle, and persistence of stipules. African *Manniophyton* (subtribe Crotonogyninae) is distinguished by its vining habit, palmate venation, and stinging hairs; the other two genera, *Crotonogyne* and *Cyrtogonone*, are quite similar and share characters such as dioecy and fused petals. The mainly African Grosserinae is the largest subtribe, with seven genera, all dioecious and with free petals. The morphological variability among these genera is great and their distributions (Table 1) disparate (South America, Africa, Southeast Asia), indicative perhaps of a paraphyletic group.

MATERIALS AND METHODS

CHARACTER SELECTION

The characters used in the cladistic analysis are explained in Appendix 1; the data matrix is presented in Table 2. The character states were obtained from herbarium specimens (Appendix 2) and literature (Table 1).

The following characters were not included in the cladistic analysis because they are typical for single taxa and, therefore, are presumably autapomorphies: whorled leaves; ovary 2-locular (*Borneodendron*); amplexicaul stipules; bracts forming a

¹ We thank the Netherlands Science Foundation for the visitor grant (B 85-314) for Wolfgang Stuppy. The directors of BISH, BM, BO, and L are thanked for use of their collections. P. Baas, M. C. Roos, several anonymous reviewers, and three editors provided very useful comments.

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Table 1. Webster's classification (1994b) for the taxa mentioned in this study. References were sources of information for character states.

Tribe Aleuritideae		
Subtribe Aleuritinae		
<i>Aleurites</i>	2 species, Malesia, Australia, Pacific	Stuppy et al. (1999)
<i>Reutealis</i>	1 species, Philippines	Stuppy et al. (1999)
<i>Vernicia</i>	3 species, China, Indochina, Japan	Stuppy et al. (1999)
Subtribe Garcinae		
<i>Garcia</i>	2 species, Central America	Lundell (1945)
Subtribe Grosserinae		
<i>Anomalocalyx</i>	1 species, Brazil	Ducke (1934)
<i>Cavacoa</i>	3 species, African	Elffers & Taylor (1956)
<i>Domohinea</i>	1 species, Madagascar	Leandri (1940)
<i>Grossera</i>	7 species, African	Pax & Hoffmann (1912)
<i>Sandwithia</i>	2 species, Neotropics	Lanjouw (1932)
<i>Tannodia</i>	ca. 4 species, E. Africa, Comoros	Pax & Hoffmann (1912)
<i>Tapoides</i>	1 species, Borneo	Airy Shaw (1971)
Subtribe Crotonogyninae		
<i>Crotonogyne</i>	15 species, Africa	Pax & Hoffmann (1912)
<i>Cyrtogonone</i>	1 species, Africa	Pax & Hoffmann (1912)
<i>Manniophyton</i>	1 species, Africa	Pax & Hoffmann (1912)
Subtribe Neoboutoninae		
<i>Benoistia</i>	3 species, Madagascar	Radcliffe-Smith (1988)
<i>Neoboutonia</i>	3 species, Madagascar	Pax & Hoffmann (1914)
Tribe Crotonaeae		
<i>Paracroton</i>	4 species, tropical Asia	
Tribe Jatrophaeae		
<i>Deutzianthus</i>	2 species, Indochina, Sumatra	
Tribe Ricinocarpeae		
Subtribe Bertyninae		
<i>Borneodendron</i>	1 species, Borneo	

cone (*Cavacoa*); submarginal abaxial glands present, crater-like; stigmas bifid to multifid (*Crotonogyne*); staminate receptacle with disc-like glands (*Cyrtogonone*); pilose receptacle (*Domohinea*, now a synonym of *Tannodia*, see Radcliffe-Smith, 1998); thick sepals (*Grossera*); liana; stinging hairs; raised glands on abaxial surface of leaves (*Manniophyton*); lobed stipules; seeds carunculate (*Neoboutonia*); branches 5-angular; stigmas bifid to multifid (*Reutealis*); hair tuft domatia on lower leaf surface (*Tannodia*); glands at apex of petiole slenderly stalked [*Vernicia cordata* (Thunb.) Airy Shaw]; clavately stalked (*Vernicia montana* Lour.).

Some characters, including several used in Webster's (1994b) keys, were not included in the phylogenetic analysis, partly because they were too variable to permit the discrimination of states (e.g., inflorescence position; inflorescence type; flower size; fruit and inflorescence pubescence), or because the states could not be scored for many taxa [e.g., anther dehiscence; ovary tapering gradually vs. abruptly into the style (important within *Vernicia*), petal venation].

OUTGROUP SELECTION

The choice of an outgroup was difficult, because there is no obvious sister group to tribe Aleuritideae. The presence of a sister group is not a requisite (Nixon & Carpenter, 1993), but may facilitate character polarization. *Deutzianthus*, considered by Airy Shaw (1967) to be a close relative of *Aleurites*, probably has other affinities. Webster (1994b) placed it in a relatively distant tribe, Jatrophaeae. *Deutzianthus* was not selected as outgroup, because if Webster is correct, many homoplasious parallel developments would exist between *Deutzianthus* and subtribe Aleuritinae, and these would likely complicate the cladogram. Testing Airy Shaw's hypothesis would require that many more genera be included in the analysis, and that is beyond the scope of this article. Although Webster's classification was not based on phylogenetic analyses, the sequence of taxa shows an increase in apomorphies (for a list of synapomorphies, see Webster, 1994a). Therefore, it is logical to look for an outgroup in the tribes treated before the Aleuritideae. *Borneo-*

Table 2. Morphological data matrix for the cladistic analysis. The characters are explained in Appendix 1. Absence of a character is never noted as 0 to avoid any suggestion of primitiveness. Unknown characters due to insufficient material are marked as missing (—). *Borneodendron* and *Paracroton* are the outgroups.

Taxon	Character number																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>Borneodendron</i>	2	2	2	1	1	1	2	1	1	1	1	1	1	1	?	2	3	1	1	1	—	1	1	1	1
<i>Paracroton</i>	2	2	2	1	2	1	2	2	1	1	1	1	3	2	1	2	2	2&3	1	1	1	2	2	1	1
<i>Aleurites</i>	2	1	2	2	2	2	2	1	1	1	3	2	2	2	1	2	2	3	1	1	1	1	3	2	1
<i>Reutealis</i>	2	1	2	2	2	1	1	1	1	1	3	2	2	2	1	1	2	2	1	1	—	1	3	1	1
<i>Vernicia</i>	2	1	1	1	2	2	1	3	1	1	3	2	2	2	1	1	2	2	1	1	—	1	3	1	2
<i>Garcia</i>	2	1	1	1&2	1	1	2	1	1	1	1	2	2	3	1	3	1	1	1	1	1	1	2	1	1
<i>Anomalocalyx</i>	1	1	1	1	1	1	2	1	1	1	1	2	2	2	1	2	1	1	1	1	1	2	2	1	1
<i>Cavacoa</i>	1	1	1	1	1	1	2	1	2	1	1	2	2	2	1	2	3	1	1	1	1	2	2	1	1
<i>Domohinea</i>	1	1	1	1	1	1	2	1	1	1	2	2	2	2	1	1	2	2	1	1	2	1	2	1	1
<i>Grossera</i>	1	1	1	1	2	1	2	2	2	1	1	2	2	2	1	2	3	1	1	1	1	2	2	1	1
<i>Sandwithia</i>	1	1	1	1	1	1	2	1	1	1	1	2	2	2	1	2	1	1	1	1	1	2	2	1	1
<i>Tannodia</i>	1	1	1	1	1	1	2	1	1	1	2	2	2&3	2	1	1	2	2	1	1	2	2	2	1	1
<i>Tapoides</i>	1	1	1	1	1	1	2	1	1	1	1	2	2	2	1	1	2	2	1	1	1	2	2	1	1
<i>Crotonogyne</i>	1	1	3	1&2	2	1	1&2	1	1	1	1	2	2	2	2	1&2	1	1	3	1	1	2	2	1	1
<i>Cyrtogonone</i>	1	1	3	2	2	1	2	1	1	1	1	2	2	2	1	2	1	1	—	1	1	—	—	—	—
<i>Manniophyton</i>	1	1	3	2	2	2	1	1	1	1	3	2	2	2	2	1&2	1	1	3	1	1	2	2	1	1
<i>Benoistia</i>	1	1	1	1	1	1	2	1	1	2	1	2	2	1	?	2	1	1	2	1	1	3	2	1	1
<i>Neoboutonia</i>	1	1	2	1&2	2	1	1	1	1	2	3	2	2	1	?	2	1	1	2	2	1	2	2	1	1

dendron (tribe Ricinocarpeae, subtribe Bertyinae) and *Paracroton* [tribe Crotonaeae; formerly and better known as *Fahrenheitia* (Balakrishnan & Chakrabarty, 1995)] are outgroup candidates, because they have been well described in the literature and abundant material was available to check characters.

CLADISTIC ANALYSIS

The cladistic analysis was performed with PAUP version 3.1.1 (Swofford, 1993). A Branch and Bound search was performed with furthest addition of taxa, and Mulpars invoked. Statistical significance of the results was evaluated with the aid of a Bootstrap Analysis, Decay Indices up to the level $D = 6$ (retaining all trees five steps longer than the most parsimonious trees), and a Permutation Tail Probability (PTP) test (Siddall, 1993). The Bootstrap (200 replicates) and Decay analyses were also performed with PAUP 3.1.1 (Swofford, 1993), with settings for: Heuristic search, TBR, Furthest, Mulpars. Siddall's PTP test was performed in conjunction with Hennig86 (Farris, 1988), with settings: characters unordered, mh*; bb*. Character optimizations were studied with MacClade version 3 (Maddison & Maddison, 1992).

RESULTS

Seven most parsimonious cladograms were found and are summarized in the strict consensus tree (Fig. 1): length 66, Consistency Index (CI) = 0.67, Retention Index (RI) = 0.67, RC = 0.45. All cladograms comprise the monophyletic subtribes Aleuritinae, Crotonogyninae, Garciinae, and Neoboutoninae. Subtribe Aleuritinae is sister group to the outgroup *Paracroton*, and these together form a clade with part of subtribe Grosserinae (the monophyletic group *Domohinea*, *Tannodia*, and *Tapoides*). Subtribe Neoboutoninae is sister group to the three former subtribes (Aleuritinae, Grosserinae, Crotonogyninae), and subtribe Garciinae is sister group to all other subtribes in tribe Aleuritideae.

The Probability Tail Permutation test (Faith & Cranston, 1991; Källersjö et al., 1992) indicated that the data matrix contains a significant amount of cladistic information ($P = 0.001001$; $a^* = 0.000376$).

A strict consensus tree of all cladograms up to 69 steps, Decay Index 4, only resulted in a polytomy for all groups. A strict consensus of the 4446 trees of up to 68 steps, Decay Index 3, showed subtribe Aleuritinae as a clade, and the strict consensus of 308 trees of up to 67 steps, Decay Index

2, also showed the clade taxa *Domohinea* and *Tannodia* (Fig. 1).

DISCUSSION

The matrix comprised several polymorphic taxa. MacClade provides the most parsimonious optimization for the polytypic characters by choosing one state. The other state is considered to be an autapomorphy and is counted as a step. The following optimizations are suggested:

Character 4 (pubescence of abaxial leaf surface): (sub)glabrous (state 1) for *Garcia* (subtribe Garciinae) and *Neoboutonia* (subtribe Neoboutoninae); densely hairy (state 2) for *Crotonogyne* (subtribe Crotonogyninae).

Character 7 (shape of leaf blade base): cuneate (state 2) for *Crotonogyne* (subtribe Crotonogyninae).

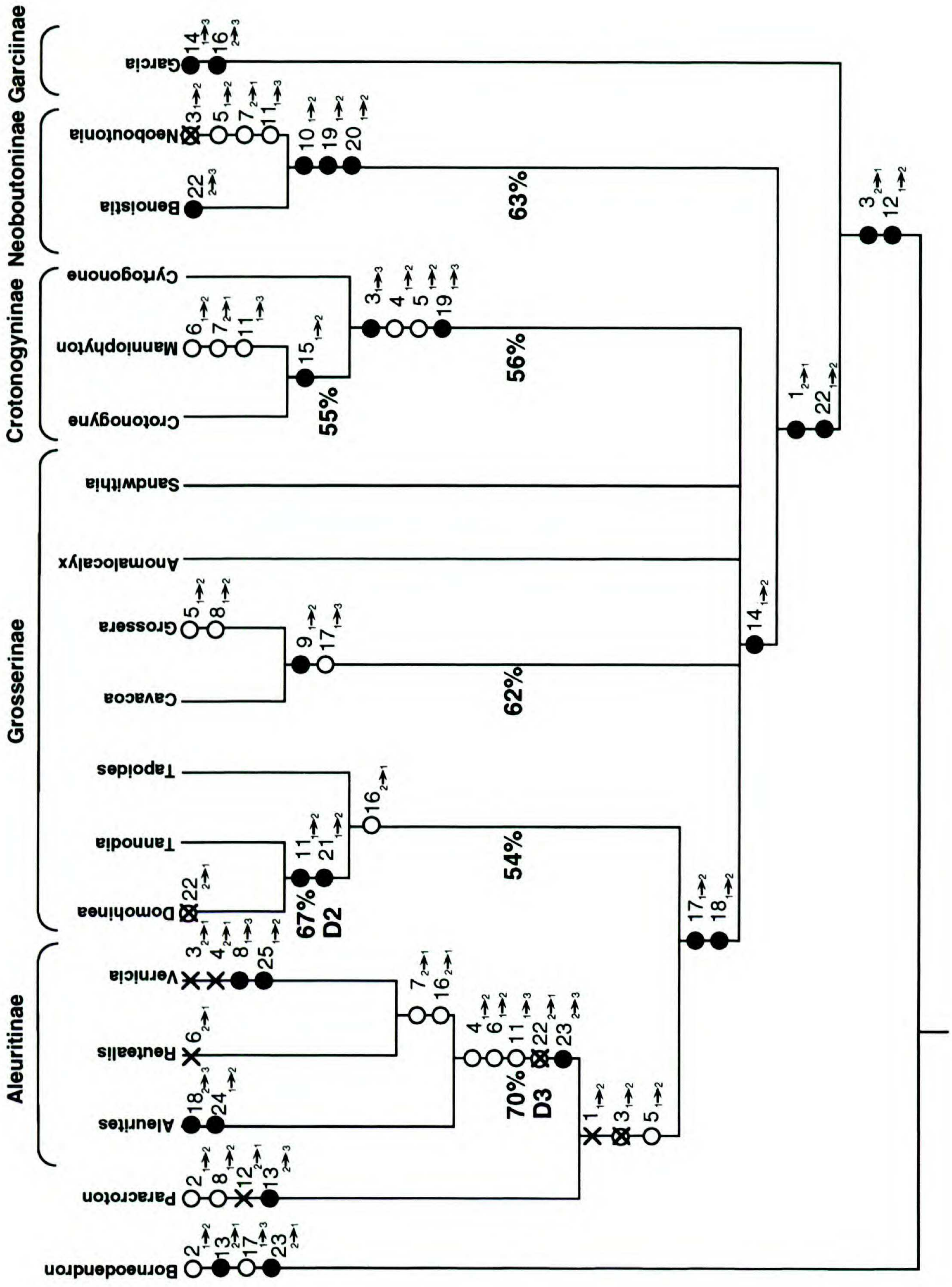
Character 13 (number of staminate sepals): 2 to 4 sepals (state 2) for *Tannodia* (subtribe Grosserinae).

Character 16 (number of stamens): 12 to 40 (state 2) for *Crotonogyne* and *Manniophyton* (subtribe Crotonogyninae).

Character 18 (arrangement of stamens): ordered in two series (state 2) for *Paracroton*.

Several of the optimizations (Fig. 1) can be interpreted differently. The characters at the root are now interpreted as either typical for the outgroup *Borneodendron* (2, 13, 17, 23) or for the ingroup (3, 12); see below. Characters 4 and 6 are regarded as synapomorphies for subtribe Aleuritinae with a reversal for *Vernicia* (ACCTRAN optimization); these characters can also be optimized as two parallel developments for *Aleurites* and *Reutealis* (DELTRAN optimization). DELTRAN optimization is used for character 2, a parallel development for *Borneodendron* and *Paracroton* (the alternative is a synapomorphy for the ingroup with a reversal for *Paracroton*). The state of character 19 is unknown for *Cyrtogonone* (subtribe Crotonogyninae); however, this character is still regarded as a synapomorphy for subtribe Crotonogyninae, thus an apiculate connective is presumed for *Cyrtogonone*.

The strict consensus cladogram (Fig. 1) is supported by a relatively high CI (0.67) and RI (0.67). Other statistical support is rather poor. Only two clades obtained a somewhat higher Decay Index (see Results). Bootstraps in this study were never 95% or higher; therefore, no clades appeared to have statistically significant support (Felsenstein, 1985). Recently, Hillis and Bull (1993, confirmed by Felsenstein & Kishino, 1993) empirically dem-



onstrated that bootstrap values of 70% or higher correspond to a probability of 95% or more that a clade is real. In this interpretation subtribe Aleuritinae (bootstrap 70%) has significant support (Fig. 1), and none of the other clades do. A bootstrap limit of 95% is very high, because it corresponds to three apomorphies for a clade without any homoplasy (Felsenstein, 1985). Morphological data matrices usually do not include many characters, and, therefore, high bootstrap support cannot be expected for all clades. The bootstrap method is purely statistical; it does not interpret the phylogenetic significance of the characters. We think that a clade with a unique character combined with a bootstrap of 60% is phylogenetically acceptable (a 60% bootstrap level corresponds to one non-homoplasious character per clade). Unique characters are considered to constitute useful characters for recognition in classifications, being reliable apomorphies.

It may appear curious that subtribe Neoboutoniae has a bootstrap of just 63%, even though it is supported by three apomorphies; this is probably due to the many homoplasious changes in *Neoboutonia* (characters 3, hairs stellate; 5, basal blade glands; 7, cordate leaf base; and 11, palmate venation). All three apomorphies (10, abaxial glandular leaf hairs; 19, connective with gland; and 20, anthers elongate) are unique; therefore, this clade is considered to be phylogenetically acceptable.

The group *Domohinea*, *Tannodia*, and *Tapoides* (54%) has no significant phylogenetic value, because character 16 (6 to 12 stamens) is not unique within tribe Aleuritideae.

Our purpose was to test the monophyly of subtribe Aleuritinae and to determine which generic classification of subtribe Aleuritinae is supported cladistically. We conclude that subtribe Aleuritinae is monophyletic: the bootstrap is high enough, the clade has a Decay Index of 3, and it possesses a divided pistillate disc as a unique character state (character 23). Airy Shaw's (1967) division of subtribe Aleuritinae into three genera is supported; at least, *Aleurites* and *Vernicia* each have two unique characters (*Aleurites*: 18, stamens in 4 series; 24, drupaceous fruit; *Vernicia*: 8, glands in leaf margin crenations; 25, seeds dorsally warty). *Reutealis* is seemingly untypically characterized by a single re-

versal (16, stamens 6 to 12); however, it possesses two unique autapomorphies: branches 5-angular, and stigmas bifid or multifid. The sister-group relationship between *Reutealis* and *Vernicia* is only supported by two parallel developments (though unique within subtribe Aleuritinae): 7 (leaf base cordate) and 16 (stamens 6 to 12).

Monophyly of subtribes Crotonogyninae and Neoboutoniae is supported in terms of unique characters, though not by significant bootstrap values or decay indices. Subtribe Garciinae is monogeneric, and, therefore, no bootstrap values or decay indices are available. *Garcia* seemingly has two unique character states (14, staminate petals 6 to 13; 16, 63 to 160 stamens); however, character 16 applies only to one of the two species in the genus, leaving only the higher number of staminate sepals as a unique character.

Subtribe Grosserinae is not supported at all; the relationships of the American genera, *Anomalocalyx* and *Sandwithia*, are still especially obscure (both genera, due to several non-included autapomorphies, received the same coding). Within subtribe Grosserinae, *Cavacoa* and *Grossera*, both African, constitute a distinct group (supported by the unique character 9, pellucid dots in leaves; and the non-unique 17, all stamens connate). The supposed relationship between *Tannodia* (including *Domohinea*) and *Tapoides* (Africa, Madagascar, Comores, Borneo) is weak (see discussion above).

The relationships between all distinct groups (lower branches in Fig. 1) are not supported by bootstrap values or Decay Indices. Characters 1 (monoecious plants) and 22 (5 pistillate sepals) are not unique; they reverse in several taxa. Characters 14 (3 to 5 staminate petals) and 22 (5 pistillate sepals), unique in this group, are not unique in the Euphorbiaceae, nor are the inner connate stamens, 17, and biseriate stamens, 18.

One of the outgroups, *Paracroton*, could not be placed parsimoniously at the base of the cladogram, because it shares various apomorphies with subtribe Aleuritinae. This suggests that tribe Aleuritideae is not monophyletic and that *Paracroton* is part of the ingroup. The major synapomorphy for tribe Aleuritideae (character 12, rupturing, connate

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Figure 1. Strict consensus cladogram for Euphorbiaceae tribe Aleuritideae (length 66 steps, including 8 steps for polymorphic taxa, CI = 0.667, RI = 0.676). Outgroups used were *Borneodendron* (tribe Ricinocarpeae subtribe Bertyinae) and *Paracroton* (tribe Crotonae). ● = apomorphies, ○ = parallel developments, × = reversals, and ⊗ = parallel reversals. The character state change is indicated for every character. Decay Indices higher than 1 and bootstraps of 50% and higher are shown.

sepals) is perhaps overvalued (sepals are free in *Paracroton*).

Another synapomorphy for tribe Aleuritideae (including *Paracroton*) is character 3 (stellate indumentum), but this character reverses several times in the cladogram and does not provide strong support. Character states 2 (red exudate), 13 (staminate sepals absent), 17 (stamens all connate), and 23 (pistillate disc absent) are considered apomorphies for the outgroup, *Borneodendron*, because these states are exceptional and their opposites, present in subtribe Aleuritideae, are common. However, more taxa have to be added to the analysis for a better evaluation of these optimizations, and that is beyond the scope of this study.

This cladistic analysis, based on morphological characters, does not reveal whether or not tribe Aleuritideae is monophyletic. The addition of more taxa is warranted for that goal.

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APPENDIX 1.

The following characters and their states (state numbers in parentheses) are included in the analysis:

1. Sexuality: dioecious (1) vs. monoecious (2).
Monoecy is often difficult to diagnose because the flowers of different sexes may open at different times, yielding functionally unisexual inflorescences. For this reason, Stuppy et al. (in press) recorded all three species in *Vernicia* to be occasionally dioecious. However, in this analysis monoecy was regarded as being typical for these species, and the occasional unisexual specimen was ignored.
2. Red exudate: absent (1) or present (2).
3. Hair type: simple only (1), simple and stellate (2), or simple and lepidote (3).

All taxa have simple hairs, though sometimes only on the very young parts. Several taxa also have stellate hairs or lepidote hairs. Subtribe Crotonogyninae all have lepidote hairs, though those of the only liana in tribe Aleuritideae, *Manniophyton*, are somewhat different: lepidote with an added upright stinging filament (inflated trichome of Webster, 1994b), giving a stellate appearance. However, the presence of stinging filaments, in this study an autapomorphy for *Manniophyton*, is perhaps typical for lianas, because they are present in all other, unrelated, Malesian lianas. Once the stinging filaments have broken off, the remaining part is perfectly scale-like and, therefore, the hairs have been coded as lepidote. Radcliffe-Smith (1988) recorded lepidote hairs for *Benoistia*; however, we have seen only simple hairs.

4. Pubescence of abaxial leaf surface: (sub)glabrous (1) or densely hairy (2).

This character was added because it may provide a syn-

apomorphy for *Aleurites* and *Reutealis*. The character states can usually be established quite easily, especially in the young parts. Only a few genera, *Crotonogyne* (subtribe Crotonogyninae), *Garcia* (subtribe Garcinae), and *Neoboutonia* (subtribe Neoboutoninae), have some species with glabrous leaves and others with densely hairy leaves; these genera are coded as polymorphic in the analysis.

5. Glands on the petiole-leaf blade transition: absent (1) or present (2).

Quite a few genera, the outgroup *Paracroton*, subtribe Aleuritinae, *Grossera* (subtribe Grosserinae), subtribe Crotonogyninae, and *Neoboutonia* (subtribe Neoboutoninae), show big glands on top of the petiole. Most taxa possess sessile glands, but a few species have stalked ones. The shape of the latter ones may vary, but this information could not be used in the analysis because the different shapes are typical for single species and, therefore, only provide autapomorphies.

6. Leaf margin: unlobed (1) or often/always lobed (2).

Lobed leaves may present a synapomorphy for *Aleurites* and *Vernicia* in subtribe Aleuritinae. Of all the other genera, only *Manniophyton* (subtribe Crotonogyninae) and *Neoboutonia* (subtribe Neoboutoninae) have lobed leaves.

7. Leaf base: cordate (1) or rounded to cuneate, attenuate, or acute (2).

Leaf bases are always cordate or cuneate within subtribe Aleuritinae. State 1 is also unambiguous within the other genera of tribe Aleuritideae, but state 2 is variable and shows overlap among the species.

8. Marginal leaf glands: absent (1), or abaxially on the teeth (2), at teeth apices (3), or in teeth sinuses or crenations.

Most taxa of tribe Aleuritideae have no glands along the leaf margins. *Paracroton* (outgroup) and *Grossera* (subtribe Grosserinae) have glands on the abaxial side of the teeth, but it is not clear if these are homologous. *Vernicia* (subtribe Aleuritinae) is the only genus of tribe Aleuritideae with glands in the sinuses of the leaf margin.

9. Pellucid dots in leaves: absent (1) or present (2).

Punctuation is only found in *Cavacoa* and *Grossera* of subtribe Grosserinae.

10. Abaxial sessile glandular hairs: absent (1) or present (2).

Small, one-celled sessile glandular hairs are found only in subtribe Neoboutoninae.

11. Venation: pinnate (1), triplinerved (2), or palmate (3).

All members of subtribe Aleuritinae have palmate venation, as do *Manniophyton* (subtribe Crotonogyninae) and *Neoboutonia* (subtribe Neoboutoninae). Palmate venation is associated with but not completely dependent on the presence of leaf lobes (character 6); leaves of *Reutealis* are never lobed, but have palmate venation. Triplinerved leaves, a special case of pinnate venation, are found only in *Domohinea* (now *Tannodia*) and *Grossera* of subtribe Grosserinae.

12. Fusion of staminate sepals: free or absent (1) or fused, rupturing spathaceously (2).

Staminate sepals connate in bud and rupturing during anthesis are typical of all members of tribe Aleuritideae. The staminate sepals are free in *Paracroton* and absent in *Blumeodendron*.

13. Number of staminate sepals: absent (1), 2–4 (2), or 5 or 6 (3).

Sepals are absent in one of the outgroups, i.e., *Borneodendron*. All other genera of tribe Aleuritideae show 2 to 4 sepals except *Tannodia* (subtribe Grosserinae) with up

to 6 sepals; the other outgroup, *Paracroton*, has 5 or 6 sepals. *Tannodia* has been coded as polymorphic.

14. Number of staminate petals: absent (1), 3–5 (or 6) (2), or 6–13 (3).

Petals are absent in the staminate flowers of *Borneodendron* and subtribe Neoboutoninae. *Garcia* (subtribe Garcinae) is the only genus with many (6–13) petals. There is a slight overlap in character states, because some genera that usually have 5 petals can sometimes exhibit variation from 5 to 6 petals within a particular inflorescence, specimen, or species.

15. Fusion of staminate petals: free (1) or connate (2).

Fusion of the staminate petals is considered typical for subtribe Crotonogyninae. However, of this group only *Manniophyton* consistently has connate petals, while *Crotonogyne* is dimorphic for this character (though coded as always present, see discussion), and *Cyrtogonone* has free petals. This character is dependent on the former one; therefore, the outgroup *Borneodendron* is coded with a question mark because the petals are lacking.

16. Number of stamens: 6–12(–14) (1), 12–40 (2), or 63–160 (3).

The coding of the states is difficult due to some overlap in states 1 and 2 and the fact that *Crotonogyne* and *Manniophyton* (subtribe Crotonogyninae) are dimorphic for states 1 and 2 and *Garcia* (subtribe Garcinae) for states 2 and 3 (though coded as possessing state 3 only to prevent too much polymorphism in the matrix): *G. nutans* Vahl has 63–160 stamens, *G. parviflora* Lundell ca. 29 stamens. This character is probably not of great importance, but it was added because it often provides an important key character in Webster's (1994b) classification.

17. Fusion of stamens: all free (1), only the inner whorl connate (2), all connate (3).

Reutealis (subtribe Aleuritinae) is the only taxon that was difficult to code: its inner stamens are connate, and the outer stamens possibly also, but this may only appear to be the case, because the outer stamens also adhere to the petals as in the other two genera of subtribe Aleuritinae. However, the other two genera, *Aleurites* and *Vernicia*, have only the inner stamens distinctly connate. Therefore, *Reutealis* has been coded also as possessing state 2.

18. Arrangement of stamens: unordered (1), ordered in 2 series (2), or ordered in (3 or) 4 series (3).

This character is dependent on the foregoing one. Taxa with free filaments always have unordered stamens. Those with (partly) connate filaments may have the stamens unordered, or ordered in 2 or 4 series. *Paracroton* is the only genus that is polymorphic for states 2 and 3.

19. Apex of connective: unmodified (1), with a gland (2), or prolonged and apiculate (3).

These three states may not be homologous. Prolongation of the connective (apiculate; present in subtribe Crotonogyninae) may be different from the presence of a gland (subtribe Neoboutoninae). However, dividing these states over one or two characters does not influence the results of the analysis.

20. Shape of anthers: short, relatively thick (1) or elongate, vermiform (2).

Anthers with a short shape (1.5–2 times as long as wide) are the more common state. The very long and thin, vermiform anthers are found only in subtribe Neoboutoninae.

21. Tubercles of pollen exine: blunt (1) or sharp (2).

Sharp exine tubercles are found only in *Tannodia* (including *Domohinea*; subtribe Grosserinae). The tubercles

of all other taxa are blunt (Punt, 1962), or the state is unknown.

22. Number of pistillate sepals: 2–4 (1), 5 (or 6) (2), or 6 (3).

There is a slight overlap in states; some taxa with 5 pistillate sepals occasionally have flowers with 6 sepals.

23. Pistillate disc: absent (1), annular (2), or divided into free lobes (3).

The staminate disc, when present, is always divided into free lobes. The pistillate disc shows more variation: it is absent in *Borneodendron*, divided into lobes in subtribe Aleuritinae, and annular in all other taxa.

24. Fruit type: capsular (1) or drupaceous (2).

Only the genus *Aleurites* (subtribe Aleuritinae) shows drupaceous fruits; all other genera are capsular.

25. Seeds: smooth (1) or dorsally warty (2).

All genera have smooth seeds except *Vernicia* (subtribe Aleuritinae; however, the seeds of *V. cordata* are still unknown).

APPENDIX 2.

Specimens examined. For some genera, of which hundreds of sheets were studied, only representative specimens covering the distribution are mentioned.

Aleurites moluccana (L.) Willd. (representative specimens): AUSTRAL ISLANDS. **Raivavae:** Raiurua, *H. St. John & F. R. Fosberg 15683* (BISH, L). AUSTRALIA. **Queensland:** Lankelly, *B. Hyland 5406* (L). BRUNEI. Berakas, *BRUN (H. Pukol) 5419* (L). CAROLINE ISLANDS. **Ponape:** Tolomail, *M. Takamatsu 984* (BISH). CHINA. **Guangdong:** Guangzhou, *H. G. Yip 279* (L). **Guangxi:** Lungchow, *H. B. Morse 646* (US). **Hainan:** Yeichow, *F. C. How 70593* (L, NY). **Yunnan:** Xishuangbanna, *K. S. Chow & P. P. Wan 80111* (BISH, NY). COOK ISLANDS. **Rarotonga:** Muriavai Valley, *W. R. Philipson 10136* (L). FIJI. **Vanua Levu:** Thakaundrove, Mbalanga, *O. Degener & E. Ordonez 14502* (NY). **Viti Levu:** Rewa, Nasinu, *J. W. Gillespie 3609* (BISH). FRENCH POLYNESIA. **Moorea:** Morioahu, Opuhohu, *H. M. Smith 98* (BISH). HAITI. Petionville, *E. C. Leonard 4831* (NY). HORNE ISLANDS. **Futuna:** Vaisei, *M. MacKee 19772* (BISH). INDONESIA. **Kalimantan Timur:** Wanariset, *Ramlanto 62* (L). **Jawa Barat:** Banjumas, *S. H. Koorders 26890* (L). **Nusa Tenggara Timur:** Ndeki, *A. Kostermans & N. Wirawan 132* (L). **Maluku:** Otimmer, *P. Buwalda 4377* (L, NY). **Irian Jaya:** Warsamson, *BW (F. A. W. Schram) 12493* (L). **Sulawesi Tenggara:** Opa Swamp, *S. Prawiroatmodjo & S. Soewoko 1823* (L). **Sumatera Utara:** Tuktuk, *J. F. Veldkamp 7185* (L). JAPAN. **Ryukyu:** Okinawa, Shimajiri, *E. H. Walker 7750* (US). LAOS. Dok Nanh, *Spire 1190* (BM). MALAYSIA. **Selangor:** Batu Caves, *K. Ogata 10241a* (L). **Sabah:** Tenom, Kulam Ayer, *SAN (Arumpad) 15316* (L). **Sarawak:** 1st Division, Telok Pinang, *S (B. Lee) 41942* (L). MANGAREVA. Duff, *F. R. Fosberg 11360* (BISH). MARIANA ISLANDS. **Guam:** Yigo, *F. R. Fosberg 35533* (BISH). MARIQUESAS. Uahuka, *E. H. Quayle 1816* (BISH). MYANMAR (BURMA). Hoho, *F. G. Dickason 9394* (L). PAPUA NEW GUINEA. **Central:** Laloki, *L. J. Brass 3644* (NY). PHILIPPINES. **Luzon:** Laguna, Los Baños, *A. D. E. Elmer 17679* (L, MO, NY). PHOENIX ISLANDS. Canton, *O. Degener 24627* (L). PITCAIRN. Parlver Valley, *H. St. John 14980*

(BISH). SAMOA. **Ofu:** *T. G. Yuncker 9540* (BISH, NY). SINGAPORE. Pulau Dumat Laut, *J. Sinclair 5291* (US). SOCIETY ISLANDS. **Huahine:** Tevairahi, *F. R. Fosberg 61154* (BISH). SOLOMON ISLANDS. **New Georgia:** Tetemara, *BSIP (Maenu'u) 6099* (L). TAIWAN. **Taitung:** Tamali-hsiang, Tamali, *Y. Endo 2181* (MO). THAILAND. **Central:** Bangkok, *A. F. G. Kerr 19563* (BM). TONGA. **Eua:** Pangai, *H. E. Parks 16077* (BISH). U.S.A. **Hawaii:** Kauai, Hanapepe River, *A. A. Heller 2431* (L, MEL, NY). VANUATU. **Malekula:** Tisbel, *W. L. Chew 307* (L). VIETNAM. Cochinchine, Bien Hoa, *C. Thorel 671* (NY, W).

Aleurites rockinghamensis (Baill.) P. I. Forst. (representative specimens): AUSTRALIA. **Queensland:** Alexandra, *B. Hyland 6726* (L). PAPUA NEW GUINEA. **Morobe:** Boana, *M. S. Clemens 8119* (L). **Northern:** Isurava, *C. E. Carr 15757* (L).

Benoistia perrieri Leandri: MADAGASCAR. Moramanga, Dec. 1908, *C. d'Alleizette s.n.* (L).

Borneodendron aenigmaticum Airy Shaw (representative specimens): MALAYSIA/SABAH. **Lahad Datu:** Pulau Sakar, *SAN (H. S. Martyn) 21605* (L); Mt. Silam, *SAN (W. Meijer) 37836* (L), *SAN (Tarmiji) 72898* (L); Tembawan Island, *KEP (J. Wyatt-Smith) 80510* (L), *SAN (P. F. Burgess) 27558* (L). **Ranau:** Bukit Hampuan, Kinabalu, *SAN (A. Gibot) 61836* (L).

Cavacoa quintasii (Pax & K. Hoffm.) J. Léonard: CONGO (ZAIRE). **Kasai:** Mweka Territ., Kahenga, *R. Dechamps 208* (L). **Orientale:** Isangi Territ., Yangambi, *J. Louis 2559* (L), *4177* (L), *9676* (L).

Crotonogyne argentea Pax: CAMEROON. Bipinde: *G. Zenker 2029* (L), *2359* (L), *3078* (L), *3668* (L), *3893* (L).

Crotonogyne gabunense Pax: GABON. Libreville, *Courtet 6485* (L).

Crotonogyne giorgii De Wild.: CONGO (ZAIRE). **Equateur:** Ingende Territ., Bolima, Luwa, *Hulstaert 1091* (L). **Léopoldville:** Inongo Territ., Lac Léopold II, *G. Gilbert 14063* (L).

Crotonogyne parviflora Prain: CONGO (ZAIRE). Ogoané, *Karmann 6485* (L).

Crotonogyne poggei Pax: CONGO (ZAIRE). **Orientale:** Isangi Terr., Yangambi, *J. Louis 6815* (L).

Crotonogyne preussii Pax: CAMEROON. Bipinde, *G. Zenker 4666* (L).

Crotonogyne zenkeri Pax: CAMEROON. Lolodorf, June 1913, *Rouyer s.n.* (L); Bipinde, *G. Zenker 822* (L). GABON. Libreville, 18 Dec. 1900, *R. P. Klaine s.n.* (L).

Domohinea perrieri Leandri: MADAGASCAR. Analamazaoho, *C. d'Alleizette 6479* (L).

Garcia nutans Rohr: FRENCH GUYANA. Cayenne, *C. d'Alleizette 6459* (L). MARTINIQUE. St. Pierre, Feb. 1868, *L. Hahn s.n.* (L).

Grossera macrantha Pax: CONGO (ZAIRE). **Léopoldville:** Moyen-Kwilu Terr., Koiyaka, Kewango, *R. Devred 2769* (L).

Grossera major Pax: CAMEROON. Lolodorf, June 1919, *C. d'Alleizette s.n.* (L); Bipinde, *G. Zenker 1805* (L), *4227* (L).

Grossera multinervis J. Léonard: CONGO (ZAIRE). **Kivu:** Kalehe Terr., vers km 110 route Kavumu-Walikale, Irangi, reserve IRSAC, *G. Troupin 4529* (L), *4700* (L).

Grossera paniculata Pax: CAMEROON. Bipinde, *G.*

Zenker 1741 (L), *1760* (L), *2070* (L), *3050* (L), *3088* (L), *3125* (L), *3231* (L), *3372* (L), *3377* (L), *3460* (L), *3532* (L), *4920* (L).

Manniophyton africanum Müll. Arg.: CAMEROON. 10 km N of Ndemba II, 30 km N of km 29 of road Bertona–Nanga Eboke, *A. J. M. Leeuwenberg 5846* (L); Yaunde, *G. Zenker 1404* (L); Bipinde, *G. Zenker 4690* (L). CONGO (ZAIRE). **Orientale:** Isangi Territ., Yangambi, Plateau Isalewi, *J. Louis 14553* (L). GABON. Nyanga, *C. d'Alleizette 6460* (L).

Neoboutonia africana Müll. Arg.: CAMEROON. Bipinde, *G. Zenker 1527* (L), *3202a* (L), *4246* (L); Yaunde, *G. Zenker 1430* (L). GABON. Libreville, *C. d'Alleizette 6517* (L).

Neoboutonia macrocalyx Pax: MALAWI. Nyassa Hochland, Station Kyimbila, *A. Stolz 2043* (L). TANZANIA. Uhehe, *W. Goetze 758* (L).

Neoboutonia melleri Prain: MALAWI. Nyassa Hochland, Station Kyimbila, *A. Stolz 444* (L), *590* (L).

Paracroton pendula (Hassk.) Miq. (representative specimens): BRUNEI. Andulau Forest Reserve, *BRUN (P. S. Ashton) 3255* (L). INDONESIA. **Jawa Barat:** Bantam, *S. H. Koorders 2604* (L). **Kalimantan Barat:** Gunung Palung Nature Reserve, on Air Putih River, 20 km SE of Talukmelano, *S. A. Mori & J. D. Mitchell 17848* (L). **Kalimantan Selatan:** Pleihari, Asam-Asam, *bb 9494* (L). **Kalimantan Tengah:** headwaters of Sungai Kehayan, 5 km NW of Tumbang Sian Logging Camp, *J. S. Burley, Tukirin et al. 820* (L). **Kalimantan Timur:** E. Kutei, Sungai Kerajaan, N of Sangkulirang, *A. Kostermans 5782* (L). **Sumatera Selatan:** Bangka, Lobok-besar, Gunung Pading, *A. Kostermans & Anta 927* (L). MALAYSIA. **Pahang:** S of Kuala Lompat, Krau Game Reserve, *KEP FRI (T. C. Whitmore) 3580* (L). **Sabah:** Labag Dist., Lokan Forest Reserve, Kinabatangan, *SAN (J. Ampuria) 36385* (L). **Sarawak:** Miri, Ulu Luak, Sungai Setap, *S (O. Haron) 21312* (L). PHILIPPINES. **Luzon:** Laguna Prov., San Antonio, *BS (A. Ramos) 23828* (L). **Mindanao:** Agusan Prov., Tungao, *PNH (D. R. Mendoza) 41965* (L). **Palawan:** Pagdanan Range, road E from San Vicente, *SHI (C. E. Ridsdale) 1511* (L). THAILAND. Peninsular, Phatthalung Prov., Tamote Falls Nature Park, *J. F. Maxwell 86–547* (L).

Paracroton zeylanicus (Müll. Arg.) Balakr. & T. Chakrab. (representative specimens): INDIA. **Kerala:** Cardamon Hills, Puliya, Munnar–Alwaye Road, ca. 15 km from Munnar, *C. E. Ridsdale 767* (L). SRI LANKA. Galle Distr., Hinidunma, *A. Kostermans 26608* (L).

Reutealis trisperma (Blanco) Airy Shaw (representative specimens): INDONESIA. **Jawa Barat:** Tjiomas, *C. A. Backer 36081* (L). PHILIPPINES. **Guimaras:** Iloilo, Miagao. **Luzon:** Batangas, *M. Ramos 1923* (L, MO); Cavite, Maragondong, *BS (E. Fénix) 5160*

(NY); Laguna, *BS (R. C. McGregor) 22912* (BM, K); Rizal, *FB (Ahern's collector) 2440* (K, L). **Mindanao:** Agusan, Butaan, *PNH (D. R. Mendoza) 42223* (L); Davao, Santa Cruz, *R. S. Williams 2852* (NY).

Tannodia cordifolia Baill.: COMORES. Mutsamdra?, *C. d'Alleizette 6484* (L).

Tapoides villamilii (Merr.) Airy Shaw: MALAYSIA. **Johore:** Mersing, Tenggaroh Forest Reserve, Compt. 101, *KEP (K. Ogata) 105167* (L). **Sabah:** Sepilok Forest Reserve, *SAN (G. H. S. Wood) 16532* (L), (*W. Meijer & Aban) 128772* (L), (*W. Meijer) 27676* (L); Jalan Trig, Leila Forest Reserve, *SAN (P. Lasan) 62527* (L).

Vernicia cordata (Hemsl.) Airy Shaw (representative specimens): INDONESIA. **Java:** *H. Zollinger 3576* (MEL). JAPAN. Hondo, *E. H. Wilson 7138* (US); Kyoto, *Tagawa-Motozi 2091* (C); Kyushu, Isso-Rindo, *K. Deguchi 5014* (NY); Nomo Saki, *Pierot 925* (L). VIETNAM. **Tonkin:** Hanoi, *C. d'Alleizette 6458a* (L).

Vernicia fordii (Hemsl.) Airy Shaw (representative specimens): CHINA. **Fujian:** Yenping, Buongkang, *H. H. Chung 3344* (BO). **Geizhou:** Tsunyi Hsien, Liang Feng Yah, *A. N. Steward et al. 256* (NY). **Guangdong:** Lung Tou Shan, *S. P. Ko 50228* (K, NY). **Guangxi:** Yung Hsien, Ta Te Tauen, *A. N. Steward & K. C. Cheo 1059* (NY). **Hubei:** Patung Hsien, *H. C. Chow 147* (NY). **Hunan:** P'ing Tou Shan, *W. T. Tsang 23509* (US). **Jiangsu:** Nanking, Drum Tower, *Y. C. Chiao 11993* (BO). **Jiangxi:** Lingchuan, *Y. Tsiang 9822* (NY). **Sichuan:** Yulei, *D. E. Boufford et al. 24035* (NY). **Yunnan:** Likiang, *J. F. Rock 5066* (NY, US). **Zhejiang:** Hangchow, *C. Y. Chiao 7969* (NY). INDIA. **Assam:** Burnihat, *W. N. Koelz 22834* (K). **Utah Pradesh:** Dehra Dun, *U. Singh 131* (NY). INDONESIA. **Jawa Barat:** Bangkelan, *J. G. B. Beumée A 913* (BO). JAPAN. **Ryukyu:** Okinawa, Yabu, *E. H. Walker et al. 6356* (L, US). SOUTH KOREA. Yongtung, *B. R. Yinger et al. 3791* (K). TAIWAN. **Chiayi Hsien:** Fanlu Hsiang, Pantienyen, *Y. R. Lin 515* (MO).

Vernicia montana Lour. (representative specimens): CHINA. **Guangdong:** Shiu Hing, *H. O. Chan 13904* (L). **Guangxi:** Won Bin, *R. C. Chin 6354* (NY). **Hainan:** Chiang Mai, Ku Tung, *C. I. Lei 495* (BO, L, NY, US). **Hong Kong:** Taipo, *S. Y. Hu 10435* (K). **Jiangxi:** Wu Yuan, *R. C. Ching 3275* (K). INDIA. **Assam:** Hmuntha, *T. R. Chand 4329* (L). INDONESIA. **Jawa Tengah:** Pengalengan, *S. M. Popta 1295* (L). **Jawa Timur:** Djembu, *B. Krayne 1* (L). MYANMAR (BURMA). **Wa States:** Pansan, *Maung Po Khant 15329* (K). PHILIPPINES. **Luzon:** Laguna, Los Baños, *FB (N. Catalan) 26923* (BO). THAILAND. **Northern:** Chiang Mai, Doi Sutep, *J. F. Maxwell 88–350* (AAU, L). VIETNAM. **Tonkin:** Taai Wong Mo Shan, *W. T. Tsang 28987* (B, C, K).