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A revision of the tribal classification of *Rhamnaceae*

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Summary. A new tribal classification of *Rhamnaceae* based on a phylogenetic analysis of *rbcL* and *trnL-F* sequences of the plastid genome is outlined here. The last classification of the family by Suessenguth recognised five tribes. Eleven tribes are now recognised, three of which are new (*Ampeloziziphеae*, *Doerpfeldieae* and *Bathiorhamneae*). The constitution of *Rhamneae* Hook. f. has been emended, and the name of one tribe has been corrected (*Zizipheae* Brongn. to *Paliureae* Reissek ex Endl.; as suggested by Schirarend & Olabi 1994) and emended. *Ventilagineae* Hook. f., *Colletieae* Reissek ex Endl. and *Gouanieae* Reissek ex Endl. are retained. *Pomaderreae* Reissek ex Endl. and *Maesopsideae* Weberb. have been resurrected, as has *Phyliceae* Reissek ex Endl., which has also been emended. Three larger groups within *Rhamnaceae* are also described on the basis of the molecular data. However, there are no morphological characters marking these groups, and they are therefore given informal names in this treatment. A morphological cladistic analysis also included here demonstrates the problems of attempting phylogenetic reconstruction if only a few morphological characters are available.

INTRODUCTION

The 50 genera and 900 species of *Rhamnaceae* are collectively cosmopolitan. They are characterised by their simple leaves, small flowers with four or five sepals that are valvate in bud, four or five stamens alternating with the sepals (obhaplostemony), anthers that are frequently enfolded by the hooded petal apices, ovaries that are usually 2 – 3(– 4 – 5)-locular, an intrastaminal, nectariferous disc and a tendency towards xeromorphism. The sepals often have a fleshy layer on the inner side that usually forms a keel and ends as a tubercle. This layer is histologically similar to the intrastaminal, nectariferous disc (Cronquist 1981). Obhaplostemony is a relatively rare feature in angiosperms, and has often resulted in *Rhamnaceae* being associated with other families such as *Vitaceae* and *Cornaceae* that also exhibit this arrangement. The xeromorphic features exhibited by some members of the family include reduced or absent leaves, crowding of leaves, shortening of branch axes, presence of thorns or spines and a low, shrubby habit. There are few plants of economic value in *Rhamnaceae*, the most notable being the fruit tree jujube (*Ziziphus jujuba*), and the ornamental shrubs *Ceanothus* and *Colletia*.

The taxonomic history of suprageneric relationships of genera now placed within *Rhamnaceae* is presented in Table 1. Adanson (1763) was the first to delimit what was to become part of *Rhamnaceae* under the name *Jujubiers*. Many of the genera he included in this group, however, have since been placed in other families such as

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TABLE 1. Taxonomic history of suprageneric classifications in *Rhamnaceae* (names in bold are those currently recognised as members of *Rhamnaceae*, those not in bold are now included in other families). Taxa sampled in the molecular analysis are indicated with an * in the Suessenguth system of this table.

AUTHOR	TRIBE/GROUP	GENERA
Jussieu (1789)	1	*Celastrus, Euonymous, Polycardia, Staphylea*
	2	*Cassine, Goupia, Ilex, Myginda, Prinos, Rubentia, Schrebera*
	3	*Mayepea,* **Rhamnus**, **Paliurus**, *Samara,* **Ziziphus**
	4	**Ceanothus**, **Colletia**, **Hovenia**, **Phylica**
	5	*Brunia, Bumalda*
	6	*Aucuba, Carpodetus,* **Gouania**, *Plectronia, Votomita*
Brongniart (1827)	n/a	**Berchemia**, **Ceanothus**, **Colletia**, **Colubrina**, **Condalia**, **Crumenaria**, **Cryptandra**, **Gouania**, **Hovenia**, **Paliurus**, **Phylica**, **Pomaderris**, **Retanilla**, **Rhamnus**, **Sageretia**, **Scutia**, **Ventilago**, **Ziziphus**
Endlicher (1840)	*Colletieae*	**Adolphia**, **Colletia**, **Discaria**, **Retanilla**
	Franguleae	**Alphitonia**, **Berchemia**, **Ceanothus**, **Colubrina**, **Condalia**, **Hovenia**, **Karwinskia**, **Noltea**, **Rhamnus**, **Sageretia**, **Scutia**, **Ziziphus**
	Gouanieae	**Crumenaria**, **Gouania**, **Helinus**, **Reissekia**
	Paliureae	**Paliurus**, **Ventilago**
	Phyliceae	**Cryptandra**, **Phylica**, **Spyridium**
	Pomaderreae	**Pomaderris**, **Trymalium**
Hooker (1862)	*Colletieae*	**Adolphia**, **Colletia**, **Discaria**, **Retanilla**, **Trevoa**
	Gouanieae	**Crumenaria**, **Gouania**, **Helinus**, **Reissekia**
	Rhamneae	**Alphitonia**, **Ceanothus**, **Colubrina**, **Cryptandra**, **Hovenia**, **Lasiodiscus**, **Nesiota**, **Noltea**, **Phylica**, **Pomaderris**, **Rhamnidium**, **Rhamnus**, **Sageretia**, **Scutia**, **Spyridium**, **Trymalium**
	Ventilagineae	**Smythea**, **Ventilago**
	Zizipheae	**Berchemia**, **Condalia**, **Microrhamnus**, **Karwinskia**, **Paliurus**, **Ziziphus**

Baillon (1877)	*Colletieae*	**Adolphia, Colletia, Discaria, Retanilla, Trevoa**
	Gouanieae	**Crumenaria, Cryptandra, Gouania, Helinus, Lasiodiscus, Nesiota, Phylica, Pomaderris, Reissekia, Spyridium, Trymalium**
	Rhamneae	**Alphitonia, Berchemia, Ceanothus, Colubrina, Condalia, Emmenosperma, Hovenia, Karwinskia, Noltea, Paliurus, Rhamnidium, Rhamnus, Sageretia, Scutia, Smythea, Ventilago, Ziziphus**
Weberbauer (1895)	*Colletieae*	**Adolphia, Colletia, Discaria, Retanilla, Trevoa**
	Gouanieae	**Crumenaria, Gouania, Helinus, Pleuranthodes, Reissekia**
	Maesopsideae	**Maesopsis**
	Rhamneae	**Alphitonia, Ceanothus, Colubrina, Cryptandra, Emmenosperma, Hovenia, Lasiodiscus, Nesiota, Noltea, Phylica, Pomaderris, Rhamnus, Sageretia, Schistocarpaea, Spyridium, Trymalium**
	Ventilagineae	**Smythea, Ventilago**
	Zizipheae	**Berchemia, Condalia, Microrhamnus, Karwinskia, Paliurus, Reynosia, Rhamnella, Rhamnidium, Ziziphus**
Suessenguth (1953)	*Colletieae*	**Adolphia*, Colletia*, Discaria*, Kentrothamnus, Retanilla, Talguenea, Trevoa***
	Gouanieae	**Crumenaria*, Gouania*, Helinus*, Pleuranthodes*, Reissekia***
	Rhamneae	**Ampelozizphus*, Alphitonia*, Ceanothus*, Colubrina*, Cormonema, Cryptandra*, Emmenosperma*, Hovenia*, Hybosperma, Lasiodiscus*, Macrorhamnus, Nesiota*, Noltea*, Oreorhamnus, Phylica*, Pomaderris*, Rhamnus*, Sageretia*, Schistocarpaea*, Scutia*, Siegfriedia*, Spyridium*, Trymalium*, *Tzellemtinia***
	Ventilagineae	**Smythea, Ventilago***
	Zizipheae	**Auerodendron, Berchemia*, Berchemiella, Chaydaia, Condalia*, Condaliopsis, Dallachya, Doerpfeldia*, Lamellisepalum, Microrhamnus, Karwinskia*, Krugiodendron*, Maesopsis*, Paliurus*, Phyllogeiton, Reynosia*, Rhamnella*, Rhamnidium*, Sarcomphalus, Ziziphus***

Rosaceae, *Aquifoliaceae* or *Celastraceae*. Jussieu (1789) divided Adanson's *Jujubiers* into six groups, two of which were merged by Brown (1814) to form *Celastraceae*. Two others were merged to form *Rhamnaceae*, which were characterized by features still used to circumscribe the family at the present time. Members of Jussieu's other two groups were placed in a number of other families. The *Jujubiers* were also split by Brongniart (1827) into the families *Celastraceae*, *Ilicineae* (including *Aquifoliaceae*) and *Rhamnaceae*, which at this stage included 18 genera. Subsequent treatments included those by Endlicher (1840), Hooker (1862), Baillon (1875), Weberbauer (1895) and Suessenguth (1953).

The most recent suprageneric or tribal classification of *Rhamnaceae* was based largely on fruit characters. Suessenguth's system (1953), which generally followed Hooker (1862), circumscribed five tribes, two of which (*Rhamneae* Hook. f. and *Zizipheae* Brongn.) were large and morphologically heterogeneous. For example *Ziziphus* and *Berchemia* were placed in *Zizipheae* because they both have fleshy fruits. However, there are a number of other characters that these two genera do not share, such as ovary position and leaf venation, indicating relationships to genera in other tribes. The other three tribes *Colletieae* Reissek ex Endl., *Ventilagineae* Hook. f. and *Gouanieae* Reissek ex Endl. appear to be more natural.

Suessenguth listed 58 genera in five tribes, but four more genera have been described since then. *Oreoherzogia* (Vent 1962) was split from *Rhamnus* but has since been sunk back into it. *Bathiorhamnus* Capuron from Madagascar does not appear to be close to any other group in the family (Capuron 1966; Richardson *et al.* in press). *Alvimiantha* Grey-Wilson from Brazil has been tentatively ascribed to *Gouanieae* (Grey-Wilson 1978). *Disaster* Gilli (1980) was ascribed to *Rhamnaceae* but subsequently transferred to *Sterculiaceae* (Van Steenis 1982). The genus *Tzellemtinia* Chiov. has been transferred to *Euphorbiaceae* and synonymized with *Bridelia* Willd. (Friis & Vollesen 1980).

Some of the genera recognized by Suessenguth are now regarded as congeneric with others in *Rhamnaceae*. These include *Cormonema* Reissek ex Endl. (=*Colubrina* Rich. ex Brongn., Standley 1925 & Cowan 1952), *Microrhamnus* A. Gray (=*Condalia*, Johnston 1962), *Hybosperma* Urb. (=*Colubrina*, Johnston 1963b), *Sarcomphalus* P. Browne (=*Ziziphus* Mill., Johnston 1964), *Phyllogeiton* (Weberb.) Herzog (=*Berchemia* Neck. ex DC., Johnston 1972), *Chaydaia* Pit. (=*Rhamnella* Miq., Yamazaki 1973), *Macrorhamnus* H. Perrier (=*Bathiorhamnus* Capuron 1966), *Talguenea* Miers (=*Trevoa* Miers ex Hook., Tortosa 1992), *Lamellisepalum* Engl. (=*Sageretia* Brongn.), and *Oreorhamnus* Ridl. (=*Rhamnus* L.). Prior to our molecular analysis (Richardson *et al.* in press) *Rhamnaceae* therefore comprised five tribes and 49 genera.

Suessenguth's classification (1953) was evaluated using DNA sequences from three regions of the plastid genome, *rbcL*, the *trnL* intron and the *trnL-F* intergene spacer (hereafter referred to as the *trnL-F* region), from 42 genera of *Rhamnaceae* and representatives of the related families *Elaeagnaceae*, *Barbeyaceae*, *Dirachmaceae*, *Urticaceae*, *Ulmaceae*, *Moraceae* and *Rosaceae* (Richardson *et al.* in press). Here we also present a morphological phylogenetic analysis of *Rhamnaceae*. Problems with the use of morphological characters include reliance on a small number of characters to delimit tribes, such as the use of fruit characters by Suessenguth (1953). Other characters used by Suessenguth (1953) are also potentially prone to developmental plasticity, e.g.

disc and ovary position. There is a lack of morphological characters that can be used for phylogenetic analyses at the suprageneric level. A combined morphological and molecular analysis is also undertaken in a total evidence approach.

METHODS

Sequence data were analyzed using the parsimony algorithm of the software package PAUP version 3.1.1 for Macintosh (Swofford 1993). Tree searches were conducted under the equal weights criterion (Fitch 1971) with 1000 random sequence additions and TBR (tree bisection-reconnection) swapping, but permitting only five trees to be held at each step. The limit on the number of trees held at each step was implemented to cut down the time spent searching on suboptimal trees. All shortest trees collected in the 1000 replicates were then used as starting trees for another round of heuristic search, and all these trees were swapped on to completion. Successive approximations weighting (SW; Farris 1969) was then carried out on these trees with a limit of ten trees per replicate and ten replicates per round, after which all trees collected were used as starting trees in a search without a tree limit so that all trees at this length were collected prior to the next round of re-weighting. Further such rounds continued until tree lengths were the same in two consecutive rounds. Characters were reweighted according to their rescaled consistency indices, with a base weight of 1000. This procedure was designed to downweight or eliminate characters that were highly homoplasious. One thousand replicates of the bootstrap (Felsenstein 1985) were then carried out with the successive weights applied. We applied the following scheme of support: bootstrap values of 50 – 74% represent weak support, 75 – 84% moderate support, and 85 – 100% strong support.

Morphological characters

In the morphological study 18 unordered characters were scored (Tables 2, 3), most of which Suessenguth (1953) had suggested to be diagnostic for genera or tribes. The operational taxonomic units for this study were the individual species included in the molecular analysis, plus *Barbeya* (*Barbeyaceae*) and *Dirachma* (*Dirachmaceae*), which were used as outgroups in these analyses because they are the sister group to *Rhamnaceae* in molecular analyses (Thulin *et al.* 1998; Richardson *et al.* in press). Information about character states was derived from studies of literature (e.g. Suessenguth 1953; Hoffmann 1991; and monographs of individual genera listed with taxonomic descriptions) and herbarium specimens.

1. In some genera the seed remains attached to the torus after dehiscence. This is coded as a two-state character.
2. Disc present/absent is a simple two-state character.
3. For cases in which a disc is present, there are three character states. The disc may be 1: adnate to the calyx tube and the ovary, i.e. filling the calyx tube, 2: adnate to the calyx tube only, i.e. the ovary is free, or 3: adnate to the ovary only.
4. Leaf margins can be revolute or more or less flat in *Rhamnaceae*, a two state character.

TABLE 2. Characters used in the morphological analysis of *Rhamnaceae*.

Character	Character state
1. seed attachment	1. attached to torus after dehiscence
	2. falling from torus after dehiscence
2. disc presence/absence	1. disc present
	2. disc absent
3. disc position	1. adnate to calyx tube and ovary
	2. adnate to calyx tube or free
	3. adnate to ovary only
4. leaf margin	1. revolute
	2. not revolute
5. nitrogen fixation	1. present
	2. absent
6. number of locules per ovary	1. usually 3
	2. 2 or 4
	3. 1
7. endosperm	1. present
	2. absent
8. fruit	1. capsule
	2. fleshy
	3. samara
9. leaf venation	1. palmate
	2. pinnate
10. stellate hairs	1. present
	2. absent
11. fruit with longitudinal wings	1. absent
	2. present
12. fruit with apical wing	1. absent
	2. present
13. ovary position	1. superior
	2. semi-inferior
	3. inferior
14. habit	1. trees or shrubs
	2. climbers or herbs
15. leaf position	1. alternate
	2. opposite
	3. whorled
16. tendrils	1. present
	2. absent
17. calyx keel	1. present
	2. absent
18. arrangement of floral parts	1. obhaplostemonous
	2. not obhaplostemonous

5. Some groups in *Rhamnaceae* form symbiotic associations with bacteria, a two-state character.
6. In most genera of *Rhamnaceae*, the number of locules per ovary is usually either two or three. *Maesopsis* is an exception with one locule per ovary. In certain instances individuals or species with two locules per ovary may also have four locules per ovary and individuals or species with three locules per ovary may have four locules per ovary. However, in the majority of cases taxa have either two or three locules per ovary, so this character is given three states: number of locules per ovary (1), (2 or 4), or usually (3).
7. Presence/absence of endosperm.
8. Fruits either fleshy, a capsule or a samara.
9. Leaf venation is either pinnate or palmate.
10. Hairs are either simple or stellate.
11. Longitudinal wings in the tribe *Gouanieae* are derived from the ovary wall. This character has two states: fruit longitudinal wings present/absent.
12. Apical wings in the tribe *Ventilagineae* are derived from the ovary wall and the style. This character has two states: fruit apical wings present/absent.
13. The scoring of the disc and ovary position characters is problematic because it is often not clear which state to assign for each taxonomic unit. Within some genera these characters are not discrete due to developmental plasticity. However, because of the limited number of characters available for this study we have decided to include these characters in the analysis. Ovary position is scored as superior, semi-inferior or inferior.
14. The habit character is coded as either trees/shrubs or climbers/herbs. In many genera different species can be either trees or shrubs (the distinction is arbitrary). The only herb in the family is *Crumenaria* in tribe *Gouanieae*. The herbaceous habit of this species appears to be a reduction from the climbing form present in all other genera in this tribe. We therefore coded habit as a two-state character i.e. trees/shrubs or climbers/herb.
15. Leaves may be arranged alternately, opposite or in whorls.
16. Tendril presence/absence is a simple two-state character.
17. Sepals may have a keel running along their midrib or not.
18. Flowers obhaplostemonous/flowers, not obhaplostemonous.

The morphological data set and the combined morphological/molecular data sets were analysed using the same strategy as for the molecular analysis except that SW was not applied. This was done because bootstrapping with SW applied is potentially unreliable if there is little variability in the data set (as is the case with the morphological data set; too few characters to get a clear picture of their performance).

Results

The molecular analysis (Richardson *et al.* in press) produced 324 Fitch trees with a length of 2559 steps, a CI = 0.59 (0.48 excluding autapomorphies) and RI = 0.70. With SW there was only one tree with two trichotomies. The SW tree length was 1 068 277 steps, CI = 0.85 (0.71 excluding autapomorphies), and RI = 0.88. Fig. 1

TABLE 3. Morphological matrix for *Rhamnaceae*. Numbers in parentheses after species names represent the number of the species indicated in Figures 1 – 3 (e.g. *Spyridium* 2 in these figs is *S. complicatum*).

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Sageretia thea (Osbeck) M. C. Johnst.	2	1	2	2	2	2	1	2	2	2	1	1	3	1	2	2	1	1
Rhamnus lycioides L. (1)	2	1	2	2	2	2	1	2	2	2	1	1	1	1	1	2	1	1
Rhamnus cathartica L. (2)	2	1	2	2	2	2	1	2	2	2	1	1	1	1	1	2	1	1
Rhamnus frangula L. (3)	2	1	2	2	2	2	1	2	2	2	1	1	1	1	1	2	1	1
Rhamnella franguloides (Maxim.) Weberb.	2	1	2	2	2	2	1	2	2	2	1	1	3	1	1	2	1	1
Krugiodendron ferreum (Vahl) Urb.	2	1	2	2	2	2	1	2	2	2	1	1	?	1	1	2	1	1
Rhamnidium elaeocarpum Reissek	2	1	2	2	2	2	2	2	2	2	1	1	1	1	2	2	1	1
Karwinskia humboldtiana (Roem. & Schult) Zucc.	2	1	2	2	2	2	1	2	2	2	1	1	1	1	2	2	1	1
Condalia microphylla Cav.	2	1	2	2	2	2	1	2	2	2	1	1	1	1	3	2	1	1
Scutia buxifolia Reissek	2	1	2	2	2	2	2	2	2	2	1	1	1	1	1	2	1	1
Berchemia discolor (Klotzsch) Hemsl.	2	1	2	2	2	2	1	2	2	2	1	1	1	1	1	2	1	1
Reynosia uncinata Urb.	2	1	2	2	2	3	1	2	2	2	1	1	1	1	2	2	1	1
Maesopsis eminii Engl.	2	1	2	2	2	3	1	2	2	2	1	1	1	1	2	2	1	1
Ventilago viminalis Hook. (1)	2	1	1	2	2	2	2	3	2	2	1	2	2	2	1	2	1	1
Ventilago leiocarpa Benth. (2)	2	1	1	2	2	2	2	3	2	2	1	2	2	2	1	2	1	1
Bathiorhamnus cryptophorus Capuron	2	1	1	2	2	1	1	2	1	2	1	1	1	1	1	2	1	1
Ampeloziziphus amazonicus Ducke	2	1	1	2	2	1	2	2	1	2	1	1	3	2	1	2	1	1
Doerpfeldia cubensis Urb.	2	1	3	2	2	2	1	2	1	2	1	1	1	1	1	2	1	1
Ceanothus coeruleus Lag. (1)	2	1	1	1	1	1	1	1	2	2	1	1	1	1	2	2	1	1
Ceanothus thyrsiflorus Eschw. (2)	2	1	1	1	1	1	1	1	2	2	1	1	1	1	2	2	1	1
Gouania mauritiana Lam.	2	1	1	2	2	1	1	1	1	2	2	1	3	2	1	1	1	1
Reissekia smilacina Endl.	2	1	1	2	2	1	1	1	2	2	2	1	3	2	1	1	1	1
Crumenaria erecta Reissek	2	1	1	2	2	1	1	1	?	2	2	1	3	2	1	2	1	1
Helinus integrifolius Kuntze	2	1	1	2	2	1	1	1	2	2	2	1	3	2	1	1	1	1
Pleuranthodes hillebrandii (Oliv.) Weberb.	2	1	1	2	2	2	1	1	?	2	2	1	3	2	1	1	1	1
Schistocarpaea johnsonii F. Muell.	2	1	?	?	2	1	1	1	2	2	1	1	1	1	1	2	1	1

Colubrina asiatica Brongn. (1)	2	1	1	2	2	1	1	1	2	2	1	1	3	1	1	2	1	1
Colubrina reclinata (L'Hér.) Brongn. (2)	2	1	1	2	2	1	1	1	2	2	1	1	3	1	1	2	1	1
Lasiodiscus mildbraedii Engl.	2	1	1	2	2	1	1	1	2	2	1	1	3	1	2	2	1	1
Emmenosperma alphitonioides F. Muell.	1	1	1	2	2	2	1	1	2	2	1	1	?	1	2	2	1	1
Alphitonia excelsa Reissek	1	1	1	2	2	1	1	1	2	2	1	1	3	1	1	2	1	1
Smythea lanceolata Summerh.	2	1	1	2	2	2	2	1	2	2	1	2	2	2	1	2	1	1
Paliurus spina-christi Mill.	2	1	1	2	2	2	2	2	1	2	1	1	2	1	1	2	1	1
Ziziphus glabrata Roxb. (1)	2	1	1	2	2	2	2	2	1	2	1	1	2	1	3	2	1	1
Ziziphus ornata Miq. (2)	2	1	1	2	2	2	2	2	1	2	1	1	2	1	3	2	1	1
Hovenia dulcis Thunb.	2	1	1	2	2	1	1	1	1	2	1	1	1	1	1	2	1	1
Phylica pubescens Aiton (3)	2	1	1	1	2	1	1	1	2	2	1	1	3	1	1	2	1	1
Phylica polifolia (Vahl) Pillans (2)	2	1	1	1	2	1	1	1	2	2	1	1	3	1	1	2	1	1
Phylica stipularis L. (4)	2	1	1	1	2	1	1	1	2	2	1	1	3	1	1	2	1	1
Phylica nitida Lam. (1)	2	1	1	1	2	1	1	1	2	2	1	1	3	1	1	2	1	1
Phylica tropica Baker (5)	2	1	1	1	2	1	1	1	2	2	1	1	3	1	1	2	1	1
Nesiota elliptica (Roxb.) Hook. f.	2	1	1	1	2	1	1	1	2	2	1	1	3	1	2	2	1	1
Noltea africana (L.) Rchb.	2	1	1	2	2	1	1	1	2	2	1	1	2	1	1	2	1	1
Discaria chacaye (G. Don) Tortosa	2	1	2	2	1	1	1	1	1	2	1	1	2	1	2	2	1	1
Colletia ulicina Gillies & Hook.	2	1	2	2	1	1	1	1	2	2	1	1	2	1	2	2	1	1
Adolphia infesta (Humbl., Bonpl. & Kunth) Meisn.	2	1	2	2	1	1	1	1	?	2	1	1	1	1	2	2	1	1
Trevoa trinervis Miers	2	2	?	2	1	1	1	2	1	2	1	1	2	1	2	2	1	1
Spyridium cf. *forrestianum* (1)	2	1	1	1	2	1	1	1	2	1	1	1	3	1	1	2	1	1
Spyridium globulosum (Labill.) Benth. (3)	2	1	1	1	2	1	1	1	2	1	1	1	3	1	1	2	1	1
Spyridium complicatum F. Muell. (2)	2	1	1	1	2	1	1	1	2	1	1	1	3	1	1	2	1	1
Cryptandra cf. *spyridioides* F. Muell.	2	1	1	1	2	1	1	1	2	1	1	1	3	1	1	2	1	1
Trymalium ledifolium Fenzl (1)	2	1	1	1	2	1	1	1	2	1	1	1	3	1	1	2	1	1
Trymalium floribundum Steud. (2)	2	1	1	1	2	1	1	1	2	1	1	1	3	1	1	2	1	1
Pomaderris rugosa Cheeseman	2	1	1	1	2	1	1	1	2	1	1	1	2	1	1	2	1	1
Siegfriedia darwinioides C. A. Gardner	2	1	1	1	2	1	1	1	2	1	1	1	3	1	2	2	1	1
Barbeya oleoides Schweinf.	2	2	?	2	2	3	2	?	2	1	1	1	?	1	2	2	2	2
Dirachma socotrana Schweinf.	2	?	?	2	2	?	1	?	2	?	1	1	?	1	1	2	2	2

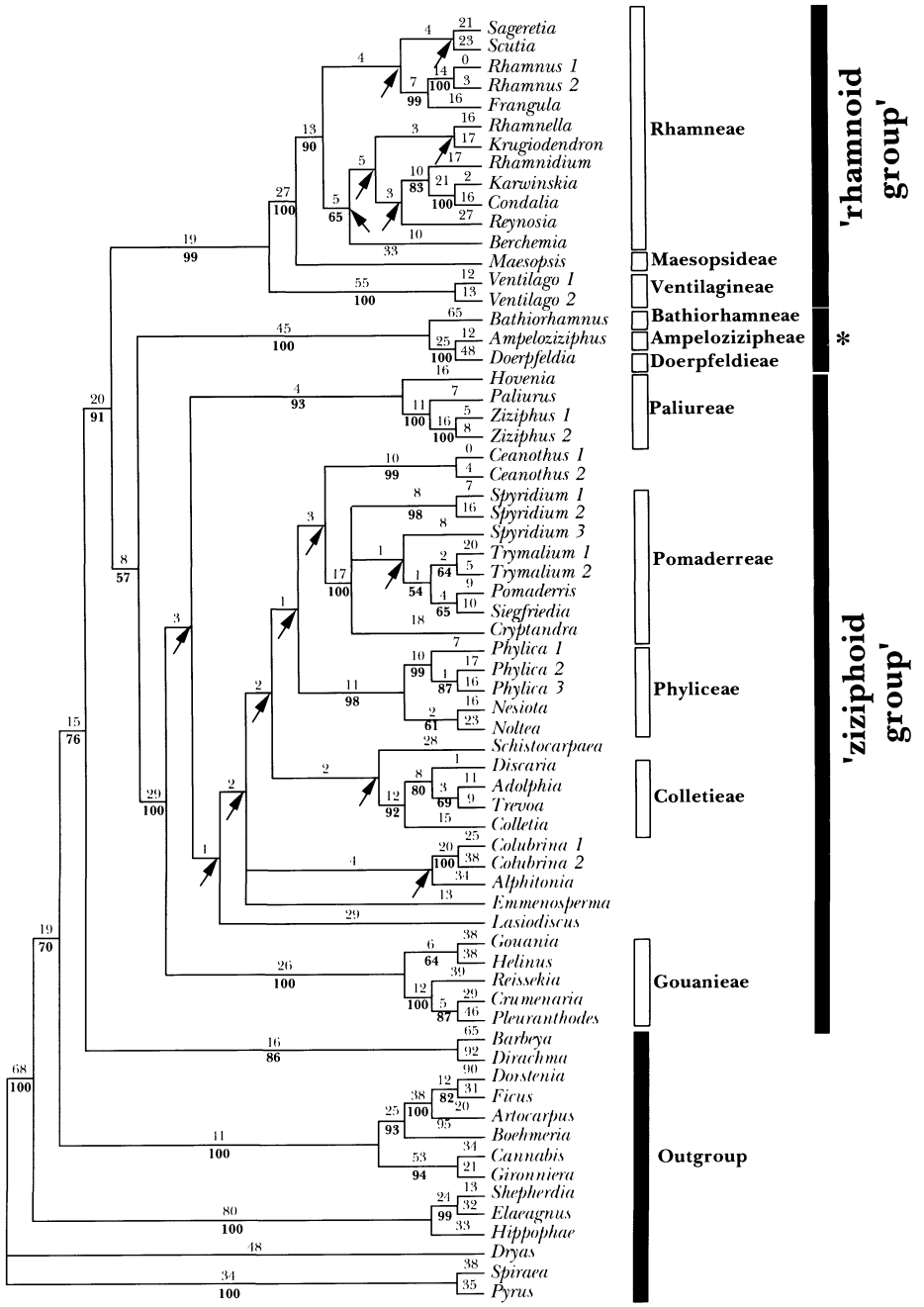

FIG. 1. The single optimal successively weighted tree from a combined parsimony analysis of *rbcL* and *trnL-F* nucleotide sequences (Richardson *et al.* in press), with its Fitch lengths (above branches), bootstrap percentages (below), and arrows indicating branches not present in the strict consensus of the Fitch trees. The tribes of *Rhamnaceae* and the informal infra-familial groups circumscribed in this paper are indicated (the 'ampeloziziphoid group' is indicated by an asterisk). The length of the tree is 2559 steps, CI = 0.59 and RI = 0.70.

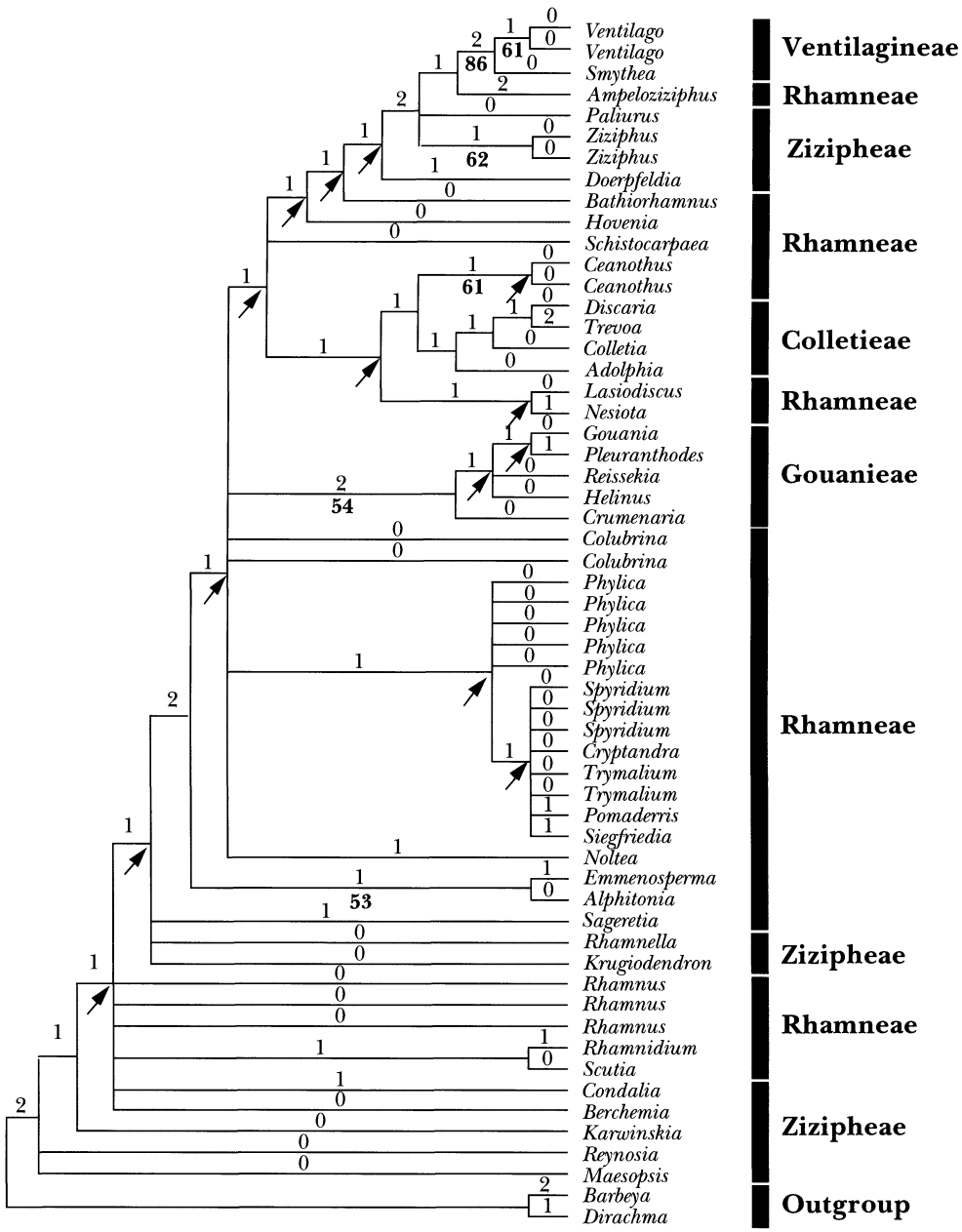

FIG. 2. One of 5000 trees from a morphological analysis of *Rhamnaceae*. Branch lengths are above branches, and bootstrap percentages are below. Branches that collapse in the strict consensus tree are indicated by an arrow. The length of the trees is 52 steps, CI=0.44 and RI=0.83. The tribal placement of each genus according to Suessenguth (1953) is indicated.

shows the single SW tree with Fitch branch lengths (ACCTRAN optimization) and SW bootstrap values; branches collapsing in the strict consensus of the Fitch trees are marked with an arrow. The Fitch length of this tree was 2559 steps (i.e., it was one of the trees found with equal weights). The informal sub-familial and formal tribal groups delimited here are indicated on this figure.

The morphological analysis produced >5000 trees with a length of 52 steps, CI = 0.44 and RI = 0.83. One of the trees from the heuristic search is shown in Fig. 2. The strict consensus of these trees indicated that *Rhamnaceae* were monophyletic although there is no bootstrap support for this. Suessenguth's tribes (indicated in Fig. 2) *Ventilagineae, Gouanieae* and *Colletieae* are also monophyletic according to the strict consensus of these trees with *Ventilagineae* being strongly and *Gouanieae* weakly supported by the bootstrap. Suessenguth's tribes *Zizipheae* and *Rhamneae* are polyphyletic. A group of Australian genera form another monophyletic group delimited in this paper as a separate tribe (*Pomaderreae* Reissek ex Endl.).

The combined morphological and molecular analysis produced 216 trees with a length of 1727, CI = 0.64 (0.49 excluding autapomorphies) and RI = 0.76. One of the trees from the heuristic search is shown in Fig. 3 with our formal tribal delimitations indicated. The topology of the combined morphological/molecular trees is more or less the same as that of the molecular analysis. In the molecular analysis the 'rhamnoid group' is sister to the rest of *Rhamnaceae* whereas in the combined analysis relationships between the three major clades are unresolved. In the combined analysis *Alphitonia* and *Emmenosperma* comprise a clade as do *Paliureae* and *Gouanieae*, and *Lasiodiscus* is sister to *Colubrina* but these relationships are not apparent from the molecular analysis alone. Resolution of relationships among genera within *Pomaderreae* and *Rhamneae* in the combined trees is better than in the molecular trees (e.g. *Berchemia* is resolved as sister to a clade containing *Rhamnella, Krugiodendron, Reynosia, Rhamnidium, Karwinskia* and *Condalia*). Individual morphological characters were mapped onto one of the combined trees to visualise their evolution (Fig. 4).

Discussion

The molecular data strongly supported the monophyly of *Rhamnaceae* with its closest relatives being *Dirachmaceae* and *Barbeyaceae* and showed that Suessenguth's tribes *Rhamneae* and *Zizipheae* were polyphyletic (Figs 1 and 3). They also indicated three highly supported clades not reflected by morphological or anatomical characteristics. Such groups were described as "cryptic clades" (Wojciechowski *et al.* 1993) in a study that identified a clade of aneuploid North American *Astragalus* strongly supported by three different lines of genotypic evidence (chromosomal, nuclear rDNA and plastid DNA). However, there were no morphological characters to support this grouping, and the authors suggested that it should be given an informal name. We have likewise adopted informal names for the three major "cryptic clades" identified here and therefore only formally recognise groups defined by morphological characters in addition to the DNA sequence information. Although the molecular trees are unresolved with respect to certain groups, other groups are clearly defined and strongly supported by the bootstrap (90% or more).

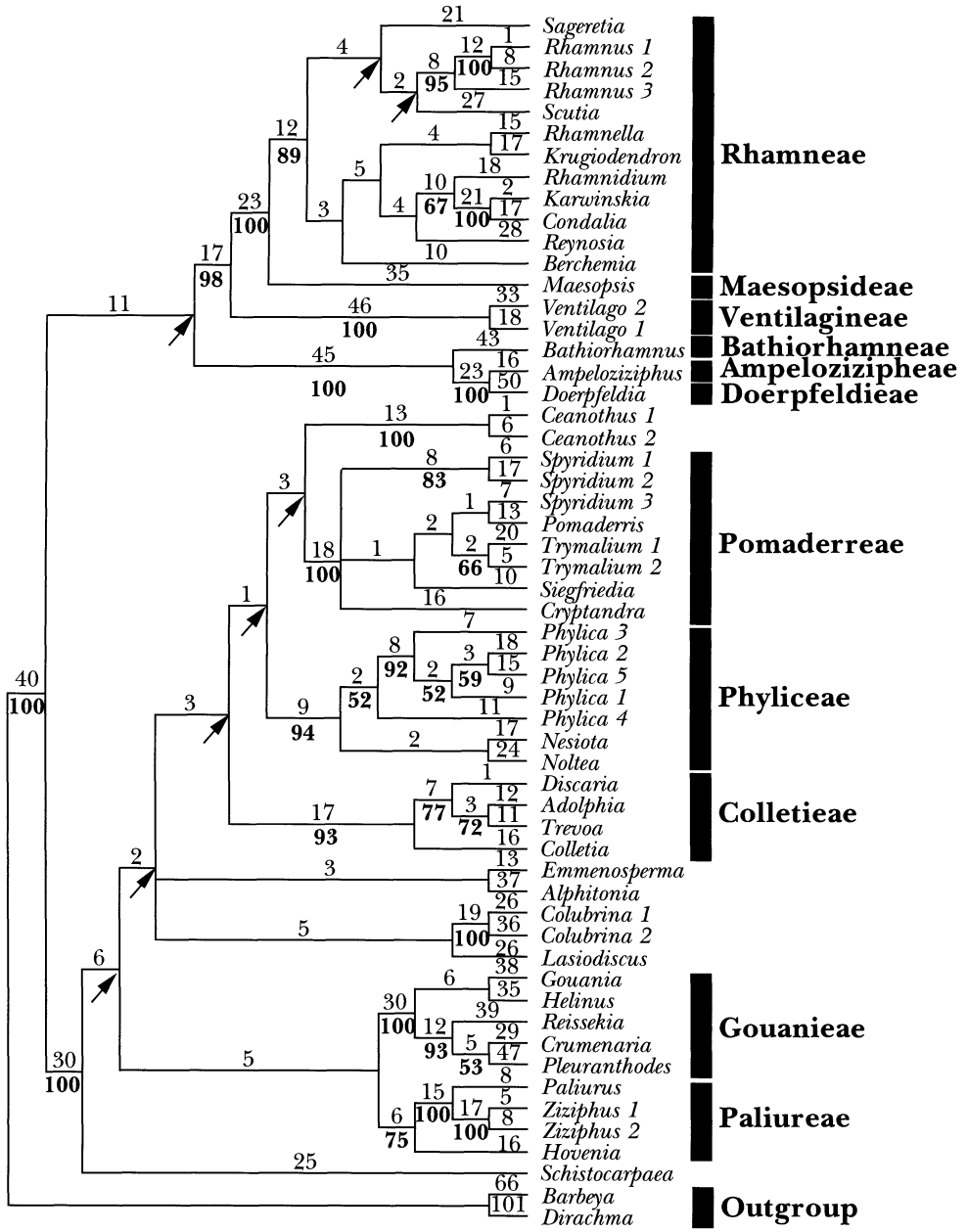

FIG. 3. One of the 216 trees from a combined morphological and molecular analysis of *Rhamnaceae*. Branch lengths are above branches, and bootstrap percentages are below. Branches that collapse in the strict consensus tree are indicated by an arrow. The length of the trees is 1727, CI=0.64 and RI=0.76. The tribes of *Rhamnaceae* circumscribed in this paper are indicated.

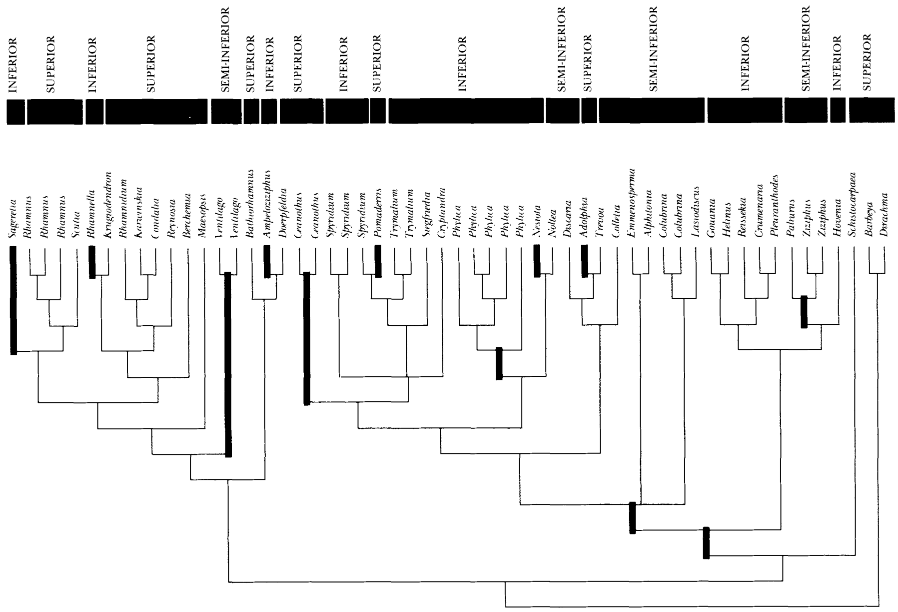

Figure 4.2. Ovary position.

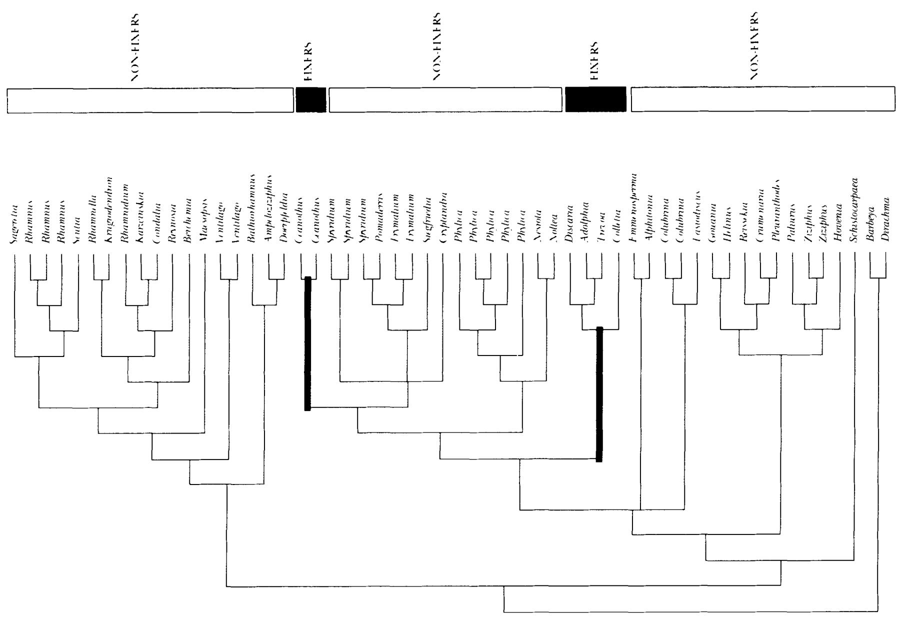

Figure 4.1. Nitrogen fixation

FIG. 4. Morphological character states mapped onto a combined morphological and molecular tree. Thick black bars represent character state changes, grey bars represent equivocal changes. 4.1. nitrogen fixation; 4.2. ovary position; 4.3. fruit appendages; 4.4. fruit type; 4.5. habit; 4.6. pubescence.

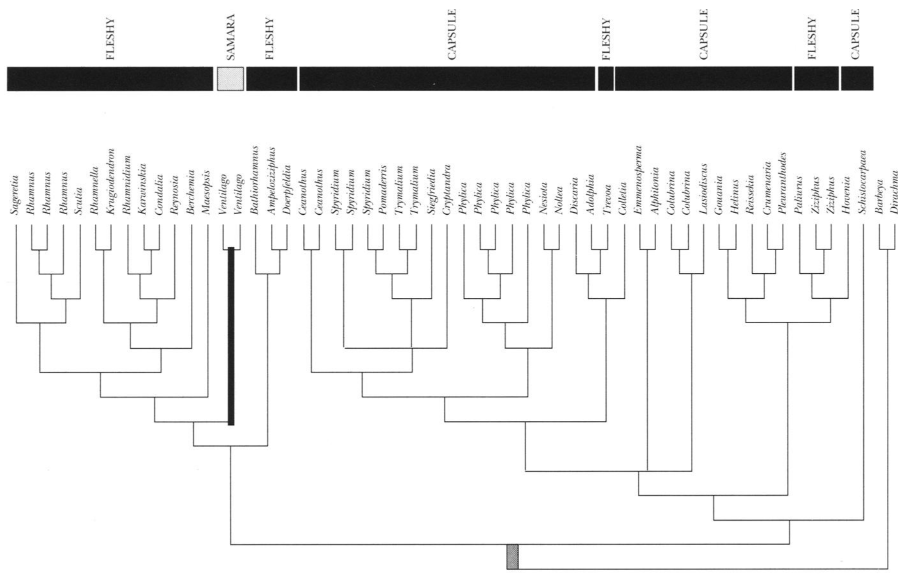

Figure 4.4. Fruit.

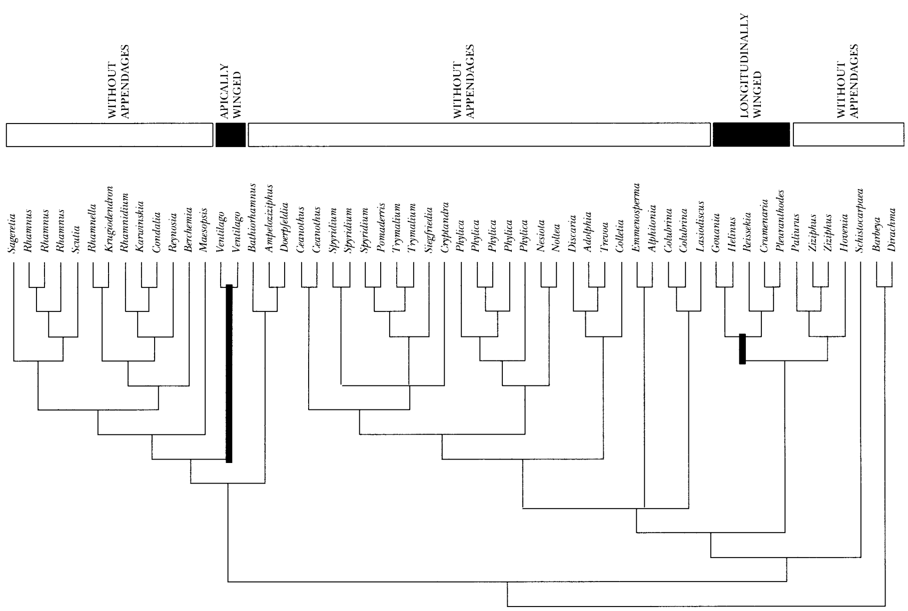

Figure 4.3. Fruit appendages.

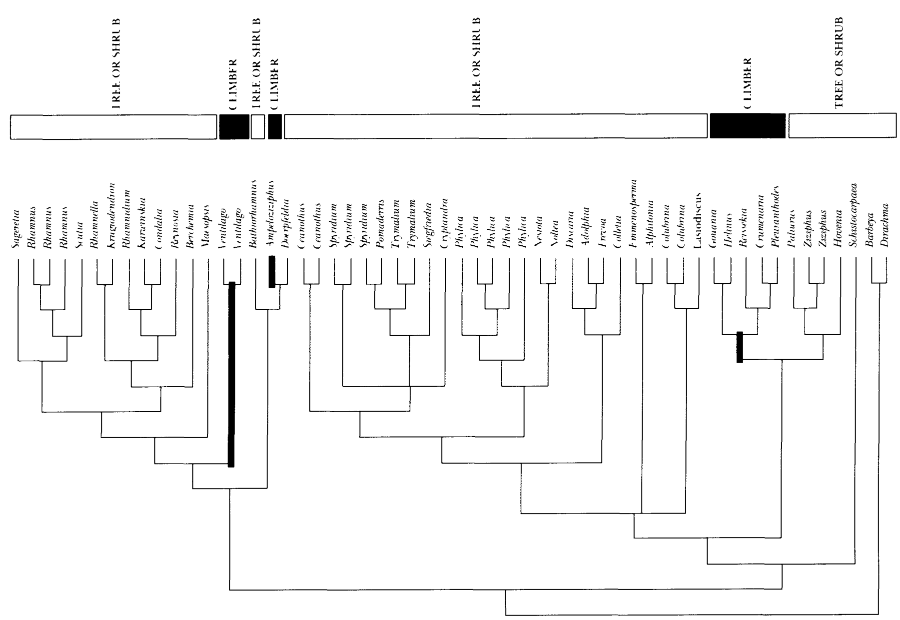

Figure 4.5. Habit.

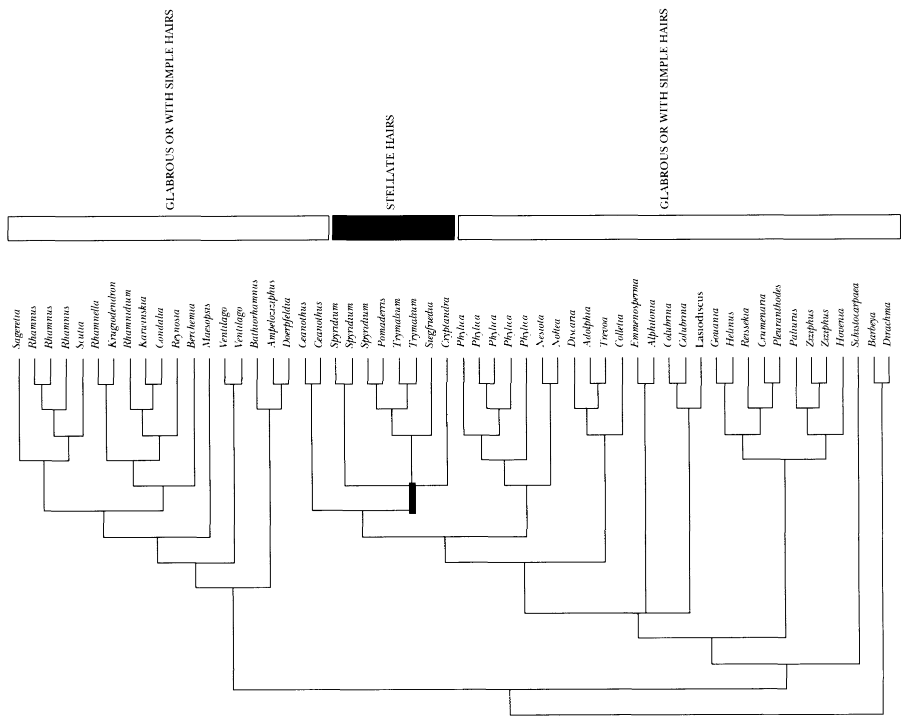

Figure 4.6. Plant pubescence.

The morphological trees (Fig. 2) do not show the three major groups evident in the molecular trees presumably because convergent evolution obscures the relationships determined by the molecular data. The morphological trees do identify most of the tribal groups delimited here, although bootstrap support for these groups is low (largely due to the paucity of morphological characters), and relationships between them are not resolved in the strict consensus tree. Suessenguth's tribes *Rhamneae* and *Zizipheae* are not monophyletic but *Gouanieae*, *Colletieae* and *Ventilagineae* are.

These analyses indicate the need for reassessment of certain morphological characteristics, and more in-depth study may reveal differences in structure confirming their independent development. These results also illustrate the difficulties involved in estimating phylogeny using only a few morphological characters. The length of the morphological tree is 52 steps, but these characters take 66 steps on the combined morphological and molecular tree. This shows that the addition of molecular data detects more homoplasy than the morphological data alone indicates. A more detailed study using more morphological characters and more accurate coding may result in better resolution and bootstrap support. The fact that the topology of the combined morphological/molecular analysis (Fig. 3) is more or less identical to that of the separate molecular analysis is expected, as more molecular characters (480 informative base positions) were available than morphological ones (18). Differential weighting of morphological and molecular characters could be tried with greater weight being assigned to morphological characters, but this is a highly subjective procedure and is based on the assumption that morphology is better than DNA data.

Some morphological characters were useful in providing added support for some weakly supported or unsupported groups indicated by the molecular trees. For example, morphology indicates a close relationship between the genera *Alphitonia* and *Emmenosperma* (seed attached to the torus after dehiscence is a synapomorphy for this group) and *Colubrina* and *Lasiodiscus*, although these relationships still have no bootstrap support.

Species of *Ceanothus* and in some genera of *Colletieae* engage in root nodular fixation of nitrogen in a symbiotic association with the actinomycete bacterium *Frankia* (Baker & Schwintzer 1990). Soltis *et al.* (1995) showed that all root-nodulating angiosperms fall within one large clade and may share a genetic predisposition to nodulation, even though most of the members of this clade do not nodulate. Fig. 4.1 shows the distribution of nitrogen-fixing taxa, indicating that ability to fix nitrogen appears either to have developed twice in parallel within the ziziphoid group or been present in the ancestor of this group and subsequently lost. The relationships between groups within this ziziphoid clade are not clearly resolved, and it could be that *Ceanothus* and the *Colletia*, *Discaria*, *Trevoa* group are sister taxa, in which case root nodulation has arisen only once (with a subsequent loss of this feature in *Adolphia*). Also, the ability to fix nitrogen has not been extensively investigated in other groups in the ziziphoid clade, and it may be that some of these groups also have nitrogen-fixing capabilities. The combined tree could be used to direct the search for other such taxa. Fig. 4.2 shows that ovary position, which is likely to be highly adaptive or developmentally

plastic, is homoplasious, and development of such characters needs to be well studied before making definite conclusions about homology. Apically and longitudinally winged fruits are derived characters in *Ventilagineae* and *Gouanieae* respectively (Fig. 4.3). The ancestral fruit form within *Rhamnaceae* cannot be determined from this data (Fig. 4.4). Fleshy fruits could have been the ancestral form with the development of capsules in the 'ziziphoid group' and capsules or samara in *Ventilagineae* and with reversals in the *Ziziphus/Paliurus* clade and *Trevoa* (*Colletieae*). However, it is equally likely that capsules could have been the ancestral form with independent changes to fleshy fruits or samara. Fig. 4.5 shows the distribution of habit types, indicating that the climbing habit has developed three times from an arborescent ancestral state (some species of *Berchemia* not included in this analysis are also climbers). Stellate hairs are a synapomorphy for the Australian tribe *Pomaderreae* (Fig. 4.6).

We recognize tribes only if they have strong bootstrap support in the molecular analysis and are well-defined morphologically (the new system is summarized in Table 4).

Description of Informal Groupings

'Rhamnoid' group

This clade can be divided into three subgroups, the first of which comprises *Rhamneae* and includes genera such as *Rhamnus* and *Berchemia* with fleshy fruits, superior ovaries and a nectariferous disc either partly or totally adnate to the calyx tube. The inter-relationships of the genera within this first group are not well resolved. The second subgroup, *Maesopsideae* Weberb., consists only of the monotypic genus *Maesopsis*, which is a sister to *Rhamneae*. The third subgroup is composed of *Ventilagineae*, which has strong support as sister to the *Maesopsis-Rhamneae* alliance. This is a tribe of climbers with apically winged fruits and semi-inferior ovaries. No sequence data have been gathered for *Smythea*, which is the only other genus previously placed in this tribe; however, this genus is morphologically similar to *Ventilago* and therefore included in *Ventilagineae*.

'Ampeloziziphoid' group

This clade consists of three highly divergent genera with palmately veined leaves and fleshy fruits. Brazilian *Ampeloziziphus* is a climbing monotypic genus with semi-inferior ovaries and a thick nectariferous disc. *Doerpfeldia*, a monotypic genus from Cuba, is a tree with small leaves and a superior ovary thinly covered by the nectariferous disc. The two species of *Bathiorhamnus* from Madagascar are trees with a superior ovary and a thick nectariferous disc. There are, however, no obvious morphological similarities linking these genera, and the high levels of molecular divergence between them indicate that they are only distantly related. It is likely that they are remnants of formerly more diverse and widespread groups and should each be recognized at tribal level because of their highly divergent nature.

TABLE 4. Summary of revised tribal classification of *Rhamnaceae*.

Tribe	Genera included	Distribution
Paliureae Reissek ex Endl.	*Paliurus, Ziziphus, Hovenia*	tropics and warm temperate regions
Colletieae Reissek ex Endl.	*Adolphia, Colletia, Discaria, Kentrothamnus, Retanilla, Trevoa*	South America, Australasia
Phyliceae Reissek ex Endl.	*Nesiota, Noltea, Phylica*	southern Africa, Atlantic and Indian Ocean islands
Gouanieae Reissek ex Endl.	*Alvimiantha, Crumenaria, Gouania, Helinus, Pleuranthodes, Reissekia*	tropical and warm Americas, Africa, Madagascar, NW India, Indian Ocean Islands
Pomaderreae Reissek ex Endl.	*Blackallia, Cryptandra, Pomaderris, Siegfriedia, Spyridium, Trymalium*	Australasia
Rhamneae Hook. f.	*Auerodendron, Berchemia, Berchemiella, Condalia, Dallachya, Karwinskia, Krugiodendron, Reynosia, Rhamnella, Rhamnidium, Rhamnus, Sageretia, Scutia*	tropics to northern temperate regions
Maesopsideae Weberb.	*Maesopsis*	tropical Africa
Ventilagineae Hook. f.	*Smythea, Ventilago*	Old World tropics
Ampeloziziphеae J. E. Richardson	*Ampeloziziphus*	Brazil, Peru
Doerpfeldieae J. E. Richardson	*Doerpfeldia*	Cuba
Bathiorhamneae J. E. Richardson	*Bathiorhamnus*	Madagascar
Genera *incertae sedis*	*Ceanothus*	USA
	Emmenosperma	Australia, New Guinea, New Caledonia, Fiji
	Schistocarpaea	Australia
	Alphitonia	Malaysia, Australia, Polynesia, Hawaii
	Colubrina	tropical and warm areas in the Americas, Africa and southeast Asia
	Lasiodiscus	Africa, Madagascar

'Ziziphoid' group

This clade comprises genera that usually have semi-inferior to inferior ovaries and capsular fruits. There are, however, exceptions to this, e.g. *Ziziphus* and *Paliurus* have fleshy fruits. In addition some genera of *Colletieae* have superior ovaries or fleshy fruits. Within the ziziphoid group, there are a number of other well-supported subgroups including Suessenguth's more derived tribes *Colletieae* and *Gouanieae*. *Gouanieae* are climbers with tendrils and longitudinally winged fruits; *Colletieae* are strongly armed trees or shrubs. The Australian tribe, *Pomaderreae*, is characterised by being the only group in the family with stellate hairs. *Ziziphus*, *Paliurus*, and *Hovenia* comprise another strongly supported tribe, *Paliureae* Reissek ex Endl. (Schirarend & Olabi (1994) noted that the name *Paliureae* predates *Zizipheae*). *Hovenia* appears to have a close relationship with *Ziziphus* and *Paliurus* in that these genera all have palmately veined leaves, cymose inflorescences, a base chromosome number of x = 12 and a similar pollen exine structure. On the basis of this and molecular evidence *Hovenia* is placed in *Paliureae*. A strongly supported, predominantly South African clade, *Phyliceae*, consisting of *Phylica*, *Nesiota*, and *Noltea* is also distinct and generally characterized by having an ericoid shrubby habit, inferior ovaries and leaves with revolute margins and tomentose undersurfaces.

Colubrina includes trees or shrubs with the nectariferous disc filling the receptacle and surrounding the ovary, and it is thought to be closely related to *Lasiodiscus* (Johnston 1971; Figueiredo 1995) as they are morphologically similar and could eventually be treated as a distinct tribe. However, in the combined molecular and morphological analysis the *Colubrina* and *Lasiodiscus* clade has <50% bootstrap support, so there is insufficient evidence to recognize this group at the present.

The affinities of a number of other genera are unclear. The arborescent genus *Alphitonia* from Malaysia, Australia and the western Pacific and the Australian *Emmenosperma* both have red arillate seeds that persist on the receptacle after dehiscence. However, there is <50% bootstrap support for this relationship, so further evidence is necessary to group these two genera together in a separate tribe. The North American genus *Ceanothus* is characterised by having receptacles and nectariferous discs persisting on the pedicel. The species of *Ceanothus* included in this analysis form a strongly supported monophyletic group for which relationships with other clades are unresolved.

Key to the Tribes

1. Fruit with apical appendages, longitudinal wings or with a dry membranous ring around the apex 2
   Fruit without such appendages, wings or dry membranous rings 4
2. Shrubs, fruit with a dry membranous ring around the apex .. *Paliureae* (*Paliurus*)
   Climbers or herbs, fruit not as above.....3
3. Fruit with longitudinal wings; ovary inferior, 3-locular; tendrils present; endosperm present ... *Gouanieae* (*Gouania*, *Crumenaria*, *Reissekia*, *Pleuranthodes*)
   Fruit with apical appendages, ovary semi-inferior, 2-locular; tendrils absent; endosperm absent ..... *Ventilagineae*

4. Infructescence axis succulent; disc usually hairy ..... *Paliureae* (*Hovenia*)
   Infructescence axis not succulent; disc not hairy 5
5. Strongly armed trees or shrubs; roots usually bearing nitrogen-fixing nodules; leaves opposite ..... *Colletieae*
   Combination of characters not as above 6
6. Fruit fleshy 7
   Fruit a capsule 12
7. Leaf venation pinnate 8
   Leaf venation palmate 9
8. Ovary 1-locular; style laterally attached to fruit ..... *Maesopsideae*
   Ovary 2- or 4-locular; style apically attached to fruit ..... *Rhamneae*
9. Ovary 3-locular 10
   Ovary 2- or 4-locular 11
10. Climber; ovary semi-inferior; endosperm absent ..... *Ampelozizipheae*
    Tree; ovary superior; endosperm present ..... *Bathiorhamneae*
11. Disc adnate to ovary only; ovary superior; endosperm present ..... *Doerpfeldieae*
    Disc adnate to ovary and calyx-tube and filling calyx tube; ovary semi-inferior; endosperm absent ..... *Paliureae* (*Ziziphus*)
12. Plant stellate-hairy ..... *Pomaderreae*
    Plant glabrous or with simple hairs 13
13. Nitrogen fixing nodules present; petals sometimes blue; North America ..... *Ceanothus*
    Nitrogen fixing nodules absent; petals never blue; not usually found in North America 14
14. Climber with tendrils ..... *Gouanieae* (*Alvimiantha*)
    Tree or shrub 15
15. Seed persisting on receptacle after dehiscence 16
    Seed not persisting on receptacle after dehiscence 17
16. Exocarp thin and leathery; ovary usually 2-locular ..... *Emmenosperma*
    Exocarp thick, spongy and crumbly at maturity; ovary usually 3-locular ..... *Alphitonia*
17. Leaves opposite 18
    Leaves usually alternate 19
18. Leaf margin not revolute; stipules interpetiolar ..... *Lasiodiscus*
    Leaf margin revolute; stipules not interpetiolar ..... *Phyliceae* (*Nesiota*)
19. Ovary semi-inferior; branches not clustered 20
    Ovary superior; branches not clustered ..... *Schistocarpaea*
    Ovary inferior; branches clustered ..... *Phyliceae* (*Phylica*)
20. Plant glabrous; leaf margins always toothed ..... *Phyliceae* (*Noltea*)
    Plant sometimes hairy; leaf margins not always toothed ..... *Colubrina*

Taxonomy

Tribe **Paliureae** *Reissek ex Endl.* in Benth. & Hook. f., Gen. Pl., 1095 (1840) [*Zizipheae* Brongn.]. Type genus: *Paliurus* Mill. Some characteristics taken from Chun & Tsiang (1939); Johnston (1963a, 1964); Schirarend & Olabi (1994).

Trees or shrubs. Branches spinose or unarmed. Leaves alternate or fasciculate, venation palmate or 3-nerved at base with midrib pinnately branched (*Hovenia*). Stipules persistent or caducous. Inflorescences axillary or terminal cymes, inflorescence-axis sometimes becoming succulent (*Hovenia*). Petals usually present. Ovary semi-inferior to superior, 2-(3- or 4-) locular. Nectariferous disc adnate to ovary and calyx-tube and filling calyx-tube, sometimes hairy (*Hovenia*). Style bi- or trifid. Fruit dry with a wide membranous ring around the apex (*Paliurus*), fleshy (*Ziziphus*) or a capsule (*Hovenia*). Seed with or without endosperm, coat membranaceous or papery. Pollen exine reticulate-rugulate, striate-rugulate, rugulate or fossulate-perforate. Chromosome numbers 2n = 12, 24, 26, 36, 40, 48, 72. New and Old World tropics and warm temperate regions, southern Europe to Japan.

Three genera: *Paliurus* Mill., *Ziziphus* Mill. (including *Sarcomphalus* R. Br.) and *Hovenia* Thunb.

Tribe **Colletieae** *Reissek ex Endl.* in Benth. & Hook. f., Gen. Pl., 1099 (1840). Type genus: *Colletia* Comm. ex Juss. Some characteristics taken from Johnston (1971, 1973); Tortosa (1983, 1989, 1992, 1993).

Trees or shrubs, strongly armed, branches green, decussate, forming spines. Roots of most genera bearing nitrogen-fixing nodules. Leaves opposite, small, often caducous, venation palmate or pinnate. Stipules absent or present and persistent or falling early. Inflorescences axillary, with flowers solitary or in cymes. Petals present or absent. Ovary (2-)3-locular, inferior, semi-inferior or superior. Nectariferous disc annular, 5-lobed, adnate to calyx tube or absent. Style 2- or 3-lobed or trifid. Fruit a capsule or fleshy. Seed coat leathery, endosperm present. Pollen exine striate-rugulate, rugulate, fossulate-insulate or fossulate-perforate. Chromosome number 2n = 22 (*Colletia, Discaria*). Predominantly South American but also in North America, New Zealand and Australia.

Six genera: *Adolphia* Meisn., *Colletia* Comm. ex Juss., *Discaria* Hook., *Kentrothamnus* Suess. & Overkott, *Retanilla* (DC.) Brongn. and *Trevoa* Miers ex Hook. (including *Talguenea* Miers ex Endl.).

Tribe **Phyliceae** *Reissek ex Endl.* in Benth. & Hook. f., Gen. Pl., 1100 (1840) emend. J. E. Richardson. Type genus: *Phylica* L. Some characteristics taken from Pillans (1942).

Unarmed ericoid shrubs or trees. Branches often clustered, parallel and erect. Leaves alternate or opposite, usually densely tomentose beneath, leaf margins usually revolute (sometimes toothed and not revolute, *Noltea*), venation pinnate. Stipules absent in all but one species of *Phylica* or present and caducous (*Nesiota*) or persistent (*Noltea*). Inflorescences capitate to spicate, paniculate or flowers solitary, terminal or axillary. Bracts leafy or short and scarious. Ovary usually inferior (sometimes semi-inferior), completely or mostly fused to the receptacle, 3-(4-) locular. Nectariferous disc epigynous or slender and covering the inside of the calyx tube, sometimes hairy (*Nesiota*). Style obscurely 3-lobed or trifid. Fruit a capsule, 3-locular; locules 1-seeded, dehiscent. Seeds arillate (at least in *Phylica*), endosperm

present. Pollen exine reticulate, reticulate-rugulate or fossulate-perforate. Southern and eastern Africa, St Helena, Tristan da Cunha, Madagascar, Mauritius, Réunion and New Amsterdam.

Three genera: *Nesiota* Hook. f., *Noltea* Rchb. and *Phylica* L.

Tribe **Gouanieae** *Reissek ex Endl.* in Benth. & Hook. f., Gen. Pl., 1102 (1840). Type genus: *Gouania* Jacq. Some characteristics taken from Grey-Wilson (1978).

Unarmed climbers or herbs (*Crumenaria*), tendrils present. Leaves alternate, petiolate, entire, venation pinnate or palmate. Stipules usually caducous. Inflorescences small cymes. Ovary inferior, (2 -)3-(4-) locular. Nectariferous disc epigynous, fleshy, stellate or margins 5-angled. Style trifid. Fruit a capsule, 3-locular, loculicidally dehiscent, usually with longitudinal wings that lie above the septum of the locules; locules 1-seeded. Seed coat leathery; endosperm present, fleshy. Pollen exine striate, striate-reticulate, rugulate, radiate-rugulate or perforate to fossulate-perforate. Chromosome number 2n = 22 (*Helinus*). Tropical and sub-tropical America, Africa, Madagascar, Indian Ocean islands and Asia.

Six genera: *Alvimiantha* Grey-Wilson, *Crumenaria* Mart., *Gouania* Jacq., *Helinus* E. Mey. ex Endl., *Pleuranthodes* Weberb. and *Reissekia* Endl.

Gouanieae are the only tribe in the family that have fruits with longitudinal wings lying above the septum of the locules.

Tribe **Pomaderreae** *Reissek ex Endl.* in Benth. & Hook. f., Gen. Pl., 1101 (1840). Type genus: *Pomaderris* Labill. Some characteristics taken from Gardner (1932, 1941); Keighery (1978).

Shrubs or small trees with stellate hairs. Leaves opposite or alternate, venation pinnate. Stipules caducous or persistent. Inflorescence with flowers solitary in axils, cymose or clustered into glomerules. Ovary usually inferior or semi-inferior (rarely superior, *Blackallia*), 3- (or 4-) locular. Nectariferous disc surrounding base of ovary and adnate to calyx tube. Style 3-lobed or trifid. Fruit a capsule, exocarp thin; locules 1-seeded, dehiscent. Seed with a small aril, endosperm present. Pollen exine verrucate (*Pomaderris*), fossulate-perforate or fossulate-insulate. Chromosome numbers 2n = 24, 36, 48 (*Pomaderris*). Australasia.

Six genera: *Blackallia* C. A. Gardner, *Cryptandra* Sm., *Pomaderris* L., *Siegfriedia* C. A. Gardner, *Spyridium* Fenzl and *Trymalium* Fenzl.

Pomaderreae may be distinguished from other tribes in *Rhamnaceae* by their stellate hairs.

Tribe **Rhamneae** *Hook. f.* in Benth. & Hook. f., Gen. Pl. 1: 373 (1862) emend. J. E. Richardson. Type genus: *Rhamnus* L. Some characteristics taken from Grisebach (1866); Mueller (1875); Urban (1902 – 03; 1924b); Nakai (1923); Wolf (1938); Johnston (1962, 1974).

Trees, shrubs or climbers, sometimes armed. Leaves opposite, sub-opposite or alternate, entire or serrate, venation pinnate. Stipules sometimes absent, often

caducous. Inflorescence solitary, fasciculate, umbellate or racemose to cymose, axillary or terminal. Petals present or absent. Ovary superior (rarely inferior), free, 2-(1- or 4-) locular. Nectariferous disc lining base of calyx tube or free. Styles 2, often persistent on apex of fruit. Fruit fleshy, 1 – 4-locular. Seeds without endosperm or endosperm thin or fleshy. In mature seeds hilum next to radicle. Pollen exine reticulate to rugulate or perforate to fossulate-perforate. Chromosome number 2n = 12, 20, 24, 26. Found throughout the range of the family except southern South America.

Thirteen genera: *Auerodendron* Urb., *Berchemia* Neck. ex DC. (including *Phyllogeiton* (Weberb.) Herzog, *Berchemiella* Nakai, *Condalia* Cav., (including *Condaliopsis* (Weberb.) Suess., *Microrhamnus* A. Gray), *Dallachya* F. Muell., *Karwinskia* Zucc., *Krugiodendron* Urb., *Reynosia* Griseb., *Rhamnella* Miq. (including *Chaydaia* Pit.), *Rhamnidium* Reissek, *Rhamnus* L. (including *Oreoherzogia* W. Vent, *Oreorhamnus* Ridl.), *Sageretia* Brongn. (including *Lamellisepalum* Engl.), *Scutia* (DC.) Brongn.

Tribe **Maesopsideae** *Weberb.* in Engler & Prantl, Nat. Pflanzenfam. 128: 399 (1895). Type genus: *Maesopsis* Engl. Some characteristics taken from Schirarend & Süss (1985).

Trees, unarmed. Leaves opposite or alternate, strongly toothed with glands at tips of teeth, venation pinnate. Stipules present. Inflorescence an axillary pseudoraceme. Petals present. Ovary superior, free, 1-locular, without a prominent placenta. Nectariferous disc lining the inside of the calyx-tube. Style laterally attached to the fruit, tetrafid. Fruit fleshy, 1-seeded. In mature seeds radicle opposite to hilum; endosperm copious, taking up most of volume of seed. Pollen exine suprabaculate. Chromosome number 2n = 18. Tropical Africa.

One genus: *Maesopsis* Engl.

Maesopsis differs from all other genera in *Rhamnaceae* in its single-celled ovary and a style laterally attached to the fruit (rather than apically).

Tribe **Ventilagineae** *Hook. f.* in Benth. & Hook. f., Gen. Pl. 1: 371 (1862). Type genus: *Ventilago* Gaertn. Some characteristics taken from Banerjee & Mukerjee (1970).

Climbers or rarely small trees, unarmed, tendrils absent. Branches rigid, glabrous. Leaves alternate, venation pinnate. Stipules caducous. Inflorescences umbellate cymes or fascicled, or arranged in axillary or terminal panicles. Calyx spreading. Ovary semi-inferior to inferior, more or less sunk into nectariferous disc, 2-locular. Nectariferous disc fleshy, tuberculate. Style with 2 short stigmatic lobes or with two arms with separate stigmas. Fruit samaroid and indehiscent or capsular and dehiscent with an apical appendage. Seed without endosperm. Pollen exine fossulate-perforate, perforate, reticulate-rugulate, striate-rugulate or rugulate. Chromosome number 2n = 24. Old World tropics.

Two genera: *Ventilago* Gaertn., *Smythea* Seem. ex A. Gray.

This tribe is unique in *Rhamnaceae* in its fruits with a pronounced apical appendage.

Tribe **Ampeloziziphеae** *J. E. Richardson* **tribus nov.** Plantae scandentes; venae foliorum palmatim dispositae; ovarium semi-inferum triloculare; fructus carnosi; semina endospermium carentia. Typus generis: *Ampeloziziphus* Ducke. Some characteristics taken from Ducke (1935).

Climbers, unarmed, tendrils absent. Leaves distichous, alternate, venation palmate, 5-nerved, the external vein on each side slender and sometimes almost obsolete. Stipules setaceous, caducous. Inflorescences axillary clustered cymes, or composed of several clustered cymes forming a panicle. Calyx tube shortly turbinate; lobes subequal. Ovary semi-inferior, included in and united to calyx tube and nectariferous disc, 3-locular. Nectariferous disc thick, flat on surface, annular. Style trifid at apex. Fruit fleshy, 3-locular with one seed per locule, base stipitate, stalk surrounded by persistent lobes of calyx; exocarp thick and fleshy; stone hard but thin walled. Seeds with endosperm and aril absent. Pollen exine fossulate-perforate. Chromosome number unknown. Northern South America.

One genus: *Ampeloziziphus* Ducke.

Tribe **Doerpfeldieae** *J. E. Richardson* **tribus nov.** Arbores; venae foliorum palmatim dispositae; ovarium biloculare, disco nectarifero tenuiter obtectum; fructus carnosi; semina endospermium instructa. Typus generis: *Doerpfeldia* Urb. Some characteristics taken from Urban (1924a).

Trees, unarmed. Leaves alternate, often emarginate, otherwise entire, venation palmate, 3-nerved. Stipules caducous. Flowers axillary, solitary. Flower bud globose. Petals absent. Ovary superior, pseudobilocular. Nectariferous disc thinly covering the ovary and attached to the calyx-tube. Style bifid. Receptacle short. Fruit fleshy, more or less unequally 2-locular, smaller locule empty; exocarp thin; calyx-tube remaining attached to lower quarter of fruit; endocarp bony. Seed with endosperm. Pollen exine rugulate. Chromosome number unknown. Cuba.

One genus: *Doerpfeldia* Urb.

Doerpfeldia is the only genus in *Rhamnaceae* to have a nectariferous disc thinly covering the ovary. All other genera have thick discs broadly attached to the ovary or thin discs that line the inside of the calyx tube or thin discs that are at least partially free from the ovary.

Tribe **Bathiorhamneae** *J. E. Richardson* **tribus nov.** Arbores; venae foliorum palmatim dispositae; ovarium superum triloculare; fructus carnosi; semina endospermium instructa. Typus generis: *Bathiorhamnus* (H. Perrier) Capuron. Some characteristics taken from Capuron (1966).

Trees, unarmed. Leaves alternate, venation palmate, 3-nerved with nerves converging at apex, margins entire to toothed. Stipules small. Inflorescence fasciculate, axillary. Sepals punctate-pellucid. Ovary superior, 3-locular. Nectariferous disc thick, broadly attached to ovary. Style trifid. Fruit fleshy, base encircled with an annular scar, (1- or 2-) 3-locular, septicidally dehiscent; locules indehiscent. Seed with endosperm, without aril, coat leathery. Chromosome number unknown. Madagascar.

One genus: *Bathiorhamnus* Capuron (including *Macrorhamnus* H. Perrier).

GENERA *INCERTAE SEDIS*

The following taxa have been given an *incertae sedis* status because their position is ambiguous in both molecular and morphological trees. Further study should give a clearer idea of their relationships to others.

Ceanothus L. Some characteristics taken from Van Rensselaer & McMinn (1942).

Shrubs or small trees, sometimes spinescent. Roots of most species bearing nitrogen-fixing nodules. Leaves alternate or opposite, venation palmate or pinnate, deciduous or evergreen. Stipules caducous or persistent. Inflorescences terminal composite panicles or axillary racemes. Petals present. Ovary 3 – (4)-locular, superior, more or less immersed in nectariferous disc. Disc adnate to ovary and calyx tube, annular, subpentagonal, glandular. Style trifid. Fruit a capsule, 3-locular, base of calyx tube circumscissile around base of capsule, 3-ribbed, separating at maturity into three parts, exocarp leathery to weakly fleshy; locules dehiscent, crustaceous, bivalved, 1-seeded. Receptacle and disc persistent on the pedicel, remaining intact during endocarp dehiscence. Seeds smooth, convex at one side, sometimes arillate, endosperm present. Pollen exine fossulate-perforate, fossulate-insulate or rugulate. Chromosome number 2n = 24. North America. A genus of 55 species.

Emmenosperma F. Muell. Some characteristics taken from Mueller (1862 – 63).

Trees, unarmed. Leaves sub-opposite, entire, leathery, venation pinnate. Stipules absent. Inflorescences repeatedly trichotomous panicles. Calyx 5-lobed; lobes deciduous. Ovary superior, 2 –(3)-locular. Nectariferous disc thin, lining the base of the receptacle. Style filiform, bifid. Stigma bi-(tri-)fid. Fruit a capsule, 2 –(3)-locular, septicidally dehiscent; locules dehiscent; exocarp thin and leathery; endocarp osseous-crustaceous, splitting unequally. Seeds persisting on receptacle after dehiscence, erect; aril and endosperm present. Pollen reticulate or fossulate-perforate. Chromosome number unknown. Australia. A genus of three species.

Schistocarpaea F. Muell. Some characteristics taken from Mueller (1891).

Trees, unarmed. Leaves alternate, venation pinnate. Stipules caducous. Inflorescences terminal and axillary panicles. Bracts small. Calyx deeply 5-lobed; lobes semi-lanceolate, deciduous. Ovary superior, 3-locular, almost fully emerged from disc. Nectariferous disc slightly undulate at margin. Style trifid. Fruit a capsule, calyx-tube persistent and surrounding base; exocarp crustaceous, irregularly trivalved; endocarp receding, thinly papery; locules splitting to base along inner side, ruptured and twisted on outer side. Seeds without albumen, testa chartaceous. Pollen fossulate-perforate. Chromosome number unknown. Australia. A monotypic genus.

Alphitonia Reissek ex Endl. Some characteristics taken from Braid (1925).

Trees, sometimes large, unarmed. Branches rust-red, tomentose. Leaves alternate, venation pinnate, entire, indumentum weakly to strongly developed. Stipules subulate, villose, caducous. Inflorescences subterminal, paniculate racemes. Ovary semi-inferior, (2 –)3-locular. Nectariferous disc adnate to ovary and calyx tube and filling calyx tube. Style 2- or 3-lobed. Fruit a capsule; margin of receptacle reaching bottom third or middle half of fruit; exocarp thick, spongy; endocarp of 2 or 3 hard, coriaceous locules; locules dehiscing down the ventral suture and partially down the dorsal suture; exocarp, endocarp and portions of the receptacle falling away; seeds persisting on the remainder of the receptacle, arillate, endosperm cartilaginous, coat hard or tough. Pollen exine fossulate-perforate, rugulate, striate-rugulate or reticulate. Chromosome number unknown. Malaysia, Australia, West Pacific islands, New Caledonia. A genus of six species.

Colubrina Rich. ex Brongn. Some characteristics taken from Johnston (1971).

Shrubs or trees, armed or unarmed, rarely scandent. Leaves alternate or opposite (*C. oppositifolia*), venation pinnate or palmate, often glandular. Stipules lateral and basal or interpetiolar, usually caducous. Inflorescence cymes or small thyrses, sessile and umbel-like or shortly stalked, few-flowered and corymb-like, or rarely flowers solitary. Flower-buds more or less glabrous to densely hairy. Ovary semi-inferior, 3 –(4)-locular. Nectariferous disc large, nearly filling the receptacle and often hiding the ovary, remaining united from the lower fifth to the upper half of the fruit. Styles trifid. Fruit a capsule; mesocarp thin, dry, leathery to brittle and flaky; endocarp crustaceous or cartilaginous; locules dehiscent. Receptacle and disc breaking irregularly as endocarp dehisces into separate locules. Seeds with endosperm, sometimes with a small aril. Pollen exine rugulate to fossulate-perforate. Chromosome number 2n = 16, 24. Tropical and sub-tropical regions of the Americas, Africa and south east Asia. A genus of thirty one species.

Lasiodiscus Hook. f. Some characteristics taken from Figueiredo (1995).

Trees or shrubs, unarmed. Leaves opposite, pinnate or palmate, often with minute, glandular teeth. Stipules interpetiolar, usually caducous. Inflorescences axillary, usually a compound partial dichasium, with branches tending to scorpioid cymes, sometimes fascicle-like or umbel-like, others dividing in trichotomies at first branching. Flower buds sub-glabrous to densely hairy. Ovary inferior or semi-inferior, 3-locular. Nectariferous disc fleshy, covering the ovary from the insertion of the petals and stamens to the base of the style. Fruit a capsule; locules dehiscent. Seeds with endosperm. Pollen exine rugulate to fossulate-perforate. Chromosome number unknown. Tropical Africa and Madagascar. A genus of twelve species.

Some chromosome numbers were taken from Raven (1975), Darlington & Wylie (1982), Kumar & Subramaniam (1986) and Jarolimova (1994).

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