

## Phylogeny of the *Polygalaceae* and its taxonomic implications

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**Key words:** *Polygalaceae*, *Carpolobieae*, *Ancylotropis*, *Pteromonnia*. — Taxonomy, phylogeny, cladistics.

**Abstract:** The phylogeny of the *Polygalaceae* is analysed cladistically. The two tribes *Xanthophylleae* and *Moutabeae* are maintained in their former circumscription while a new tribe, the *Carpolobieae*, comprising the African genera *Carpolobia* and *Atroxima* is detached from the *Polygalaceae*. Within the *Polygalaceae*, the genera *Polygala* and *Monnina* appears to be polyphyletic. It is concluded that *Monnina* subg. *Monninopsis* and *M.* subg. *Pterocarya* are better recognized as independent genera, here described as *Ancylotropis* and *Pteromonnia*, respectively. More work needs to be done before taxonomical decisions are made regarding *Polygala*, *Bredemeyera* and *Comesperma*, which are often joined in a single genus, are found to be only distantly related.

The 17 genera of *Polygalaceae* included in this study (Table 1) represent the ones most commonly recognized as members of the family (for discussion, see Selection of taxa in Material and methods). With this circumscription the family appears to be naturally coherent (ERDTMAN 1952, LEINFELLNER 1972, STYER 1977, VERKERKE 1985).

CHODAT (1896) divided the *Polygalaceae* into three tribes, the *Polygaleae*, the *Moutabeae*, and the *Xanthophylleae*. This classification has been maintained ever since. Since CHODAT's treatment was published, three new genera have been described and the genus *Diclidanthera* transferred to the tribe *Moutabeae* and the original differential characters for the tribes have proven to be insufficient. Even the emendation of the *Moutabeae* suggested by VAN ROYEN & VAN STEENIS (1952) subsequent to the description of *Eriandra* is partly overruled by the recent addition of the genus *Balgoya* (MORAT & MEIJDEN 1991). As a matter of fact, with the present circumscription it is very difficult to point at characters unequivocally defining the tribe *Moutabeae* in relation to the *Polygaleae*. In contrast, the tribe *Xanthophylleae* with its incompletely septate fruits with more than one ovule per carpel seems well defined. Within the last 15 years the current tribal classification has been disputed. STYER (1977) found that wood anatomical evidence tied together the traditional *Moutabeae* genera but did not exclude the possibility that other genera, especially those that are lianas, would conform to this group as well. Results

Table 1. Genera included in the *Polygalaceae*, the acronyms used for each, and their intrafamilial position

Genus	Acronym	Tribus (CHODAT 1896)
<i>Atroxima</i>	ATRO	<i>Polygaleae</i>
<i>Bredemeyera</i>	BRED	—
<i>Carpolobia</i>	CARP	—
<i>Comesperma</i>	COME	—
<i>Epirixanthes</i>	EPIR	—
<i>Monnina</i> subg. <i>Monnina</i>	MONm	—
<i>M.</i> subg. <i>Monninopsis</i> CHODAT	MONi	—
<i>M.</i> subg. <i>Pterocarya</i> (DC.) CHODAT	MONp	—
<i>Muralita</i>	MURA	—
<i>Nylandtia</i>	NYLA	—
<i>Polygala</i>	POLY	—
<i>Polygala venenosa</i> JUSS.	POLv	—
<i>Salomonina</i>	SALO	—
<i>Securidaca</i>	SECU	—
<i>Balgoya</i>	BALG	<i>Moutabeae</i>
<i>Barnhartia</i>	BARN	—
<i>Diclidanthera</i>	DICL	—
<i>Eriandra</i>	ERIA	—
<i>Moutabea</i>	MOUT	—
<i>Xanthophyllum</i>	XANT	<i>Xanthophylleae</i>

from studies on ovule and seed anatomy (VERKERKE 1984, 1985, 1991) and floral vascular anatomy (ERIKSEN 1993) do not support the current tribal boundaries. Although the system has been challenged, no alternatives have so far been proposed. A cladistic analysis combining evidence from a large number of characters seems to be the best tool in an attempt to elucidate the phylogeny of the *Polygalaceae*.

My interest in the intrafamilial relationships within the *Polygalaceae* was caused by an ongoing systematic study of the genus *Monnina* and this is reflected in the aim of this study which has been to provide answers to the following questions: (1) do the results from a cladistic analysis confirm or reject the present tribal subdivision?, (2) if rejected which is the alternative system?, (3) is *Monnina* a monophyletic genus in its present circumscription?, (4) which tribe does it belong to?, and (5) which genera are the nearest relatives of *Monnina*?

### Material and methods

**Selection of taxa.** The ingroup contains taxa of which the polygalaceous nature has been substantiated. The systematic position and circumscription of the majority of genera included are unambiguous, but in the cases where taxonomists have disagreed on these matters my choice will need an explanation.

When the genus *Diclidanthera* was first described by MARTIUS in 1827 its systematic position was uncertain and over the years it has been placed in a number of different families (*Ebenaceae*, *Styraceae*, and *Sapotaceae*) and even in a family of its own, the *Diclidantheraceae*. With the discovery of the genus *Barnhartia*, described by GLEASON in

1926, its connection with the *Polygalaceae* became obvious and, supported by pollen morphological (ERDTMAN 1944) and wood anatomical (STYER 1977) evidence, its position in this family is now widely accepted. Also the genus *Xanthophyllum* has from time to time been considered to constitute a monotypic family, the *Xanthophyllaceae* as is the case in the treatment of CRONQUIST (1988). However, recent investigations on ovular ontogeny and seed coat anatomy (VERKERKE 1984), wood anatomy (BRIDGWATER & BAAS 1982), and a broad spectrum of morphological details (MEIJDEN 1982) all lead to the conclusion that there are no serious reasons to detach *Xanthophyllum* from the *Polygalaceae*.

In *Polygala* several species or species groups (either considered as sections or subgenera), have a history as independent genera (*Acanthocladus* KLOTZSCH ex HASSK., *Badiera* DC., *Polygaloides* HALLER (sect. *Chamaebuxus* DC.), *Monrosia* GRONDONA, *Phlebotaenia* GRISEB., and *Semeiocardium* HASSK.). HUTCHINSON (1967) recognized two of these, *Acanthocladus* and *Badiera*, at the generic level. BLAKE (1916) argues that "although the species groups are well defined they are so regularly graduated that the separation of any one of them would involve in consistency the recognition of all". Although an interesting issue, the infrageneric structure of *Polygala* has not been the object of this study. Material has been available of only one of the above mentioned groups, viz., *Polygala venenosa* JUSS. belonging to the sect. *Chamaebuxus* according to CHODAT (1893). This species has been treated separately and, consequently, the genus *Polygala* is taken in the strict sense.

The genera *Salomonina* and *Epirixanthes* have often been united (BENTHAM & HOOKER 1862, CHODAT 1896, HUTCHINSON 1967), and *Comesperma* has by some authors been considered as a section of *Bredemeyera* (CHODAT 1893, STEENIS 1968), but all are here treated separately in an attempt to test the mutual connexions. The two minor sections of *Bredemeyera* in the sense of STEENIS (1968), viz., *Hualania* and *Melchiora* are not included here due to lack of data. *Hualania* was accepted as a genus by HUTCHINSON (1968) and *Bredemeyera papuana* STEENIS which constitutes the sect. *Melchiora* was transferred to *Comesperma* by PEDLEY (1984).

The genus *Monnina*, which I am currently studying in greater detail, consists in its present circumscription of three subgenera which differ considerably in appearance and, above all, in fruit type. To decide whether *Monnina* is a monophyletic genus the subgenera *Pterocarya* and *Monninopsis* are treated as separate terminal taxa in the analysis. *Monnina weddelliana* CHODAT from sect. *Stipulatae* CHODAT was found to have a floral vascular anatomy similar to that of *M.* subg. *Pterocarya* (ERIKSEN 1993). In all other characters as well, it is coded for as *M.* subg. *Pterocarya*, and has, therefore, been included in that subgenus. A few other species from *M.* sect. *Stipulatae* show affinity to *M. weddelliana* but due to insufficient data on their fruit anatomy and floral vascular anatomy the systematic position of these species will not be discussed here.

The systematic position of *Emblingia*, a monotypic Australian genus, is uncertain (ERDTMAN & al. 1969) and although included in the *Polygalaceae* by CRONQUIST (1988) it is excluded from this study.

The outgroup was selected from among the families which according to CRONQUIST (1988) are most closely related: *Vochysiaceae*, *Trigoniaceae*, and *Tremandraceae*.

The *Vochysiaceae* is the largest of the families (c. 200 spp., CRONQUIST 1988) and was revised by STAFLEU (1948, 1952, 1953, 1954). The floral structure is generally extremely specialized, with a spur arising from one of the calyx lobes (KOPKA & WEBERLING 1984), often a single petal, and always only a single stamen. Comparison of the floral morphology between *Polygalaceae* and *Vochysiaceae* would involve serious difficulties.

The *Tremandraceae* is unusual in the order by having regular flowers and would in that respect be easier to deal with. However, its wood anatomy, studied by CARLQUIST (1977), is according to BRIDGWATER & BAAS (1982) indeed very different from that of the *Polygalaceae*, implying that it may not be as closely related as supposed by CRONQUIST. In many other respects the *Tremandraceae* is very poorly known.

The family finally chosen as an outgroup, the *Trigoniaceae*, is a small family consisting of 3 genera, viz., *Trigonia* (26 spp. from America), *Trigoniastrum* (1 spec. from Malaysia), and *Humbertodendron* (1 spec. from Madagascar). It has recently been monographed (LLERAS 1978) and information on ovules and seeds is provided by BOESEWINKEL (1987). Regarding wood anatomy the *Trigoniaceae* show remarkable similarities with *Xanthophyllum* (BRIDGWATER & BAAS 1982).

**Selection of characters.** The procedure of selection has in this case been a question of finding the characters for which the character state of the majority of genera could be determined. All characters found to fulfil, or nearly fulfil the following requirements are included in the matrix: (1) showing a reasonable degree of intrageneric constancy, (2) showing some intergeneric variation, and (3) data available (or could be made available) for the selected taxa.

**Data gathering.** Morphology was studied on dried specimens from the herbaria AAU, GB, GH, L, LY, MO, NY, PH, S, US (acronyms according to HOLMGREN & al. 1990). A representative material of 1–4 species from each genus was selected for direct observations and further information was obtained from the literature (see Appendix). Flowers rehydrated in water were dissected and their morphology studied under a stereo lens.

Data on floral vascular anatomy were obtained by sectioning and staining flower buds (for a detailed description of materials and methods, see ERIKSEN 1993). For determination of stomata type, dried leaves were boiled in 10% HNO<sub>3</sub> a few minutes, the lower and upper epidermis were removed and studied in light microscope. In order to supplement the chemical data on saponine content collected by KASSAU (1931), the method of RIZK (1982) was adopted with some modifications. An amount of 0.05 g dried leaf material was crushed, boiled in 5 ml distilled water in a test tube and filtered. After cooling, the extract was shaken vigorously for 15 s and allowed to rest for 15–20 min. before it was classified for saponine content (froth less than 5 mm = negative, froth more than 5 mm = positive). A list of material used for the saponine test is provided in the Appendix.

Presence or absence of aluminium was tested according to CHENERY (1948). Ca. 2.5 × 2.5 cm of dry, crushed leaf material was placed in a test tube with 1 ml of Aluminon reagent and heated for 5 min. in a boiling water bath. The Aluminon reagent consists of 0.75 g ammonium aurine tricarboxylate, 200 g ammonium acetate, 15 g gum acacia, and 189 ccm concentrated hydrochloric acid, dissolved separately, mixed and made up to 1500 ml. The reagent is bright orange and shifts to red when reacting with aluminium in the heated test tube. The material tested for aluminium content is listed in the Appendix.

**The characters.** Characters and character states used are enumerated in Table 2. Below the definition and homology of character states are discussed only for problematic characters.

**Glands.** The glands found in the *Polygalaceae* are either sessile or stalked and either discoid or crateriform (Fig. 1 A). They occur at the stem nodes (even in inflorescences) and on various parts of the leaf (petiole and blade). The shape of the glands is useful only at the specific level, whereas the position has a value at the generic level. The nodal glands have often been labelled stipules but WEBERLING (1974) has shown that they are not of stipular nature. In the *Vochysiaceae* both true stipules and nodal glands of the same type as in *Polygalaceae* occur indicating that the glands are not homologous with stipules. Consequently, all glands in the *Polygalaceae* must be interpreted as homologous structures irrespective of their position.

**Inflorescence.** Axillary inflorescences occur in all taxa to some extent, even in those having terminal inflorescences, whereas the reverse is not true. Taxa in which the growth of the axes is determinate are coded as having terminal inflorescences, and those having proliferate inflorescences or indeterminate growth of the axes as lacking terminal inflorescences.

**Calyx.** The degree of fusion of the sepals is distinct although the difference between

character state 1 “more and less free from base” and 2 “synsepalous at base” might seem vague. The majority of the taxa coded with character state 1 have their sepals completely free from base but in some species of a few genera the two abaxial sepals are connate to a varying degree. The genera with synsepalous sepals have, on the other hand, all five sepals connate, sometimes with one more profound slit abaxially (Fig. 1 B).

**Corolla.** Pentamerous corollas occur in rare cases in genera otherwise having trimerous corollas. CHODAT (1893) observed five petals in *Polygala*, and rudiments of the two lateral petals are reported for *Muraltia* (LEVYNS 1949) and *Securidaca* (KRÜGER & al. 1988). Generally, these occasional deviations from the normal state in a genus have not been considered as polymorphisms.

**Stamen number.** Variation in number of stamens within species is not uncommon but as argued above these aberrations have not affected the coding of the basic number of stamens in a genus. *Eriandra* is reported to have seven to ten stamens (ROYEN & STEENIS 1952), eight and ten stamens have been reported for *Diclidanthera* (STYER 1977), and I have observed a specimen of *Polygala* with seven stamens instead of the usual eight. In *Monnina* subg. *Pterocarya* some species have a constantly reduced number of stamens, viz. six instead of the usual eight, and the same species have in their cleistogamous flowers on the side branches the number further reduced to four. Since this autapomorphy is not important at the generic level it was disregarded in the matrix.

**Pollen grains.** The pollen grains of the *Polygalaceae* are polycolporate (Fig. 1 K), the number of colpi ranging from 7 to 21 (up to 28 reported by ERDTMAN 1952). The number of colpi is correlated with pollen grain size (LEVYNS 1954) and varies moderately even within species. No distinct classes of colpi numbers was found, and the character state limits were therefore set such that the number of multistate taxa was minimized.

**Fruit.** To determine fruit type I have relied entirely on the information given in the literature, especially on the elaborate studies on ovules and seeds by VERKERKE (1984, 1985, 1991).

**Nectary.** The nectary in *Bredemeyera*, which is situated on the staminal sheath, is unique in the family (Fig. 1 G). It might be homologous with the other nectary types but to avoid misinterpretations it has been coded as a separate character. The nectaries at the base of ovaries, irrespective of their shape, all receive their vascular support from the staminal traces (JAUCH 1918, pers. obs.) and are considered homologous (Fig. 1 L–M). There is a transition from the annular nectary through a staminal ring with a unilateral process to the entirely unilateral nectary but each step is clearly defined. Lack of nectary, on the other hand, is probably associated with a shift either in mating system (becoming autogamous) or of pollinator (to pollen-eating flies) and this state could, theoretically, arise from any of the other. Directionality has not been imposed on this character.

**Aril.** In many genera some kind of appendage is found on the seed. Three types of arils can be distinguished: (1) the exostome aril or caruncle, which is an outgrowth from the outer integument near the hilum, (2) the funicular aril, resulting from a swelling of the attached part of the funiculus, and (3) the chalazal aril, which is an outgrowth from the chalazal part of the seed coat. These structures are analogous with the common function of promoting dispersal and are, therefore, distinguished as different characters.

**Endosperm.** The endosperm amount is that of the ripe seed. The data originate from the studies of VERKERKE (1984, 1985, 1991) who distinguishes four classes of endosperm amount, viz., copious, considerable amount, scanty, and none. How this estimation was carried out is not explained but I assume that it is based on a more or less subjective judgement. In my analysis only two character states are recognized, viz., none to scanty and considerable amount to copious since the number of multistate taxa is thereby minimized.

**Endotesta cells.** According to VERKERKE (1984, 1985, 1991) endotesta cells measuring 7–30 µm are short, and those measuring 19–70 µm long. Representatives of some

Table 2. Characters and states used in the cladistic analyses

1	<b>Predominant growth habit</b> 1 – trees or shrubs 2 – herbs or subshrubs 3 – lianas	13	<b>Filaments</b> 1 – free from each other, $\pm$ united with corolla 2 – united into a tube, free from corolla 3 – united into a sheath, free from or united with corolla
2	<b>Stomata</b> 1 – paracytic 2 – anemocytic 3 – cyclocytic 4 – none	14	<b>Anther attachment</b> 1 – dorsifix 2 – basifix
3	<b>Glands</b> 1 – on leaf 2 – at nodes 3 – absent	15	<b>Number of microsporangia</b> 1 – 3- or 4 2 – 2
4	<b>Saponine content</b> 1 – saponines absent 2 – saponines present	16	<b>Anther dehiscence</b> 1 – ventral, longitudinal slit 2 – marginal slit 3 – ventral, falciform slit
5	<b>Aluminium accumulation</b> 1 – present 2 – absent	17	<b>Pollen grains</b> 1 – 3–5 porate 2 – 7–9 colporate 3 – 10–21 colporate
6	<b>Inflorescence type</b> 1 – paniculate, secondary branches racemose 2 – paniculate, secondary branches paniculate 3 – racemose 4 – single flower	18	<b>Carpel number</b> 1 – 3 2 – 2 3 – 4–5 4 – 7–8
7	<b>Presence of terminal inflorescences</b> 1 – absent 2 – present	19	<b>Ovule number per carpel</b> 1 – 1 2 – > 1
8	<b>Calyx lobes</b> 1 – lobes $\pm$ free from base 2 – synsepalous at base 3 – tubular, tube $\pm$ as long as lobes	20	<b>Fruit</b> 1 – capsule 2 – berry 3 – drupe 4 – samara
9	<b>Calyx persistence</b> 1 – calyx caducous in fruit 2 – calyx persistent in fruit	21	<b>Seed indument</b> 1 – pubescent 2 – glabrous
10	<b>Corolla merism</b> 1 – 5-merous 2 – 3-merous	22	<b>Style shape</b> 1 – straight 2 – curved or geniculate
11	<b>Corolla shape</b> 1 – abaxial petal $\pm$ flat 2 – abaxial petal boat-shaped	23	<b>Style apex and stigma</b> 1 – entire with one stigmatic area 2 – bifid with two stigmatic areas 3 – bifid with one stigmatic area
12	<b>Stamen number</b> (in <i>Trigoniaceae</i> including staminodes) 1 – 4 2 – 5 3 – 7 4 – 8–10	24	<b>Nectary on filaments</b> 1 – no 2 – yes

Table 2 (continued)

25	<b>Nectary on receptacle</b> 1 – annular 2 – annular with process 3 – unilateral 4 – none	31	<b>Inner integument of ripe seed</b> 1 – not crushed 2 – crushed
26	<b>Exostome aril</b> 1 – absent 2 – present	32	<b>Calcium oxalate crystals in seed coat</b> 1 – absent 2 – present
27	<b>Chalazal outgrowth</b> 1 – absent 2 – present	33	<b>Endotesta cells</b> 1 – short 2 – long
28	<b>Funicular aril</b> 1 – absent 2 – present	34	<b>Cotyledons</b> 1 – flat 2 – thick
29	<b>Initiation of outer integument</b> 1 – subdermally 2 – dermally	35–49	<b>Contribution of vascular strands to gynoecium/androecium from different perianth positions</b> 1 – no contribution 2 – contribution
30	<b>Endosperm</b> 1 – none to scanty 2 – considerable amount to copious		

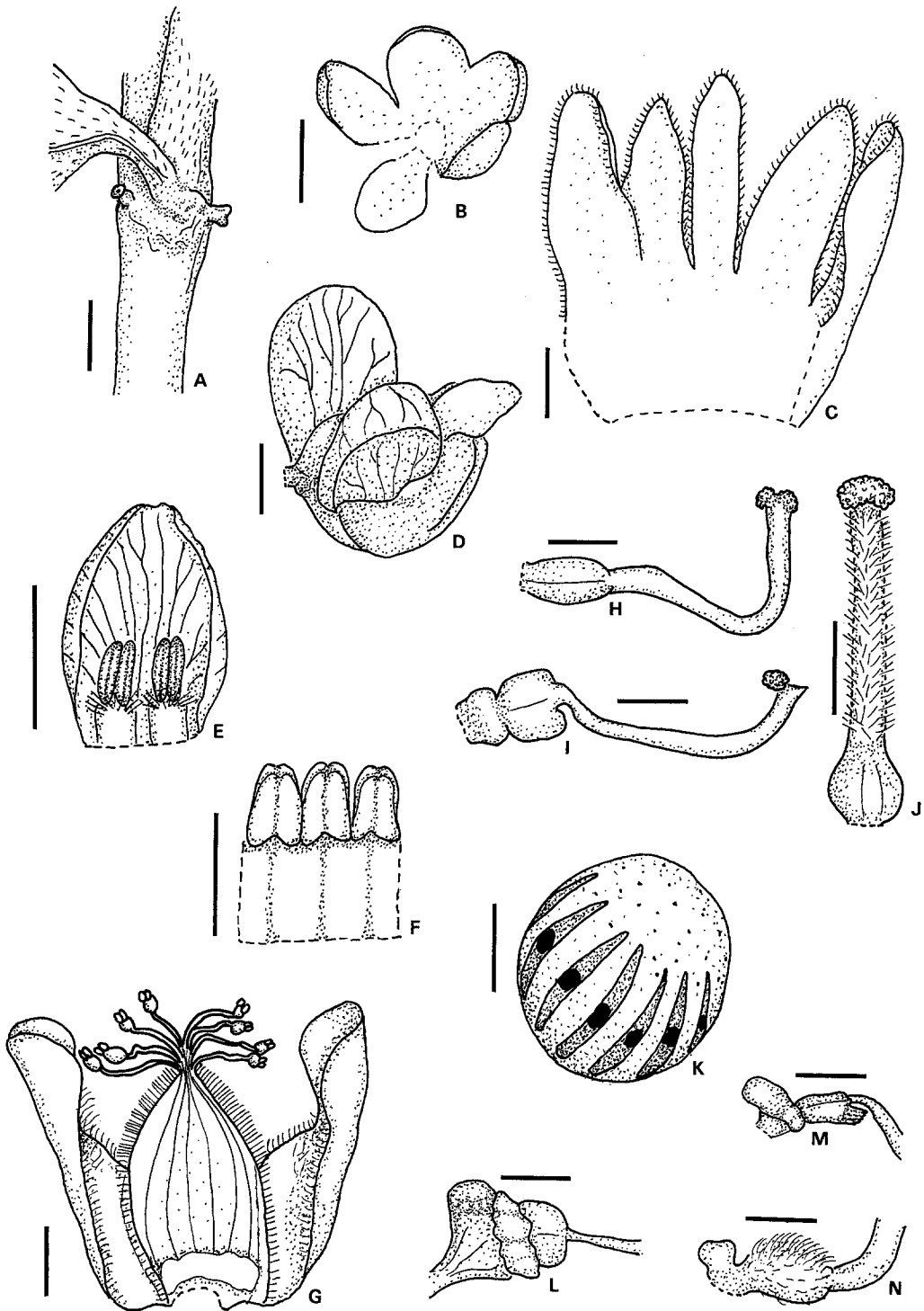
genera with endotesta cells measuring between 19 and 30  $\mu\text{m}$  are sometimes classified as short, sometimes as long, which might seem a little odd. However, the classification of endotesta cells as long or short might be a matter of relative length compared to the surrounding cells and not necessarily a reflection of their absolute length. Without further knowledge on how the delimitation was carried out, I have relied on the judgements expressed in the above mentioned papers.

**Vascular anatomy.** For each of the ten vascular strands present in the receptacle of the flowers the contributions to the vascularization of the androecium and gynoecium, respectively, have been analyzed. In all genera the strand supporting the adaxial sepal does not participate in the vascularization of any other genera. All such non-informative strands have been excluded.

**Cladistics.** Analyses were undertaken with the PAUP program (SWOFFORD 1989). Default settings were used throughout, except that multistates were interpreted as polymorphisms in accordance with character codings. No constraints were imposed on the data set. The character matrix used is given in Table 3.

In all analyses the heuristic search algorithm was applied. The general heuristic search does not necessarily find the shortest tree and if it does, all possible minimal trees might not be included. The search result often improves by selecting the random addition sequence in a number of replicates. A heuristic search with random addition sequence run in 50 replicates was applied to the data matrix.

The bootstrap method was used to give a measure on the strength of the clades. The settings were 100 replicates and simple addition sequence.





An alternative way to obtain a measure on the strength of the clades is to use the heuristic search with random addition sequence and save not only the shortest trees but also trees one or more steps longer and construct a consensus tree. The clades not collapsing in the resulting consensus tree are considered to be strong. Here all trees one and two steps longer than the shortest tree, respectively, were kept.

## Results

The heuristic search with random addition sequence resulted in six equally parsimonious trees. Two tree-islands in the sense of MADDISON (1991) were found, differing in the two clades associating the three taxa *Securidaca*, *Bredemeyera*, and *Polygala venenosa*. A representative tree from each of these two islands is shown in Figs. 2 and 3, respectively.

In the strict consensus tree of the six most parsimonious trees (Fig. 4) the topology is partly unresolved for the clade representing the majority of the tribe *Polygaleae* (except *Atoxima* and *Carpolobia*), whereas the internal topology of the tribe *Moutabeae* remains resolved. *Atoxima* and *Carpolobia* are isolated on a separate clade. The genera *Bredemeyera* and *Comesperma* do not share a common closest ancestor and uniting the two genera would result in a paraphyletic taxon. The same could be argued for *Salomonina* and *Epirixanthes* and the three subgenera of *Monnina*.

The strength of the clades turned out to be quite low. In the 50% majority rule bootstrap consensus tree the basal clades upheld are those comprising the genera *Atoxima* and *Carpolobia* (98%), the tribe *Polygaleae* s. str. (52%), and the tribes *Moutabeae* and *Xanthophylleae* (49%), respectively. Among terminal clades, the

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Fig. 1. Details of vegetative and floral morphology. The numbers in brackets refer to character states. *A Monnina weddelliana* CHODAT (LUTEYN & DORR 13600, GB) showing nodal glands (3 : 2). *B Eriandra fragrans* VAN ROYEN & VAN STEENIS (STEVENS 54706, L) showing a basally synsepalous calyx (8 : 2). *C Diclidanthera elliptica* MIERS (GARDNER 5002, US, isosyntype) showing a tubular calyx (8 : 3). *D Monnina arbuscula* CHODAT (MOLAU & ERIKSEN 2797, GB) showing an entire flower with a calyx with five free lobes, and a trimerous corolla with a boat-shaped abaxial petal (8 : 1, 10 : 2, 11 : 1). *E Xanthophyllum exelsum* BLUME ex MIQ. (anonymous s.n., S) showing a petal with two adnate but mutually free filaments, and longitudinally dehiscent anthers (13 : 1, 16 : 1). *F Balgoya pacifica* MORAT & MEIJDEN (redrawn from MORAT & MEIJDEN 1991, Fig. 1: 8) showing filaments united into a tube, and anthers opening by marginal slits (13 : 2, 16 : 2). *G-H Bredemeyera laurifolia* (ST. HIL. & MOÇ.) KLOTZSCH ex A. W. BENN. (PABST 4395, AAU). *G* showing the petal-stamen sheath with a nectary at base, and anthers dehiscing by short, falciform slits resulting in pore-like openings (13 : 3, 16 : 3, 24 : 2), *H* showing a geniculate, apically bifid style with two stigmatic areas (22 : 2, 23 : 2). *I Comesperma flava* DC. (STRID 21496, S) showing a curved, apically bifid style with one stigmatic area (22 : 2, 23 : 1). *J Barnhartia floribunda* GLEASON (SANDWICH 507, S) showing a straight, apically entire style with one stigmatic area (22 : 1, 23 : 1). *K Monnina denticulata* CHODAT (HARLING & ANDERSSON 14297, GB) showing a 15-colporate pollen grain (17 : 3). *L Polygala venenosa* JUSS. (MODIGLIANI s.n., LY) showing an annular disc (25 : 1). *M Securidaca* spec. (BRANDBYGE & al. 36151, AAU) showing an annular disc with a unilateral process (25 : 2). *N Monnina parviflora* (BONPL.) H. B. K. (CLEEF 2707, US) showing a unilateral nectary (25 : 3). Bars: *A, C, D*: 2 mm, *B*: 5 mm, *E-J, L-N*: 1 mm, *K*: 1  $\mu$ m



clades including *Diclidanthera* and *Eriandra* (52%) and *Muraltia* and *Nylandtia* (71%) are relatively strong.

Frequencies, listed in the bootstrap frequency table, have been applied to the clades in the strict consensus tree from the heuristic search (Fig. 4). This is done

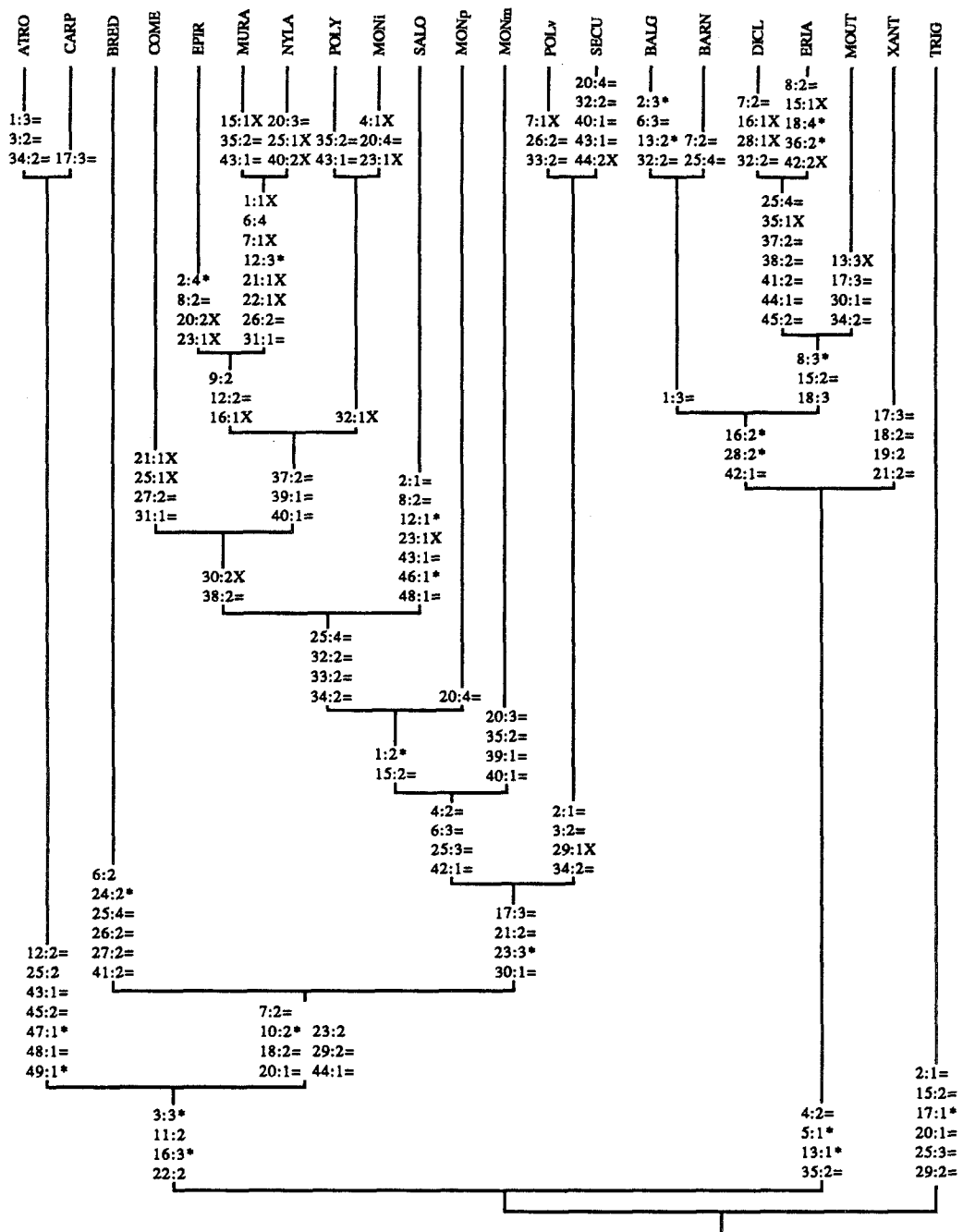


Fig. 2. Tree no. 2 of six equally parsimonious trees. *Polygala venenosa* and *Securidaca* occurring on a terminal clade. The symbols following each character state are \* apomorphy, = parallelism, X reversal, character states not followed by a symbol occur as transformations on internal nodes in terminal taxa

with the purpose of visualizing the weak points in the topology of the tree. It must be emphasized that many of the clades in this strict consensus tree are otherwise contradicted and, therefore, not included in the bootstrap consensus tree.

Saving all trees which are two steps longer than the shortest tree or shorter results in a strict consensus tree with a single clade, viz. the one including *Atoxima* and *Carpolobia*. The strict consensus tree of all trees which are one step longer

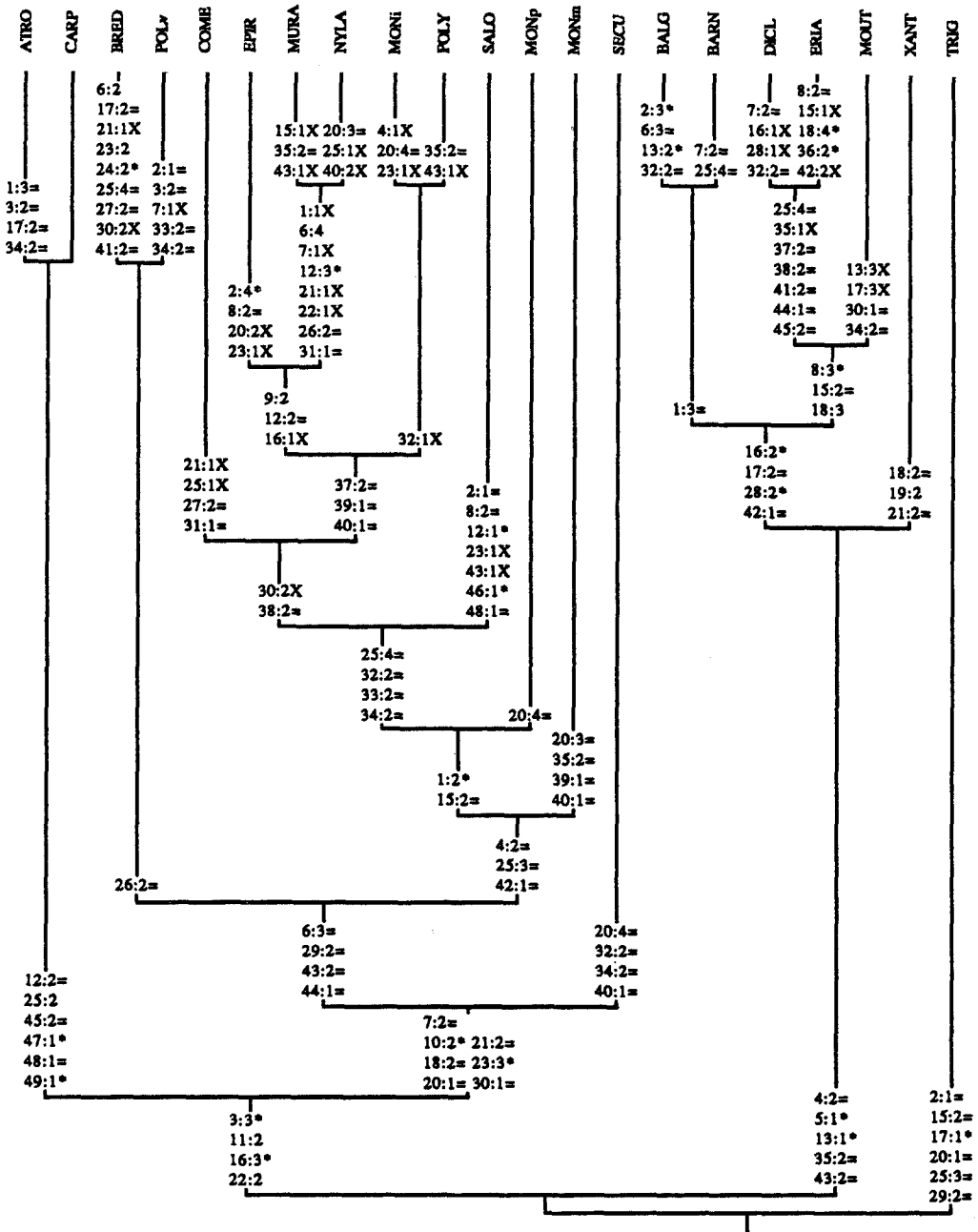


Fig. 3. Tree no. 5 of six equally parsimonious trees. *Polygala venenosa* is occurring on the same terminal clade as *Bredemeyera*. Symbols as in Fig. 2

than the shortest tree or shorter comprises one additional clade, viz., the remaining part of the tribe *Polygaleae*.

### Conclusion

The result of the cladistical analysis is not contradictory to the present tribal subdivision. On the other hand, the stability of most of the clades is low, and it cannot be excluded that the addition of a single conflicting character will change the topology of the consensus tree radically. Yet, to maintain the present tribes as the backbone in the systematic subdivision of the family seems to be the most appropriate solution until further data has accumulated. That the classification remains unaltered might seem strange since it has been challenged independently by VERKERKE (1985) and ERIKSEN (1993). However, the results obtained in the two studies are pointing in different directions. The tribes are reflecting floral morphology remarkably well. However, even when excluding all characters associated with floral morphology (characters 8, 10–13, 22–25, and 44–49) and analyzing the reduced matrix the boundaries of all tribes except *Xanthophylleae* remains unchanged. It is interesting to note that by disregarding the floral characters the association of the tribes is reversed. *Xanthophyllum* appears at an internal node in the *Polygaleae* associated with *Securidaca* and *Polygala venenosa* instead of close to the *Moutabea* and the *Moutabeae* becomes the sister group of *Atroxima* and *Carpolobia*.

According to the strict consensus tree the sister group of the genus *Xanthophyllum* is the tribe *Moutabeae* and the tree topology does not contradict a union of the two tribes *Xanthophylleae* and *Moutabeae*. However, the tribal status of *Xanthophylleae* is justified by a number of autapomorphies in the gynoecial structure, especially ovule number and ovary septation. LEINFELLNER (1972) found that the symplicate zone of the ovary is fertile and the symmarginal vascular bundle is inversed in the *Xanthophylleae*, whereas in the other tribes the synascidiate zone is fertile and the symmarginalis is normal. Furthermore, the wood anatomical structure of *Xanthophyllum* is somewhat different from that of the other tribes (BRIDGWATER & BAAS 1982).

The relationships among the *Moutabeae* genera are quite uncertain. Only *Diclidanthera* and *Eriandra* seems to be tied together more tightly. The conclusion drawn by ROYEN & STEENIS (1952) that “their conformity is different when different characters are chosen for comparison” is probably exactly what is reflected in the results of this analysis. Ignoring the recently described genus *Balgoya*, their final conclusion regarding the mutual affinities of the genera are consistent with my result as well. However, a different conclusion was reached in a study on wood anatomy (STYER 1977). *Eriandra* was found to be divergent from *Barnhartia*, *Diclidanthera* and *Moutabea*, and *Barhartia* found to be most closely related to *Diclidanthera*. Wood anatomical data were not included in the matrix in this analysis due to lack of information on particularly the tribe *Polygaleae*. The internal structure of the *Moutabeae* clade might change with the inclusion of these characters. The wood anatomy of *Balgoya* shows several similarities with the genera *Moutabea*, *Xanthophyllum*, and *Securidaca* (DÉTIENNE 1991). This is not consistent with any of the classifications suggested above and only adds to the confusion.

There is not much doubt that the two genera *Atroxima* and *Carpolobia* warrant

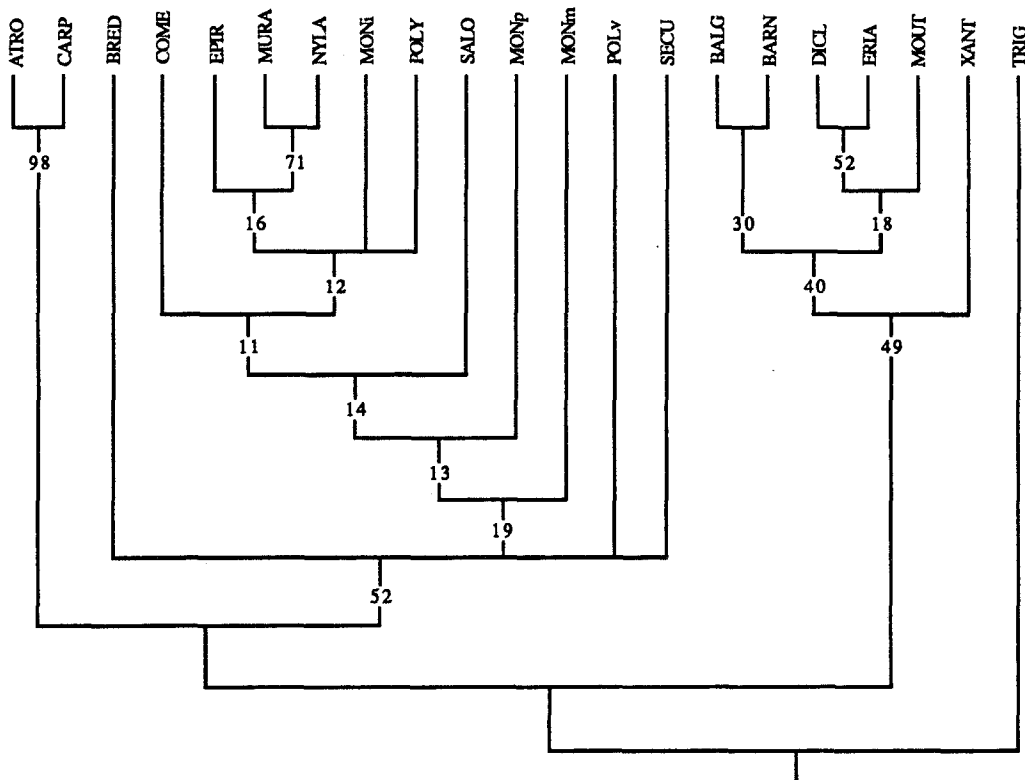


Fig. 4. Strict consensus tree of six equally parsimonious trees. The numbers indicate the frequency of occurrence of the clades in the bootstrap analysis. Some of the clades do not appear in the bootstrap consensus tree

being placed in a tribe separate from *Polygaleae*. In the taxonomic revision of the two genera (BRETELER & SMISSAERT-HOUWING 1977) the possibility of such a separation was never discussed but it turns out to be the most reliable implication of this analysis. It is the most stable clade in both of the stability tests. This new tribe differs from *Polygaleae* in fruit type, seed anatomy, corolla merism, and number of stamens (with the exception of *Epirixanthes*).

The tribe *Polygaleae* s. str., to which *Monnina* belongs, is not very well resolved (Fig. 4). Only the relation between *Muraltia* and *Nylandtia* is confirmed with conviction in the bootstrap test. My results do not support the union of the genera *Comesperma* and *Bredemeyera* but it must be emphasized that the sections *Hualania* and *Melchiora*, which are somewhat intermediate between the two genera in a number of characters, are not included in the analysis. Without considering all taxa of the complex a reliable classification is not obtained. *Salomonina* and *Epirixanthes*, the second pair of genera often united, do not share a common closest ancestor in the strict consensus tree. However, the two taxa appear together in the bootstrap consensus tree with a frequency of 0.60 indicating that they may be closer than indicated by the strict consensus tree. Summarizing, this analysis does not settle the question whether *Salomonina* and *Epirixanthes* should be joined or not.

It is very interesting to note that *Polygala venenosa* does not at all appear in the *Polygala* complex but rather together with either *Securidaca* or *Bredemeyera*, implying that a polyphyletic origin of *Polygala* s.l. is possible. It would be appropriate and necessary to look over the systematics of the entire genus before any decisions are made.

The results of the analysis shows that the genus *Monnina* is polyphyletic in its present circumscription, and yet the question of origin is not that straight forward. Tree topology is not very strong in this part and taxonomical conclusions must be drawn with caution. In the bootstrap consensus tree *Polygala* and *Monnina* subg. *Monnina* occur in the same terminal clade with a frequency of 0.15. That the two taxa are very similar is reflected in the number of common character states: of 49 characters the harmony is complete in 30 while as many as 44 characters are in accordance when those showing polymorphism in one or the other taxa are included. Differences in fruit type, occurrence of an arillus, and vascularization of the gynoecium are the only characters unequivocally separating the two. Consequently, these must be considered as key characters in the following evaluation.

The characters separating the clade including *Polygala* from *Monnina* subg. *Monnina* in the cladogram are the habit and the number of microsporangia. However, both of these characters are changing states towards the terminal taxa and thus the *Polygala* complex is only weakly supported. The annual habit is probably strongly correlated with a more autogamous mating system where pollen number, and thereby the number of microsporangia necessary, is lower. Such correlation diminishes the individual force of characters. The clade supporting the *Polygala* complex tends to collapse resulting in a trichotomy with *Monnina* subg. *Monnina*, *M.* subg. *Pterocarya*, and the remaining *Polygala* complex.

With a frequency of 0.15 *Monnina* subg. *Pterocarya* appears together with *M.* subg. *Monninopsis* in the bootstrap consensus tree. The two taxa are differing in stigma type, occurrence of a disc, and vascularization of the gynoecium, but share the samaroid fruit type. Reverting to the key characters, the subgenus *Monninopsis* is similar to *Polygala* and subg. *Pterocarya* to subg. *Monnina* in disc type and vascularization while they are differing from both *Polygala* and subg. *Monnina* in their fruit type. *Monnina* subg. *Monninopsis* is more strongly tied to the *Polygala* clade than to *Monnina* and although the strict consensus tree shows that its position is not quite clear, its separation from the rest of *Monnina* is a fact.

Assuming that subg. *Monninopsis* evolved from the *Polygala* line and subg. *Pterocarya* from the *Monnina* line, their position in the hierarchy should follow the existing taxonomical level of the group they belong to. In the *Polygaleae* the most important differential characters were found to be associated with fruits and seeds as well as with vascular anatomy of the flower. Since subg. *Monninopsis* differs from *Polygala* and subg. *Pterocarya* from the remaining part of *Monnina* in these characters both warrant being placed in genera of their own.

### Survey of systematic implications

A new tribe accomodating the two African genera *Atroxima* and *Carpolobia* is herewith proposed.

***Carpolobieae* ERIKSEN, trib. *Polygalacearum* nov.** — Type: *Carpolobia* G. DON.

Arbores, frutices vel lianae, inflorescentiis racemosis simplicibus vel compositis.

Flores irregulares, sepalis quinque liberis, petalis quinque longitudine plus minusve aequalibus, petalo abaxiali concavo (carina). Stamina quinque monadelphica, filamentis in vagina aperta connatis, antheris per rimas breves dehiscentibus. Stylus teres, curvatus, apice integro, stigmatibus capitatis. Ovarium trilobulatum, ovulo in quoque loculo singulari. Fructus baccatus, seminibus pubescentibus.

Trees, shrubs, or lianas. Leaves alternate, with or without nodal glands. Stems and branches glabrous or provided with simple, white hairs. Laminae simple, pinnately veined, entire. Flowers arranged in axillary, simple or compound racemes, each subtended by a bract and two bracteoles, irregular; sepals 5, free, equal in shape but lateral ones slight larger; petals 5, more or less equally long, the abaxial one concave (keel), the others narrowly elliptic, the basal part of all petals adnate to the staminal sheath. Stamens 5, monadelphous, the filaments united for most or all of their length into an adaxially open sheath; anthers opening by short, falciform slits; style terete, gently curved, apically undivided, the stigma capitate. Ovary 3-locular with one ovule in each locule, subtended by an adaxially enlarged disc. Fruit a berry, the seeds covered with erect and juicy or undulate and dry hairs.

Genera included: *Carpolobia* and *Atroxima*.

The tribes of *Polygalaceae* can be distinguished as follows:

- 1 a. Ovary 2-carpellate, sometimes pseudomonomerous
  - 2 a. One ovule per fertile locule, corolla 3-merous ..... *Polygaleae*
  - 2 b. More than one ovule per fertile locule, corolla 5-merous .....  
..... *Xanthophylleae*
- 1 b. Ovary 3–8-carpellate
  - 3 a. Abaxial petal concave (keel), anthers 5 ..... *Carpolobieae*
  - 3 b. Abaxial petal not concave, anthers 8–10 ..... *Moutabeae*

In the tribe *Polygaleae* the ranks of two taxa, *Monnina* subg. *Monninopsis* and *M.* subg. *Pterocarya*, are changed.

***Ancylotropis* ERIKSEN, gen. nov.** — Type: *Monnina insignis* A. W. BENN.

*Monnina* subg. *Monninopsis* CHODAT, Bull. Herb. Boissier 4: 253 (1896).

Plantae herbaceae, inflorescentiis simplicibus racemosis. Sepala inferiora plus-minusve connata, sepala lateralia aliformia, carina geniculata basi breviter unguiculata, limbo profunde tripartito. Stylus teres, tenuis, geniculatus, apice integro, stigmatibus sessilibus. Fructus indehiscens siccus alatus vel exalatus, bilocularis vel abortu subunilocularis, sepalis caducis.

Annual herbs. Leaves alternate, short-petiolate, without nodal glands. Stems and branches terete, provided with white, unicellular hairs. Laminae simple, pinnately veined, entire. Flowers arranged in simple racemes, each subtended by a bract and two bracteoles, irregular; outer sepals 3, small, herbaceous, the lower two more or less connate at base; inner sepals (wings) 2, large, lateral, petaloid; petals 3, the lower (keel) carinate, geniculate, the limb profoundly tripartite, the upper petals short, united in their lower part with the filament sheath (see below), but free from each other, forming a conduplicate petal-stamen sheath; stamens diadelphous, 8, the filaments fused into a filament sheath to which lateral margins the upper petals are adnate; style terete, delicate, geniculate, entire and hirsute at apex; stigma sessile. Ovary 2-locular, one locule sometimes abortive, at base without nectary. Fruits regularly winged or wingless samaras, the calyx caducous.



Species included:

***Ancylotropis insignis* (A. W. BENN.) ERIKSEN, comb. nova.** — Basionym: *Monnina insignis* A. W. BENN., in MARTIUS (Ed.): Fl. Bras. 13 (3): 56 (1874). — *Monnina piauhensis* CHODAT, Bull. Herb. Boissier 3: 541 (1895).

***Acylostropis malmeana* (CHODAT) ERIKSEN, comb. nova.** — Basionym: *Monnina malmeana* CHODAT, Bull. Herb. Boissier 3: 540 (1895).

***Pteromonnina* ERIKSEN, gen. nov.** — Type: *Monnina pterocarpa* RUIZ & PAV.

*Monnina* sect. *Pterocarya* DC., Prodr. 1: 340 (1824). — *Monnina* subg. *Pterocarya* (DC.) CHODAT, Bull. Herb. Boissier 4: 251 (1896).

Herbae annuae vel perennes, inflorescentiis simplicibus racemosis. Sepala libera vel raro duo inferiora basi breviter connata, sepala lateralia aliformia, carina leniter curvata, apice parum trilobata. Stylus compressus, curvatus vel geniculatus, apice bipartito, lobo superio stigma ferente. Fructus indehiscens siccus alatus vel exalatus, bilocularis vel abortu subunilocularis, sepalis caducis.

Annual or perennial herbs. Leaves alternate, short-petiolate to sessile, with or without nodal glands. Stems and branches terete, covered by unicellular hairs, either white, conical and curved or compressed and straight, or yellowish with knoblike thickenings on its outer side and  $\pm$  straight. Laminae simple, pinnately veined, entire or rarely undulate. Flowers arranged in simple racemes, each subtended by a bract and two bracteoles, irregular; outer sepals 3, small, herbaceous, free or rarely the lower two shortly connate at base; inner sepals (wings) 2, large, lateral, petaloid; petals 3, the lower (keel) carinate, the upper two united in their lower part with the filament sheath (see below), but free from each other, forming a conduplicate petal-stamen sheath; stamens diadelphous, (4-)6-8, the filaments fused for most or all of their length into a filament sheath to which lateral margins the upper petals are adnate; style compressed, geniculate to gently curved, apically unequally cleft, the upper lobe with a sessile or  $\pm$  stalked capitate or discoid stigma, the lower lobe sterile, often forming a tooth. Ovary 1- or 2-locular, subtended by a gland enlarged toward the adaxial side into a knoblike process. Fruit a regularly or irregularly winged, or occasionally wingless samara.

Species included: **Without nodal glands:**

***Pteromonnina amarella* (CHODAT) ERIKSEN, comb. nova.** — Basionym: *Monnina amarella* CHODAT, Bull. Soc. Bot. Genève sér. 2, 25: 200 (1934).

***Pteromonnina cardiocarpa* (ST. HIL.) ERIKSEN, comb. nova.** — Basionym: *Monnina cardiocarpa* ST. HIL., Fl. Bras. Merid. 2: 60 (1829).

***Pteromonnina dictyocarpa* (GRISEB.) ERIKSEN, comb. nova.** — Basionym: *Monnina dictyocarpa* GRISEB., Abh. Königl. Ges. Wiss. Göttingen 24: 23 (1879). — *M. argentina* I. M. JOHNST., Contr. Gray Herb. 81: 92 (1928). — *M. wilczekiana* CHODAT, Bull. Herb. Boissier sér. 2, 2: 531 (1902).

***Pteromonnina filifolia* (CHODAT) ERIKSEN, comb. nova.** — Basionym: *Monnina filifolia* CHODAT, Bull. Soc. Bot. Genève sér. 2, 25: 198 (1934).

***Pteromonnina fosbergii* (FERREYRA) ERIKSEN, comb. nova.** — Basionym: *Monnina fosbergii* FERREYRA, Phytologia 69: 356 (1990).

***Pteromonnina leptostachya* (BENTH.) ERIKSEN, comb. nova.** — Basionym: *Monnina leptostachya* BENTH., Pl. Hartw.: 125 (1845).

***Pteromonnina linearifolia* (RUIZ & PAV.) ERIKSEN, comb. nova.** — Basionym: *Monnina linearifolia* RUIZ & PAV., Syst. Veg. Fl. Peruv. Chil. 1: 173 (1798).

***Pteromonnina lorenziana* (CHODAT) ERIKSEN, comb. nova.** — Basionym: *Monnina lorenziana* CHODAT, Bull. Herb. Boissier 2: 168 (1894). — *M. humahuaquensis* GRONDONA, Darwiniana 7: 14 (1945). — *M. pumila* FERREYRA, Bol. Dir. Gen. Agric. Peru 17: 123 (1945).

***Pteromonnina macbridei* (CHODAT) ERIKSEN, comb. nova.** — Basionym: *Monnina macbridei* CHODAT, Bull. Soc. Bot. Genève sér. 2, 25: 199 (1934).

***Pteromonnina macrostachya* (RUIZ & PAV.) ERIKSEN, comb. nova.** — Basionym: *Monnina macrostachya* RUIZ & PAV., Revis. Gen. Pl. 3 (2): 10 (1898). — *M. arenicola* FERREYRA, J. Arnold Arbor. 27: 137 (1946). — *M. lanceolata* (POIR.) DC., Prodr. 1: 339 (1824). Basionym: *Polygala lanceolata* POIR., Encycl. 5: 498 (1804). — *Monnina weberbaueri* CHODAT, Bot. Jahrb. Syst. 42: 102 (1909). — *M. weberbaueri* var. *elongata* CHODAT, Bot. Jahrb. Syst. 42: 102 (1909). — *M. weberbaueri* var. *maxima* CHODAT, Bot. Jahrb. Syst. 42: 102 (1909). — *M. weberbaueri* var. *pachyantha* CHODAT, Bot. Jahrb. Syst. 42: 102 (1909). — *M. macrostachya* var. *pumila* A. GRAY, United States exploring expedition, botany, phanerogamia part I 15: 107 (1854).

***Pteromonnina philippiana* (CHODAT) ERIKSEN, comb. nova.** — Basionym: *Monnina philippiana* CHODAT, Bull. Herb. Boissier 2: 169 (1894).

***Pteromonnina polygonoides* (CHODAT) ERIKSEN, comb. nova.** — Basionym: *Monnina polygonoides* CHODAT, Bull. Soc. Bot. Genève sér. 2, 25: 200 (1934).

***Pteromonnina ramosa* (I. M. JOHNST.) ERIKSEN, comb. nova.** — Basionym: *Monnina ramosa* I. M. JOHNST., Contr. Gray Herb. 70: 77 (1924).

***Pteromonnina resedoides* (ST. HIL.) ERIKSEN, comb. nova.** — Basionym: *Monnina resedoides* ST. HIL., Fl. Bras. Merid. 2: 61 (1829).

***Pteromonnina rugosa* (CHODAT) ERIKSEN, comb. nova.** — Basionym: *Monnina rugosa* CHODAT, Bull. Herb. Boissier 4: 251 (1896).

***Pteromonnina rusbyi* (CHODAT) ERIKSEN, comb. nova.** — Basionym: *Monnina rusbyi* CHODAT, Mem. Torrey Bot. Club 6: 6 (1890).

***Pteromonnina wrightii* (A. GRAY) ERIKSEN, comb. nova.** — Basionym: *Monnina wrightii* A. GRAY, Pl. Wright. 2: 31 (1853). — *M. brachystachya* GRISEB., Abh. Königl. Ges. Wiss. Göttingen 19: 75 (1874). — *M. eriocarpa* CHODAT, Meded. Rijks-Herb. 27: 29 (1915). — *M. macrostachya* var. *stenophylla* O. KTZE., Revis. Gen. Pl. 3 (2): 10 (1898).

#### With nodal glands:

***Pteromonnina exalata* (A. W. BENN.) ERIKSEN, comb. nova.** — Basionym: *Monnina exalata* A. W. BENN., in MARTIUS (Ed.): Fl. Bras. 13 (3): 59 (1874). — *M. oblongifolia* ARECHAV., Anales Mus. Nac. Montevideo 4 (1): 8 (1902).

***Pteromonnina herbacea* (DC.) ERIKSEN, comb. nova.** — Basionym: *Monnina herbacea* DC., Prodr. 1: 340 (1824). — *M. graminea* CHODAT, Bot. Jahrb. Syst. 42: 103 (1909). — *M. spruceana* CHODAT, Bull. Herb. Boissier 2: 167 (1894).

***Pteromonnina macrocarpa* (CHODAT) ERIKSEN, comb. nova.** — Basionym: *Monnina macrocarpa* CHODAT, Bull. Herb. Boissier 4: 252 (1896).

***Pteromonnina pterocarpa* (RUIZ & PAV.) ERIKSEN, comb. nova.** — Basionym: *Monnina pterocarpa* RUIZ & PAV., Syst. Veg. Fl. Peruv. Chil. 1: 174 (1798). — *M. angustifolia* DC., Prodr. 1: 340 (1824). — *M. chanduyensis* CHODAT, Bull. Herb. Boissier 2: 167 (1894). — *M. pterocarpa* var. *exauriculata* CHODAT, Bull. Soc. Bot. Genève sér. 2, 25: 202 (1934).

***Pteromonnina retusa* (K. PRESL) ERIKSEN, comb. nova.** — Basionym: *Monnina retusa* K. PRESL, Reliq. Haenk. 2: 102 (1831). — *M. cuneata* ST. HIL., Fl. Bras. Merid. 2: 62 (1829). — *M. emarginata* ST. HIL., Fl. Bras. Merid. 2: 63 (1829). — *M. hilairiana* KLOTZSCH ex. HASSK. in MIQUEL, Ann. Mus. Bot. Lugduno-Batavum 1: 192 (1863). — *M. intermedia* ARECHAV., Anales Mus. Nac. Montevideo 4 (1): 10 (1902). — *M. ramosissima* ARECHAV., Anales Mus. Nac. Montevideo 4 (1): 11 (1902).

***Pteromonnina richardiana* (ST. HIL.) ERIKSEN, comb. nova.** — Basionym: *Monnina richardiana* ST. HIL., Fl. Bras. Merid. 2: 66 (1829). — *M. cordata* KLOTZSCH ex. HASSK. in MIQUEL, Ann. Mus. Bot. Lugduno-Batavum 1: 192 (1863). — *M. martiana* KLOTZSCH ex. A. W. BENN. in MARTIUS (Ed.): Fl. Bras. 13 (3): 59 (1874).

***Pteromonnina stenophylla* (ST. HIL.) ERIKSEN, comb. nova.** — Basionym: *Monnina stenophylla* ST. HIL., Fl. Bras. Merid. 2: 64 (1829).

***Pteromonnina tristaniana* (ST. HIL.) ERIKSEN, comb. nova.** — Basionym: *Monnina tristaniana* ST. HIL., Fl. Bras. Merid. 2: 65 (1829). — *M. tristaniana* var. *robusta* CHODAT, Bull. Herb. Boissier sér. 2, 1: 436 (1901). — *M. mucronata* ARECHAV., Anales Mus. Nac. Montevideo 4 (1): 9 (1902). — *M. offersiana* KLOTZSCH ex. HASSK. in MIQUEL, Ann. Mus. Bot. Lugduno-Batavum 1: 192 (1863). — *M. virescens* ARECHAV., Anales Mus. Nac. Montevideo 4 (1): 9 (1902).

***Pteromonnina weddelliana* (CHODAT) ERIKSEN, comb. nova.** — Basionym: *Monnina weddelliana* CHODAT, Bull. Herb. Boissier 4: 244 (1896). — *M. nigrescens* RUSBY, Bull. New York Bot. Gard. 4: 324 (1907).

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Appendix. Sources of information. For each taxon (acronyms defined in Table 1) the main source of information is given in brackets. In those cases information is taken from specific treatments, which are mainly studies on anatomical evidence, the character in question is given by its number followed by the reference

ATRO (BRETELER & SMISSAERT-HOUWING 1977) 20, 31–33: VERKERKE (1985). — BALG (MORAT & MEIJDEN 1991) 2: BAAS (1991); 21, 29–33: VERKERKE (1991). — BARN (STYER 1977) 2: STYER (1977). — BRED (MENDES MARQUES 1980, STEENIS 1968) 2: METCALFE & CHALK (1967); 9: KASSAU (1931); 28–33: VERKERKE (1985). — CARP (BRETELER & SMISSAERT-HOUWING 1977) 2: METCALFE & CHALK (1967); 20, 28–33: VERKERKE (1985). — COME (PEDLEY 1984) 28–33: VERKERKE (1985). — DICL (STYER 1977) 2: STYER (1977); 20, 28–29, 31–33: VERKERKE (1985). — EPIR (PENZIG 1901, WIRZ 1910) 28–33: VERKERKE (1985). — ERIA (ROYEN & STEENIS 1952) 2: STYER (1977); 3: MEIJDEN (1982); 29–33: VERKERKE (1985). — MON(m, i, p) 2: MENDES MARQUES (1989), subg. *Pterocarya*; 28–33: VERKERKE (1985). — MOUT (STYER 1977) 7, 9: AUBLET (1775); 20, 28–33: VERKERKE (1985). — MURA (LEVYNS 1954) 2: METCALFE & CHALK (1967); 29–30, 33: VERKERKE (1985); 32: RODRIGUE (1893). — NYLA 2: METCALFE & CHALK (1967); 20, 29–33: VERKERKE (1985). — POLY (CHODAT 1893, BLAKE 1916) 2: METCALFE & CHALK (1967); 28–33: VERKERKE (1985). — POLV (CHODAT 1893) 29: HASSKARL (1842); 32–33: VERKERKE (1985). — SALO (LOUREIRO 1790, SUMITHRAARACHCHI 1987) 29–33: VERKERKE (1985). — SECU (JOHNSON 1987, African spp.) 2: METCALFE & CHALK (1967); 17: COETZEE & ROBBERTSE (1985, African spp.); 23: KRÜGER & al. (1988); 28–33: VERKERKE (1985). — XANT (MEIJDEN 1982) 2: METCALFE & CHALK (1967); 25–27: VERKERKE (1985); 28–33: VERKERKE (1984). — TRIG (LLERAS 1978, AUSTIN 1967) 28–33: BOESEWINKEL (1987).

Data on saponine content are taken from KASSAU (1931) and on aluminium accumulation from CHENERY (1948). Complementary test were made where data was missing.

The saponine test was conducted on the following material: *Atroxima afzeliana* (OLIV. ex CHODAT) STAPF, ZENKER 1654 (L), *A. liberica* STAPF, sine coll. 8248 (L); *Barnhartia floribunda* GLEASON, SANDWICH 507 (S); *Diclidanthera penduliflora* MART., GENTRY & al. 18430 (AAU); *Eriandra fragrans* VAN ROYEN & VAN STEENIS, RISDALE & GALORE 33494 (L); *Polygala venenosa* JUSS., MODIGLIANI s.n. (LY); *Trigonia paniculata* WARMING, MEXIA 4705 (GB).

The specimens tested for aluminium content were: *Atroxima afzeliana* (OLIV. ex CHODAT) STAPF, ZENKER 1654 (L), *A. liberica* STAPF, sine coll. 8248 (L); *Barnhartia floribunda* GLEASON, SANDWICH 507 (S); *Bredemeyera barbeyana* CHODAT, HATSCHBACH 42931 (AAU), *B. laurifolia* (ST. HIL. & MOÇ.) KLOTZSCH ex A. W. BENN., PABST 4395 (AAU), *B. velutina* A. W. BENN., PEREIRA 638 (AAU), *Bredemeyera* spec., TORRES 493 (ECON); *Carpolobia alba* G. DON, DE GIORGI 1610 (S); *Comesperma ericinum* DC., HUBBARD 3785 (S), *C. flavum* DC., STRID 21197 (S); *Diclidanthera elliptica* MIERS, GARDNER 5002 (US), *D. penduliflora* MART., GENTRY & al. 18430 (AAU); *Eriandra fragrans* VAN ROYEN & VAN STEENIS, RISDALE & GALORE 33494 (L); subg. *Monnina*: *Monnina crassifolia* H. B. K., MOLAU & ÖHMAN 1256 (GB), *M. pachycoma* CHODAT, WEST 7036 (GH), *M. pilosa* H. B. K., HARLING 25283 (GB), *M. pseudopilosa* FERREYRA, HUMBLER 6245 (MO), *M. speciosa* TR. & PL., MCPHERSON 13011 (GB), *M. subspeciosa* CHODAT, MOLAU & ERIKSEN 2159 (GB), *M. trichoptera* DIELS, HARLING & ANDERSSON 13883 (GB), *M. weddelliana* CHODAT, BUCHTIEN 182 (US), *Monnina* spec., MOLAU & ERIKSEN 2271 (GB), subg. *Monninopsis*: *M. insignis* A. W. BENN., HARLEY 21500 (US), subg. *Pterocarya*: *M. exalata* A. W. BENN., IRWIN & al. 8207 (US), *M. leptostachya* BENTH., HARLING & ANDERSSON 13550 (GB); *Moutabea* spec., WURDACK & MONACHINO 41141 (AAU); *Muraltia heisteria* (L.) DC., SIDEY 2165 (S); *Nylandtia spinosa* (L.) DUMOR., WALL s.n. (S); *Polygala oleaefolia* ST. HIL. & MOÇ., HATSCHBACH & KOCZICKI 975 (AAU), *P. paniculata* L., HOLM-NIELSEN & al. 4485 (AAU), *P. venenosa* JUSS., MODIGLIANI s.n. (LY), *Polygala* spec., REYNEL & al. 5226 (GB); *Salomonina cantoniensis* LOUR., MÖLLER s.n. (S), *S. ovalifolia*?, KJELLBERG 2238 (S); *Securidaca* spec., CROAT 20450 (MO), *Securidaca* spec., BRANDBYGE & al. 36151 (AAU), *Securidaca* spec., GENTRY & DALY 18342 (MO); *Xanthophyllum exelsum* BLUME ex MIQ., coll. unknown s.n. (S), *X. gracile* CHODAT, JACOBS 5370 (S), *X. vitellinum* NEES, BLUME s.n. (LY).

Stomata types were studied on the following material: *Atroxima liberica* STAPF, sine coll. 8248 (L); *Bredemeyera* spec., TORRES 308 (GB); *Carpolobia alba* G. DON, DE GIORGI 1610 (S); *Comesperma ericinum* DC., WALL s.n. (S); *Monnina* subg. *Monnina*: *M. crassifolia* H. B. K., MOLAU & ÖHMAN 1256 (GB), subg. *Monninopsis*: *M. insignis* A. W. BENN., HARLEY 21500 (US), subg. *Pterocarya*: *M. amarella* CHODAT, BRUNEL 667 (GH); *Nylandtia spinosa* (L.) DUMOR., RYCROFT 3118 (S); *Polygala venenosa* JUSS., MODIGLIANI s.n. (LY); *Salomonina ciliata* DC., RAMOS & EDAÑO s.n. (S), *Securidaca* spec., SOLOMON 16807 (MO)

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