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Evolutionary relationships in the *Podalyrieae* and *Liparieae (Fabaceae)* based on morphological, cytological, and chemical evidence

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Abstract: Taxonomic relationships amongst the genera of the southern African tribes *Podalyrieae* and *Liparieae* are discussed. Data gained from morphological, cytological and chemical investigations are analyzed cladistically to determine relationships. The genus *Cadia* (tribe *Sophoreae*) is included in the investigation to establish whether it should be transferred to the *Podalyrieae*. The results clearly indicate that the *Podalyrieae* and *Liparieae* are monophyletic and that they should be united, but that *Hypocalyptus* and *Cadia* should be excluded. Within the monophyletic group, there are two distinct subclades each supported by three apomorphies. The results also show that there is a strong sister relationship between *Amphithalea* and *Coelidium*. In the taxonomic treatment the *Liparieae* are placed into synonymy under the *Podalyrieae* and two subtribes are recognized. A key to the genera in the tribe is given, followed by a synopsis of the genera.

When POLHILL (1976, 1981a, c–f) proposed a biogeographic classification for the *Podalyrieae* and *Genisteae* sensu BENTHAM (1837, 1839), he divorced the African *Podalyrieae*, *Liparieae* and *Crotalarieae* from the northern temperate *Thermopsideae* and *Genisteae*, and the Australian *Mirbelieae* and *Bossiaeeae*. He placed the genera *Cyclopia* VENT., *Podalyria* LAM. and *Virgilia* POIR. in the *Podalyrieae* on account of the more or less free stamens. *Amphithalea* ECKL. & ZEYH., *Coelidium* VOGEL ex WALP., *Hypocalyptus* THUNB., *Liparia* L. and *Priestleya* DC. were allocated to the *Liparieae*, based on the fused stamens. POLHILL (1981d, e), however, surmised that it might be sensible to amalgamate the two tribes, but added that a detailed study is needed to clarify the uncertainty regarding relationships between them.

Over the last four years, the taxonomy of the *Podalyrieae* and *Liparieae* has been the subject of intensive research (SCHUTTE 1995). A series of studies was conducted in which the morphological variation, chromosome numbers and chemical constituents in each of the genera were scrutinized to determine generic delimitations. Some fascinating results were obtained, which emanated in several substantial changes at generic level: (1) it was established that *Priestleya* is paraphyletic, resulting in *Priestleya* sect. *Aneisothea* being raised to generic level under the reinstated name *Xiphotheca* ECKL. & ZEYH. (SCHUTTE & VAN WYK 1993); (2) *Priestleya* sect. *Priestleya* was found to be congeneric with *Liparia* and included therein (SCHUTTE & VAN WYK 1994); (3) *Podalyria* also proved to be paraphyletic, which led to the description of a new genus, *Stirtonanthus* B.-E. VAN WYK & A. L. SCHUTTE (VAN WYK & SCHUTTE 1994, 1995a); (4) the genus *Calpurnia* E. MEY. (tribe *Sophoreae*) was found to be a sister group of *Virgilia* and subsequently transferred to the *Podalyrieae* (VAN WYK & SCHUTTE 1995b).

An earlier preliminary survey of phylogenetic relationships in the tribes *Podalyrieae*, *Liparieae* and *Crotalarieae* (VAN WYK & SCHUTTE 1995b), indicated that both the *Podalyrieae* and *Liparieae* are monophyletic taxa, which originated from a common ancestor. *Hypocalyptus*, however, dropped to a basal position, thereby reflecting its incongruous taxonomic position. More information has since then come to light.

In the tribe *Sophoreae*, recent anatomical, chemical and DNA studies have indicated that the genus *Cadia* FORSSK. deviates from other members of the *Cadia* group (POLHILL 1981b) in various characters, e.g. wood anatomy (GASSON 1994), alkaloids (VAN WYK & al. 1993), chloroplast DNA (DOYLE 1987, 1995). POLHILL (1994) subsequently abandoned the *Cadia* group and transferred *Cadia* to the *Sophora* group. He, however, reiterated the suggestion by VAN WYK & al. (1993), that the genus should possibly be transferred to the *Podalyrieae*.

The objectives of this paper are (1) to discuss the morphological, cytological and chemical variation in the *Podalyrieae* and *Liparieae*, (2) to re-examine evolutionary affinities amongst the genera, (3) to provide a predictive classification for the tribes, based on sound empirical evidence, and (4) to investigate the possible inclusion of *Cadia* in the *Podalyrieae*.

Morphological characters

Growth form. In the *Podalyrieae* and *Liparieae*, all the species are long-lived perennials. There is a considerable variation in growth form – from tall upright trees with a main trunk, to erect woody shrubs, to virgate, multi-stemmed shrubs, to small rounded subshrubs or sprawling shrublets. The general trend of a tree-like versus a shrub-like growth form is thus applicable as an evolutionary character.

Adaptations to survive recurrent fires have, to a large extent, influenced the life forms of the taxa. The two fire-survival strategies, sprouters (able to resprout after fire) and non-sprouters (obligate reseeders after fire), are important taxonomic characters, particularly at the specific level (SCHUTTE & al. 1995; SCHUTTE 1997c, d). At generic level, however, there are no clear-cut discontinuities and these characters appear to have evolved independently in the different genera.

Leaves. Leaves are imparipinnate in *Virgilia* and *Calpurnia*, digitately trifoliolate in *Hypocalyptus* and *Cyclopia* and simple in *Amphithalea*, *Coelidium*, *Liparia*, *Podalyria*, *Stirtonanthus* and *Xiphotheca* (Fig. 1). Petioles are invariably present in most genera, except in *Amphithalea* and *Coelidium*, where they are strongly reduced or absent and *Liparia*, where they are totally lacking. *Cyclopia* and *Liparia* have decurrent leaf bases and the leaves tend to turn black when dried.

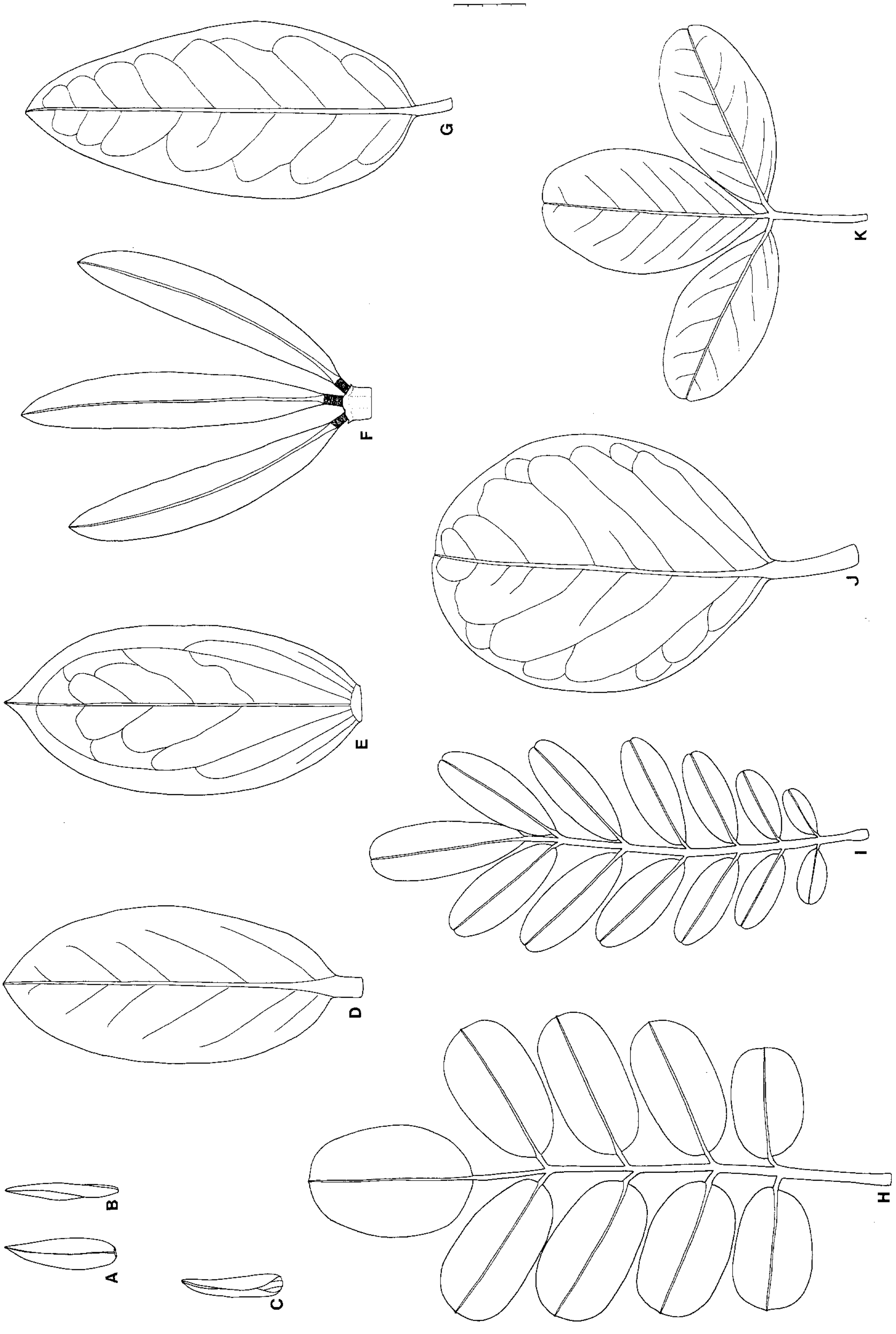

Fig. 1. Variation in leaves in the *Podalyrieae* and *Liparieae* (lower surface, vestiture not shown). *A Coelidium flavum*; *B Coelidium tortile*; *C Amphithalea ericifolia*; *D Xiphotheca fruticosa*; *E Liparia parva*; *F Cyclopia intermedia*; *G Podalyria lanceolata*; *H Calurnia intrusa*; *I Virgilia divaricata*; *J Stirtonanthus taylorianus*; *K Hypocalyptus coluteoides*. – Scale in mm

Liparia has leaves with three or more primary veins arising from the base of the lamina, in contrast to the pinnately veined leaves of the other genera. Stipules are invariably present in all the genera, albeit strongly reduced in size in *Amphithalea*, *Coelidium* and *Xiphotheca*.

It seems as if specialization in leaves occurred along the sequence of reduction as proposed by Dormer (1945, 1946) and Polhill (1981a): compound to simple; petioles present to absent; stipules conspicuous to strongly reduced.

Inflorescences. According to Polhill (1976), inflorescences tend to be rather labile in the *Papilionoideae*. In the *Podalyrieae* and *Liparieae* inflorescence structure is a useful character at both inter- and infrageneric level. Terminal, many-flowered racemes occur in *Hypocalyptus* (Fig. 2). *Virgilia* and *Calpurnia* have subterminal and axillary racemes or panicles. The rest of the *Podalyrieae* and *Liparieae* have axillary, simple racemose inflorescences, with modifications in the number of flowers, length of the peduncle and length of the inflorescence axis (Fig. 2). In *Liparia* the flowers are borne on lateral short shoots, terminating in a small apical extension of the inflorescence axis. These brachyblasts are either contracted

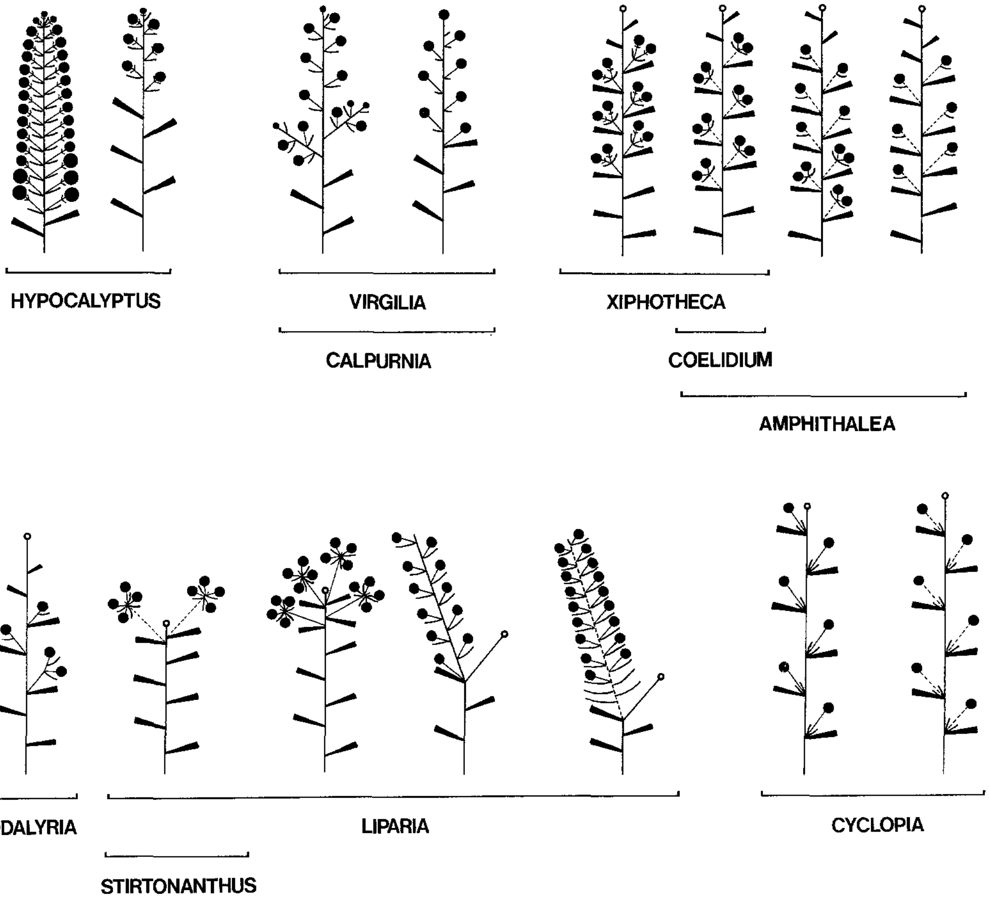

Fig. 2. Schematic representation of inflorescence structure in the *Podalyrieae* and *Liparieae*. See text for discussion

into many-flowered heads subtended by petaloid, sterile bracts, or few-flowered units in which a decrease in the length of the axis eventually leads to decussate two- or four-flowered inflorescences (SCHUTTE & VAN WYK 1994). *Xiphotheca*, *Coelidium* and several species of *Amphithalea* invariably have geminate (paired) flowers. The other species of *Amphithalea* are either bifloral at the base of the flowering branch, becoming unifloral towards the apex, or uniformly single-flowered. Specialization appears to culminate in *Cyclopia*, where the inflorescences are consistently unifloral and supported by two bracts, very rarely three or four bracts (SCHUTTE, pers. obs.), with the flower situated in the axil of the uppermost bract.

The bracts are generally sheathing (i.e. with a broad point of attachment) in the *Podalyrieae* and *Liparieae* (Fig. 3). Tridentate bracts, possibly due to an extreme reduction in leaf size and subsequent fusion with the adjacent stipules, have been observed in *Hypocalyptus*, *Virgilia*, *Stirtonanthus* and *Podalyria*. The bracts are caducous at an early stage in *Podalyria*, *Virgilia* and *Calpurnia*. *Xiphotheca* and three species of *Coelidium* have the bracts fused with the pedicel at the base. Most genera lack bracteoles, except *Hypocalyptus*, *Xiphotheca*, *Virgilia* and *Calpurnia*, where they are either conspicuous (*Hypocalyptus*, *Xiphotheca phylicoides* A. L. SCHUTTE & B.-E. VAN WYK, *X. canescens* (THUNB.) A. L. SCHUTTE & B.-E. VAN WYK, *X. elliptica* (DC.) A. L. SCHUTTE & B.-E. VAN WYK, or strongly reduced (*Virgilia oroboides* ADAMSON, *Calpurnia* and the remainder of *Xiphotheca*).

The structure and evolutionary tendencies of inflorescences in the *Fabaceae* have been discussed by WEBERLING (1989). Trends evident in the *Podalyrieae* and *Liparieae* include the following: inflorescence position terminal to axillary; inflorescence type racemose to geminate; inflorescences extended to congested; many-flowered to few-flowered to unifloral inflorescences; terminal extension of inflorescence axis absent to present; bracts persistent to caducous; bracteoles present to strongly reduced or absent.

Flowers. Calyx. In the *Podalyrieae* and *Liparieae*, the upper two calyx lobes are invariably fused higher up than the lower three lobes (Fig. 4) This character breaks down only in three species of *Calpurnia*, where the sinus between the upper two lobes is subequal to the others. According to POLHILL (1976), the *Podalyrieae* and *Liparieae* calyx type is the most ubiquitous and apparently basic form in the subfamily. However, some specialization is found in the carinal calyx lobe in *Cyclopia* and especially *Liparia*, where it is longer or larger than the upper four and often distinctly keeled. *Virgilia* has a two-lipped calyx, with the lower three lobes fused into a trifid lower lip. An intrusive calyx base is characteristic of all the genera, except *Xiphotheca*, *Amphithalea*, *Coelidium* and a few species of *Calpurnia* (Fig. 3). These taxa have attenuate calyx bases, with the receptacular part (hypanthium) often prominent. There is, however, one species of *Xiphotheca* which has an intrusive calyx base (SCHUTTE & VAN WYK 1993, SCHUTTE 1997a), but it is here regarded as a secondary development.

Corolla. There are some noteworthy patterns of divergence in the corolla of the *Podalyrieae* and *Liparieae* (Fig. 5). Apart from *Amphithalea*, *Coelidium* and *Xiphotheca*, all the genera have firmly textured flowers, adapted to pollination by large xylocopid bees and presumably also birds and small non-flying mammals (REBELO 1987, SCHUTTE & VAN WYK 1994). The flowers are yellow in all species of

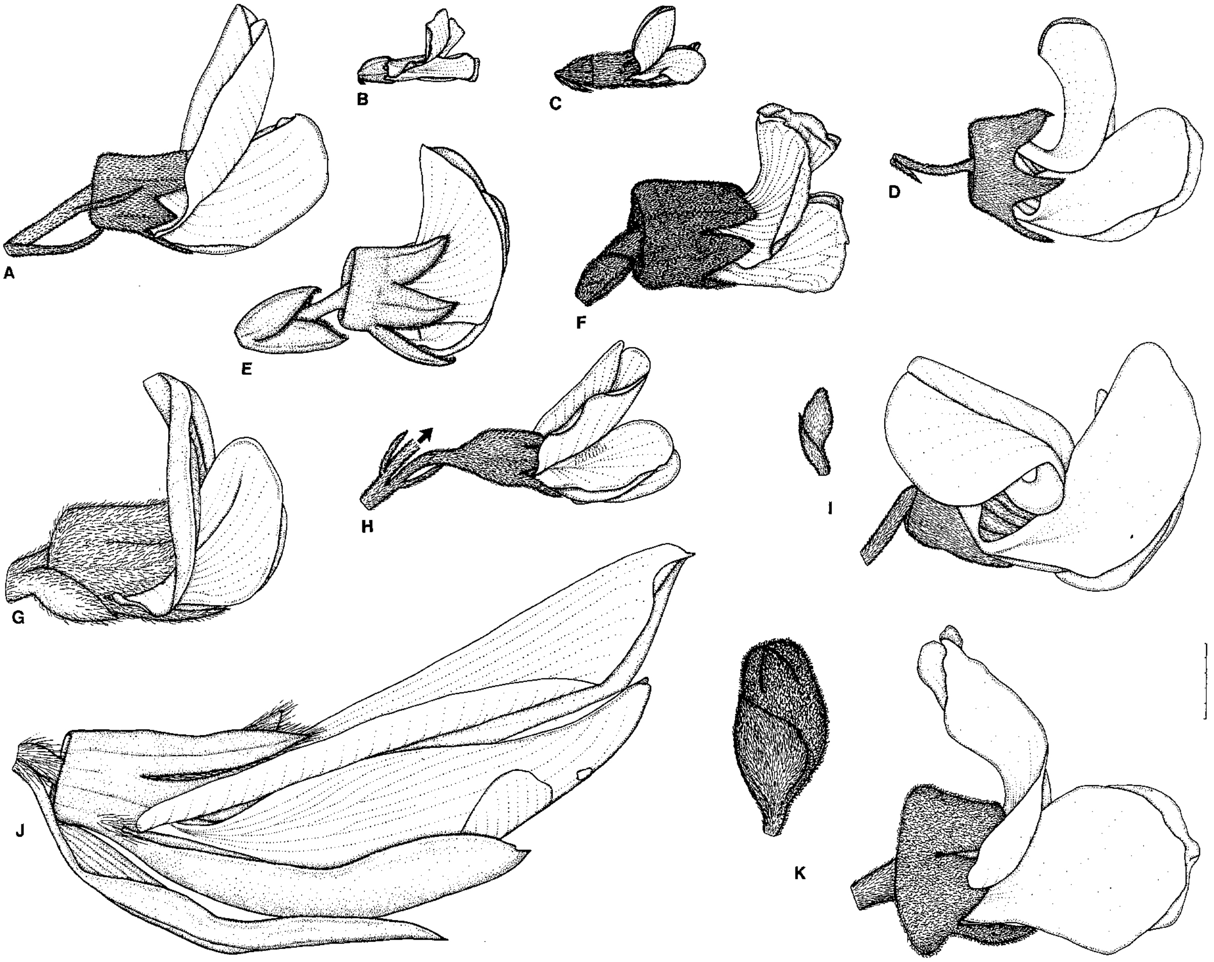

Fig. 3. Flowers of the *Podalyrieae* and *Liparieae* in lateral view (note the structure of the calyx, position of the bracts and presence or absence of bracteoles). *A Hypocalyptus coluteoides*; *B Amphithalea micrantha*; *C Coelidium tortile*; *D Calpurnia intrusa*; *E Cyclopia intermedia*; *F Stirtonanthus taylorianus*; *G Liparia umbellifera*; *H Xiphotheca phylicoides*; *I Virgilia divaricata*; *J Liparia splendens* subsp. *splendens*; *K Podalyria argentea*. – Scale in mm

Calpurnia, *Stirtonanthus*, *Cyclopia*, *Xiphotheca* and most species of *Liparia* (one species has bright orange-red flowers and two others have a lemon-yellow flower colour). White, pink or purple flowers, often with a white or dark violet nectar guide, predominate in *Virgilia Podalyria*, *Coelidium* and *Amphithalea*. *Hypocalyptus* is unusual in having magenta pink flowers with a yellow nectar guide (see discussion on anthocyanins below).

The standard petal is large, thickly textured, usually strongly reflexed, with callosities at the base and emarginate at the apex in *Liparia*, *Hypocalyptus* and members of the *Podalyrieae* (Fig. 5). Keel petals are rostrate or beaked and lack a distinct pocket or auricle. Not even the wing petals are pocketed or auriculate, but

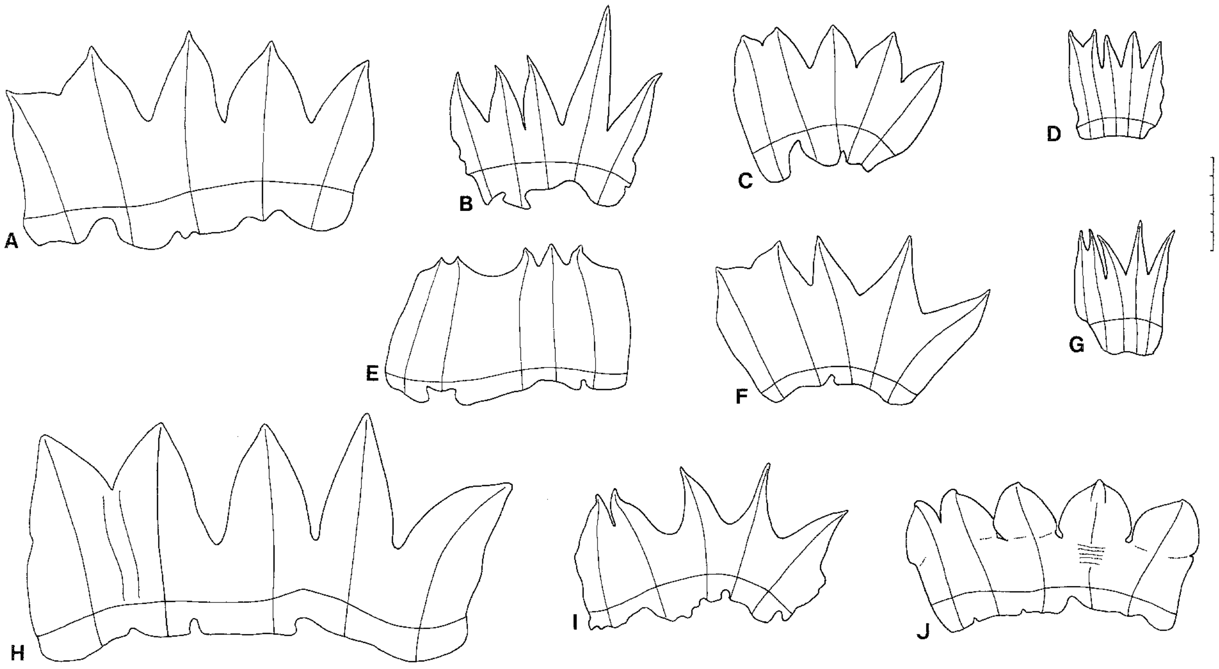

Fig. 4. Calyces of the *Podalyrieae* and *Liparieae* (opened out with the upper lobes to the left). *A Stirtonanthus chrysanthus*; *B Liparia angustifolia*; *C Xiphotheca elliptica*; *D Amphithalea ericifolia*; *E Virgilia divaricata*; *F Hypocalyptus coluteoides*; *G Coelidium tortile*; *H Podalyria myrtillifolia*; *I Calpurnia intrusa*; *J Cyclopia intermedia*. – Scale in mm

petal sculpturing is sometimes present. *Cyclopia* is exceptional in having distinct grooves on the standard petal, which probably act as nectar guides and well-developed pockets on the keel and wing petals (Fig. 5). *Amphithalea*, *Coelidium* and *Xiphotheca* have relatively unspecialized corollas with the keel petals obtuse and distinctly pocketed and auriculate (Fig. 5). In these genera the pocket on the wing petal is a thickened lobe, formed on the inside (abaxial side). Wing petal sculpturing is invariably present in the upper basal area.

Stamens. Traditionally the fusion of the stamens has been used to discern the *Liparieae* from the *Podalyrieae* (Polhill 1976, 1981d, e). In the *Podalyrieae* the stamens are free or almost free to the base, but in the *Liparieae* the degree of fusion varies from diadelphous in *Liparia*, *Xiphotheca* and *Amphithalea* to monadelphous in *Coelidium*, to a closed tube in *Hypocalyptus* (Fig. 6). In fact, the generic circumscription of *Coelidium* is based solely on this character. Both *Amphithalea* and *Coelidium* have a well-developed hypanthium, which implies that the stamens are fused into an open sheath for at least that part. This means that the only real difference between the two genera lies in the degree of fusion of the vexillary stamen (see variation in Fig. 6).

The stamens are thickened at the base in the *Podalyrieae* and the vexillary filaments are modified to form one or two nectar wells in *Cyclopia*, *Calpurnia*,

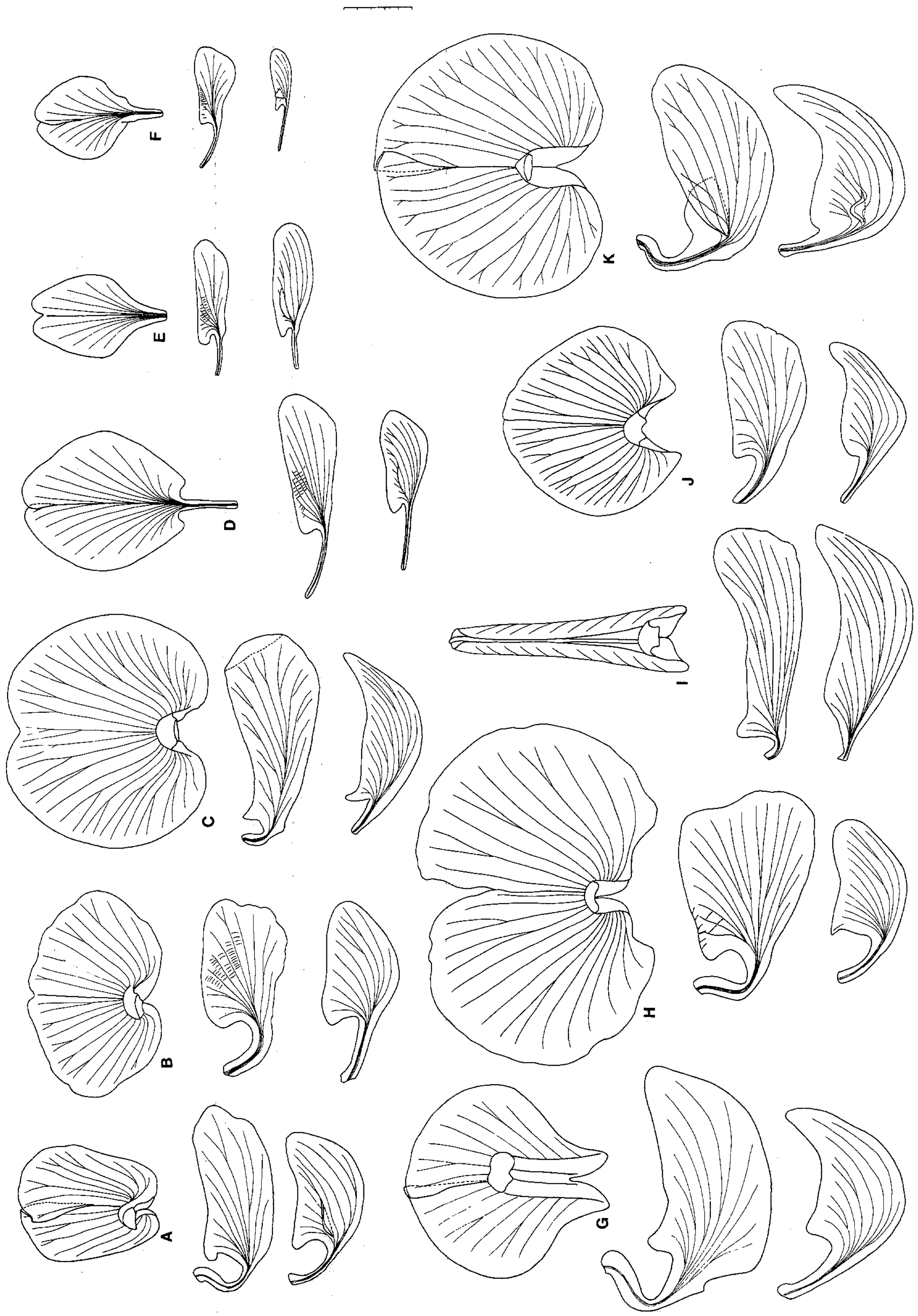

Fig. 5. Standard, wing and keel petals of the *Podalyrieae* and *Liparieae*. A *Calpurnia intrusa*; B *Stirtonanthus taylorianus*; C *Hypocalyptus sophoroides*; D *Xiphotheca reflexa*; E *Amphithalea ericifolia*; F *Coelidium flavum*; G *Virgilia divaricata*; H *Podalyria argentea*; I *Liparia parva*; J *Liparia capitata*; K *Cyclopia intermedia*. – Scale in mm

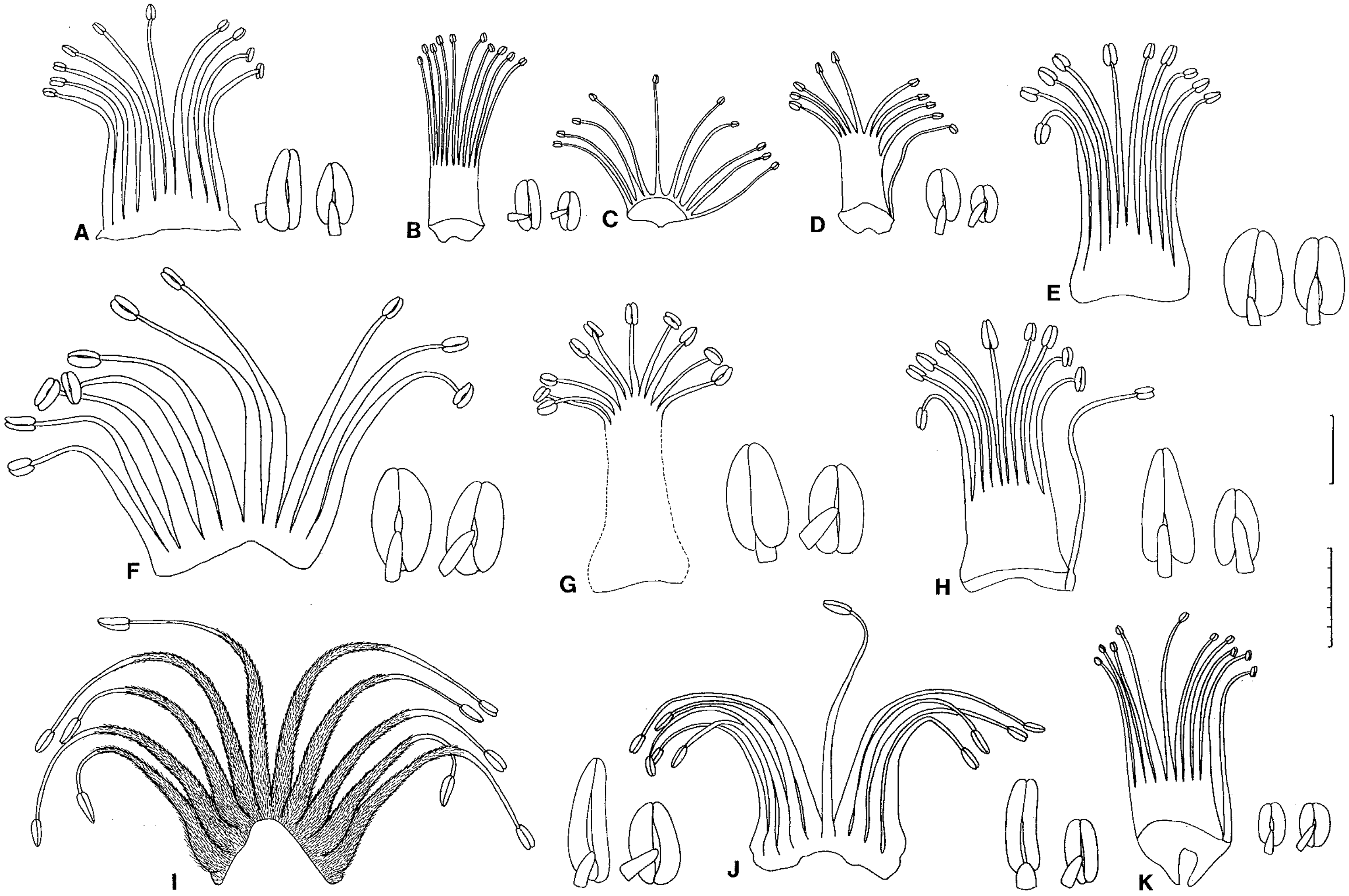

Fig. 6. Stamens and anthers of the *Podalyrieae* and *Liparieae*. *A Podalyria intermedia*; *B Coelidium flavum*; *C Coelidium parvifolium*; *D Amphithalea rostrata*; *E Calpurnia intrusa*; *F Stirtonanthus taylorianus*; *G Hypocalyptus coluteoides*; *H Liparia bonaespei*; *I Virgilia divaricata*; *J Cyclopia intermedia*; *K Xiphotheca reflexa*. Scales (upper for anthers, lower for stamens) in mm

Podalyria, *Virgilia*, *Liparia* and *Stirtonanthus*. Hairy stamens occur in *Virgilia* (Fig. 6) and one species of *Calpurnia.*

Dimorphic anthers seem to be associated with a beaked keel, those of the unspecialized flowers being less differentiated (Fig. 6). The anthers are alternately short and dorsifixed or long and basifixed or subbasifixed throughout the genera.

Pistils. *Hypocalyptus* deviates from the other genera in having the pistil stipitate. All genera have the style curved upwards and in *Podalyria*, *Stirtonanthus*, *Amphithalea* and *Coelidium* the base of the style is often hairy. The number of ovules varies from one or two in *Coelidium* (GRANBY 1980) and *Amphithalea* (GRANBY 1985), to up to thirty in *Hypocalyptus* (DAHLGREN 1972). These differences are of use only at infrageneric level.

Fruits. The significance of fruit characters (i.e. of the pods and seeds) in the taxonomy of the *Fabaceae* is well known (CORNER 1951, 1976; DAHLGREN 1975; POLHILL 1976, 1981a; ESAU 1977; DUDIK 1981; GUNN 1981a, 1981b; PATE & KUO 1981; MANNING & VAN STADEN 1987). However, POLHILL (1976) pointed out that the weighting of fruit characters at generic and tribal level has, in some instances, led to artificial segregation of otherwise natural groups.

The variation in fruit structure in the *Podalyrieae* and *Liparieae* is illustrated in Fig. 7. Pods are laterally compressed and constricted between the seeds in *Xiphotheca*, *Virgilia*, *Calpurnia* and one species of *Hypocalyptus*, but this character seems to have evolved independently in the different genera. The remaining taxa have inflated pods. Apart from *Hypocalyptus*, which has tardily dehiscent pods

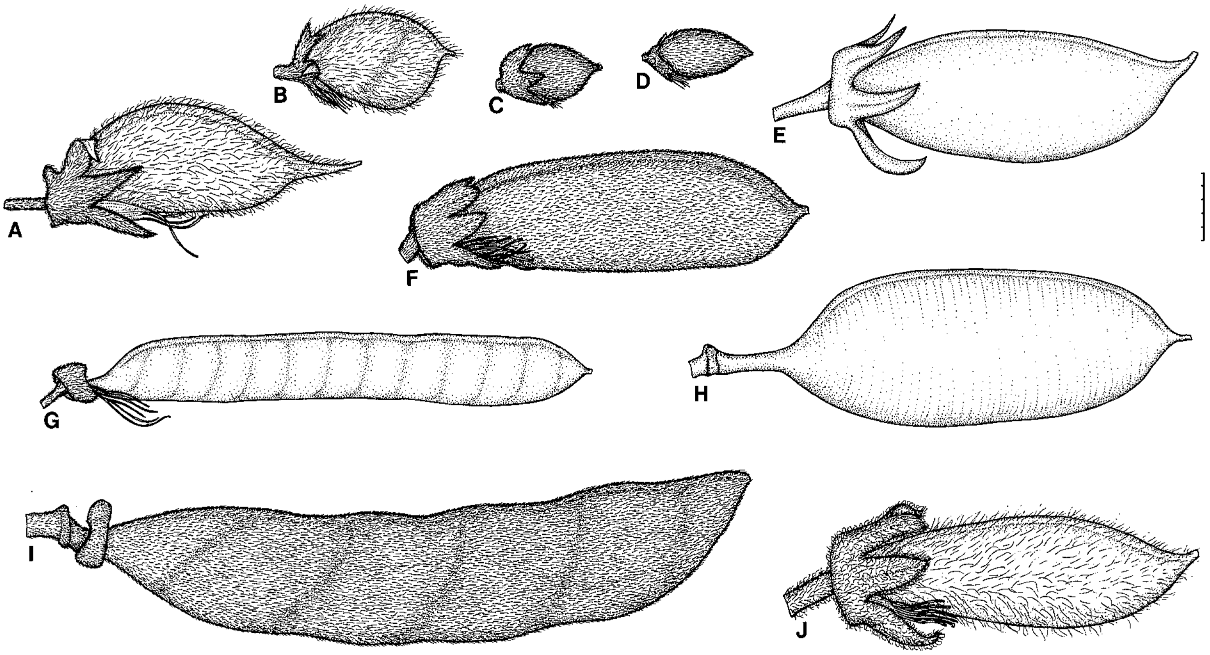

Fig. 7. Fruits of the *Podalyrieae* and *Liparieae* in lateral view. *A Liparia striata*; *B Xiphotheca guthriei*; *C Amphithalea ericifolia*; *D Coelidium vlokii*; *E Cyclopia genistoides*; *F Stirtonanthus taylorianus*; *G Calpurnia intrusa*; *H Hypocalyptus coluteoides*; *I Virgilia divaricata*; *J Podalyria myrtillifolia.* Scale in mm

(Schutte, pers. obs.), seeds are released by the explosive mechanism (Polhill 1976) in all the other genera. Both tribes have sessile, obliquely oblong to ovate pods, except in *Hypocalyptus*, where the pods are distinctly stipitate and where the three species each have a characteristic pod shape. In most genera, the pods are many-seeded, but in *Amphithalea* and *Coelidium* the number is reduced to one or rarely two seeds per pod.

Evolutionary trends in fruit characters have been discussed by Dudik (1981) and Polhill (1981a). The following trends apply in the *Podalyrieae* and *Liparieae*: legume many-seeded to one- or two-seeded; legume dehiscent to tardily dehiscent; and seed with an aril to seed without an aril.

Seeds. Characters of the seed have traditionally been regarded as conservative (Manning & Van Staden 1987, Van Staden & al. 1989). According to Polhill (1976) aril characters have previously been overweighted at the generic level, but neglected at the generic group or tribal level in the *Genisteae* sensu Bentham. In the South African *Papilionoideae*, the *Podalyrieae* and *Liparieae* represent the arillate tribes. They differ from the Australian tribes in having a collar-like aril, not hooded, channelled, papillate or with a rugose lobe distal to the radicular lobe as in the *Bossiaeeae* and *Mirbelieae* (Crisp & Weston 1987).

The aril is reduced to a non-fleshy rim aril in *Virgilia*, *Stirtonanthus* and *Calpurnia*, but thick and fleshy in the other taxa. Further specialization is found in *Coelidium* and *Amphithalea*, where the aril is prolonged towards the lens area (see Fig. 9 in Van Wyk & Schutte 1995b). *Hypocalyptus* is anomalous in having the aril continuous around the hilum, whilst all the other genera have it interrupted at the radicular end of the hilum. *Stirtonanthus* is unusual in the oblique orientation of the lens alignment (Van Wyk & Schutte 1994).

As shown by Manning & Van Staden (1987), the shape and position of the micropyle are of taxonomic importance in subfam. *Papilionoideae*. In the *Podalyrieae* and *Liparieae*, *Hypocalyptus* deviates in having an ypsaloid micropyle, which is situated outside the hilar region. The remaining genera all have a punctate micropyle situated within the hilar region (see Fig. 9 in Van Wyk & Schutte 1995b).

Secondary xylem. Baretta-Kuipers (1981) has shown that the structure of secondary wood is taxonomically useful in the *Fabaceae* at subfamily and tribal levels. She, however, omitted shrubby legumes from her study, as the xylem in these do not have all the characters of the xylem of trees (mature wood).

Since most of the genera of the *Podalyrieae* and *Liparieae* include at least some woody species, which can become 15 to 30 years old, a study of the secondary xylem of these taxa was undertaken. Two main groups are apparent: those with the vessels arranged in small, isolated, radial or tangential groups as in *Virgilia*, *Calpurnia* and *Hypocalyptus*, and those with the vessels arranged in large confluent (dendritic) groups as in *Podalyria*, *Stirtonanthus*, *Cyclopia* and all the genera of the *Liparieae*, except *Hypocalyptus* (Van Wyk & Schutte 1995b). The isolated type of arrangement is found in the supposedly more primitive tribes of the *Papilionoideae* (Metcalfe & Chalk 1950, Baretta-Kuipers 1981), which seems to indicate that the confluent type of arrangement is more advanced. According to Baas & Schweingruber (1987), Fujii & al. (1994) and Baas (pers. comm.) the diffuse arrangement of vessels is found in species occurring in tropical regions, whilst the more complex dendritic patterns are associated with species found in strongly seasonal habitats, e.g. the Cape fynbos region or other Mediterranean ecosystems. This trend has been explicitly documented by Carlquist (1987), Baas & Schweingruber (1987), Baas & al. (1988) and Wheeler & Baas (1991).

Antipodals. Antipodals in the female gametophyte have proved to be of taxonomic value at the tribal level in the Australian *Papilionoideae* (Cameron & Prakash 1990). Suggestions that the Australian *Bossiaeeae* and *Mirbelieae* may be closely related to the *Podalyrieae* and *Liparieae* (Crisp & Weston 1987), urged an investigation into the structure of antipodals in these two tribes, especially in view of the aberrant position of *Hypocalyptus* in the *Liparieae*. A detailed discussion of the results will be published elsewhere (Schutte 1997b).

It was found that the antipodals are prominent and persistent at least until anthesis in *Liparia*, *Xiphotheca*, *Amphithalea*, *Coelidium* and the genera of the *Podalyrieae*. *Hypocalyptus*, however, has inconspicuous and ephemeral antipodal cells. Thus, unlike the *Bossiaeeae* and *Mirbelieae*, antipodals are neither gigantic nor totally absent in the *Podalyrieae* and *Liparieae*. A direct affinity between the South African and Australian tribes, based on this character, seems unlikely.

Cytological characters

Chromosome counts are known for all the genera of the *Podalyrieae* and *Liparieae*. With the exception of *Cyclopia*, *Virgilia* and *Hypocalyptus*, all have $2n = 18$ (Dahlgren 1967; Granby 1980; Goldblatt 1981a; Polhill 1981d, e; Schutte 1995). *Cyclopia* and *Virgilia* are the only known polyploids, the latter a hexaploid with $2n = 54$ (Van Wyk 1986, Goldblatt 1981b) and the former, with an apparent polyploid range of $2n = 36$ (Goldblatt 1981b), 54 and ±126 (Schutte 1995). A basic chromosome number of $x = 9$ seems most likely for the two tribes, as was suggested by Goldblatt (1981a). *Hypocalyptus*, however, is atypical in having $2n = 20$, and therefore a base number of $x = 10$ (Goldblatt 1981b, Van Wyk & Schutte 1995b).

Chemical characters

Alkaloids. Virtually nothing was known about the distribution of alkaloids in the tribes *Podalyrieae* and *Liparieae* prior to our studies. Only *Virgilia* (Mears & Mabry 1971, Van Eijk & Radema 1982, Van Eijk & al. 1982) and some species of *Calpurnia* (Radema & al. 1979; Asres & al. 1986a, b) had been studied earlier and were known to contain unique combinations of quinolizidine alkaloids.

The distribution of the major alkaloids found in the genera of the *Podalyrieae* and *Liparieae* are summarized in Table 1. *Hypocalyptus* and *Cyclopia* are not included, since no alkaloids could be detected in them. Each of the other genera appears to have a characteristic combination of major alkaloids. The marked decrease in the number of compounds found in the genera of the *Liparieae* is noteworthy.

No less than 16 different alkaloids were found in *Podalyria* and *Stirtonanthus* (Van Wyk & al. 1992). Most species of *Podalyria* produce tetracyclic quinolizidine alkaloids such as sparteine, lupanine, isolupanine, 13α-hydroxylupanine and

Table 1. The distribution of major alkaloids in the genera of the *Podalyrieae* and *Liparieae*. *** present in all species examined, ** present in most species examined, * present only in a few species examined, + present in trace quantities only. *CALP Calpurnia*, *VIRG Virgilia*, *PODA Podalyria*, *STIR Stirtonanthus*, *LIPA Liparia*, *XIPH Xiphotheca*, *AMPH Amphithalea*, *COEL Coelidium*

Alkaloids	CALP	VIRG	PODA	STIR	LIPA	XIPH	AMPH	COEL
Anabasine						***		
Ammodendrine		+			*		***	***
Lupinine	*	***				***		
Epilupinine	*	***						
4β-*O*-(2′-pyrrolyl-carboxyl)-epilupinine		*						
4β-hydroxy-11-*O*-(2′-pyrrolyl-carboxyl)-epilupinine		***						
Lusitanine		*						
Sparteine		**	**	+	***	**		
α-isosparteine				+	**	**		
11,12-dehydrosparteine					**			
Lupanine		**	***	+	**			
Isolupanine			**	*	**			
17-oxolupanine			**					
3-hydroxylupanine			*					
13α-hydroxylupanine	***	**	**	***	**			
4β, 13α-dihydroxylupanine	*							
3, 13-dihydroxylupanine			*					
10, 13-dihydroxylupanine	*							
3, 4, 13-trihydroxylupanine	*							
Digittine	*							
Lebeckianine			*					
Calpurmenine	**							
Lupanine 13α-angelate	*		*	*				
Lupanine 13α-tigliate	**							
Cajanifoline			**					
Sessilifoline			*					
Pearsonine			*					
Oroboidine	***	**		***				
Calpaurine	*							
13α-pyrrolyl-carboxyl-acid-ester	**							
Aphylline			*					
Virgiline	***	***		**				
Virgiline-pyrrolyl-carboxyl-acid-ester	***	***		***	*			
Virgiboidine		***						
Dihydrovirgiboidine		**						
Virgilidone		**						
Dihydrovirgilidone		*						

cajanifoline (an ester). Some species also contain other esters (pearsonine, sessilifoline, lupanine 13α-angelate), hydroxylated lupanines and aphylline. The three species of *Stirtonanthus*, however, were found to accumulate virgiline, 13α-hydroxylupanine and two totally different esters, oroboidine and virgiline-pyrrolylcarboxylic acid ester. These two different sets of alkaloids in the two taxa, supported other deviations in morphological characters (VAN WYK & SCHUTTE 1994, 1995a) and hence, proved that they are dissimilar. In fact, the compounds contained in *Stirtonanthus* show more resemblance with *Virgilia* than with *Podalyria*.

In a detailed study of the alkaloids of *Virgilia*, a total of 44 alkaloids were detected; 43 of the quinolizidine type and one bipiperidyl alkaloid (GREINWALD & al. 1989, VEEN & al. 1991). *Virgilia* is exceptional in containing also tricyclic quinolizidine alkaloids in addition to bi- and tetracyclic compounds. The presence of virgiline and its carboxylic acid ester as major compounds in *Calpurnia*, *Virgilia* and *Stirtonanthus*, suggests a close relationship between these genera and supports the transfer of *Calpurnia* to the *Podalyrieae* (VAN WYK & SCHUTTE 1995b).

Anabasine (a bipiperidyl alkaloid) and lupinine (a bicyclic quinolizidine alkaloid) were detected as major alkaloids in *Xiphotheca*. A totally different set of alkaloids was found in *Liparia* (including *Priestleya* s. str.) where a combination of lupanine, isolupanine, 13α-hydroxylupanine, sparteine, α-isosparteine, 11,12-dehydrosparteine (all tetracyclic quinolizidine alkaloids) and minor quantities of ammodendrine (a bipiperidyl alkaloid) were located (VAN WYK & al. 1991a, b). These findings clearly support the recent reinstatement of *Xiphotheca* (SCHUTTE & VAN WYK 1993), as well as the inclusion of *Priestleya* s. str. into *Liparia* (SCHUTTE & VAN WYK 1994).

Amphithalea and *Coelidium* seem to have very few alkaloids. ARNDT & DU PLESSIS (1968) investigated the alkaloids of one species of *Coelidium*. They recorded ammodendrine as the major compound and isopiperideine and α-aldotripiperideine as minor alkaloids. A wider survey of the alkaloids of *Amphithalea* and *Coelidium* is currently in progress (VAN WYK & al., unpubl.). Ammodendrine has been detected as a major alkaloid in both genera and quinolizidine alkaloids appear to be absent. The concentration of alkaloids present in the species of *Coelidium* investigated seems to be higher than in the *Amphithalea* species, but yields are very variable, and many species have almost no detectable alkaloids.

The biogenetic pathways along which quinolizidine alkaloids are produced have been discussed by various authors (NOWACKI & WALLER 1977; SALATINO & GOTTLIEB 1980, 1981; GOMEZ & al. 1981). VAN WYK & VERDOORN (1990) used this information in the *Crotalarieae* to construct a phylogeny for the tribe. Following these authors, the biosynthetic routes in the *Podalyrieae* and *Liparieae* are illustrated diagrammatically in Fig. 8. The various steps involved in the pathways are explained in the references mentioned above and are not repeated here. Five groups are apparent: (1) a group producing bipiperidyl alkaloids as major compounds, e.g. *Coelidium*, *Amphithalea* and *Xiphotheca* (*Liparia* has ammodendrine as a major compound in one species only); (2) a group with bicyclic quinolizidine alkaloids, e.g. *Virgilia*, *Calpurnia* and *Xiphotheca*; (3) a group accumulating 13α-hydroxylupanine in all or most species, e.g. *Calpurnia*, *Virgilia*,

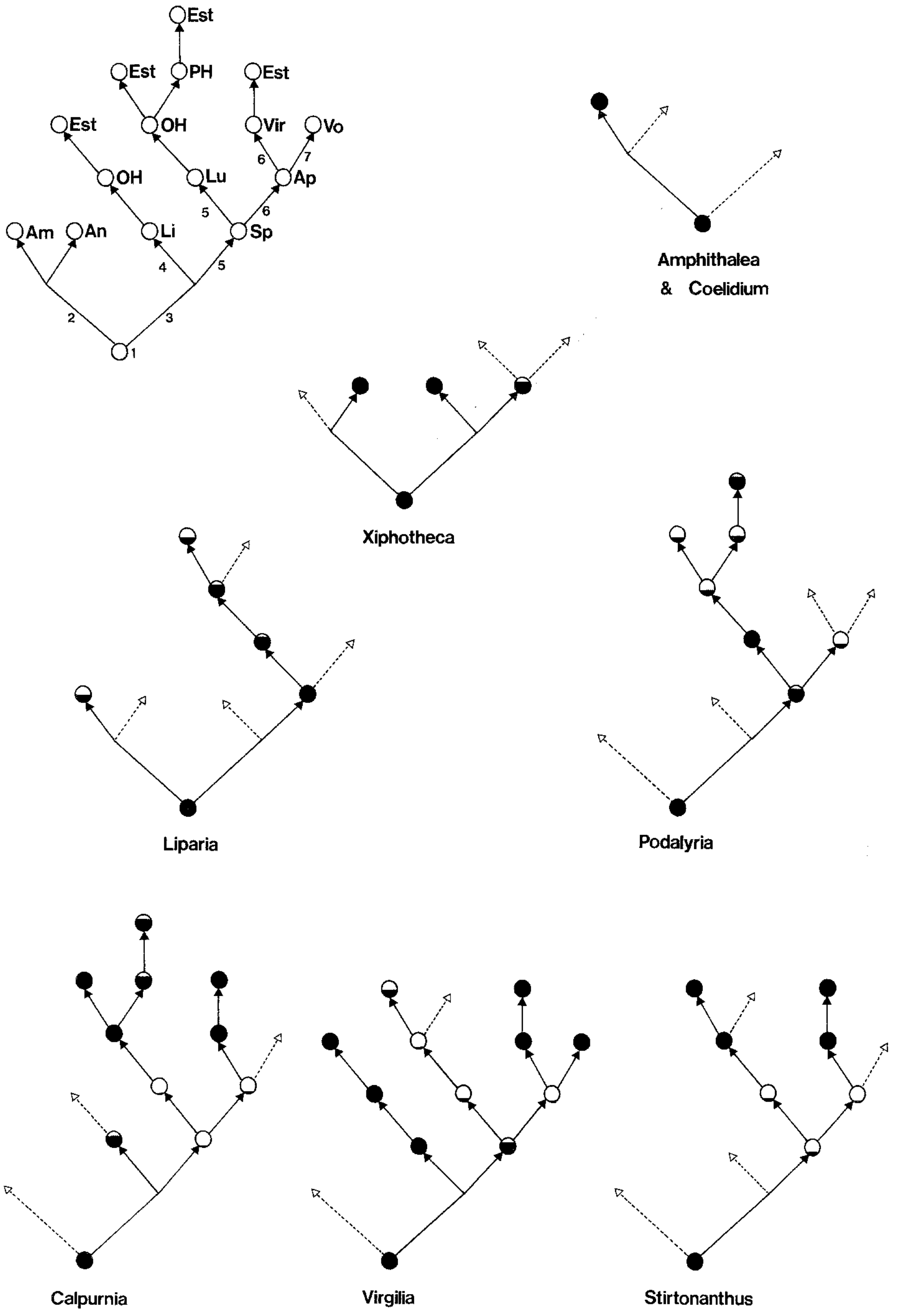

Fig. 8. Diagrammatic representation of biosynthetic pathways of *Podalyrieae* and *Liparieae* alkaloids and a comparison of the routes present in the different genera. Direction of arrows suggests increasing specialization. Biosynthetic pathways: 1 lysine pathway; 2 bipiperidyl pathway; 3 quinolizidine pathway; 4 bicyclic quinolizidine pathway; 5 tetracyclic quinolizidine pathway; 6 10-oxo pathway; 7 tricyclic quinolizidine pathway. Compounds: *Am* ammodendrine; *An* anabasine; *Li* lupinine; *Lu* lupanine; *Sp* sparteine; *Ap* aphylline; *Vir* virgiline; *Vo* virgiboidine; *OH* monohydroxylated alkaloids; *PH* polyhydroxylated alkaloids; *Est* esters of mono- and polyhydroxylated alkaloids. Solid lines indicate presence; broken lines indicate absence

Podalyria, *Stirtonanthus* and *Liparia*; (4) a group specializing in the 10-oxo pathway with subsequent esterification, e.g. *Stirtonanthus*, *Virgilia* and *Calpurnia*; (5) a group producing lupanine-type esters, e.g. *Calpurnia*, *Virgilia*, *Stirtonanthus*, *Podalyria* and *Liparia*. These different specializations are included as characters in the cladistic analyses below.

Canavanine. A detailed survey of the occurrence of canavanine, a non-protein amino acid, in legume seeds was carried out by Bell & al. (1978). Once again, *Hypocalyptus* is incongruent in being the only member of the *Podalyrieae* and *Liparieae*, which does accumulate canavanine in its seeds. All three the species tested positive for canavanine. Elsewhere, this component is known from the tribes *Desmodieae*, *Indigofereae*, *Trifolieae*, *Galegeae*, *Robinieae*, *Sesbanieae*, *Bossiaeeae* and some genera of the *Mirbelieae*, *Phaseoleae*, *Coronilleae*, *Vicieae* and *Millettieae*. Phylogenetically, the absence of canavanine is here interpreted as apomorphic at the suprageneric level.

Anthocyanins. The anthocyanins in the pink-, purple- or white-flowered species of *Virgilia*, *Podalyria*, *Coelidium*, *Amphithalea* and *Hypocalyptus* have been studied by Van Wyk & Winter (1994) and Van Wyk & al. (1995). It was established that flower pigmentation is conservative within the genera but that each of the genera contains an unique combination of anthocyanins.

Virgilia and *Podalyria* differ from each other in the presence of a coumaroyl ester, cyanidin-3-(p-coumaroylglucoside), in *Podalyria*, whilst acetic acid esters of cyanidin-3-glucoside and peonidin-3-glucoside are restricted to *Virgilia* (Van Wyk & Winter 1994). In the *Liparieae*, the flowers of *Amphithalea* and *Coelidium* accumulate esters of cyanidin-3-glucoside, but in *Amphithalea* it is esterified with acetic acid and in *Coelidium* with coumaric acid (Van Wyk & al. 1995). The 3-sophorosides of cyanidin and pelargonidin are responsible for the red flower colour in *Liparia*. All these genera contain cyanidin-3-glucoside, except *Hypocalyptus*, where malvidin-3-glucoside is the only compound present in the flower petals. This indicates that even in its floral pigments, *Hypocalyptus* deviates from the rest of the *Liparieae*.

The presence of esters of anthocyanins and cyanidin-3-glucoside in all the pink- and purple-flowered genera (excluding *Hypocalyptus*) offers additional evidence that the *Podalyrieae* and *Liparieae* are monophyletic. In particular, the accumulation of esters of anthocyanins, appears to be unique for the two tribes. All other legumes for which data are available (and *Hypocalyptus*) have glucosides only.

Cladistic analyses

Cladograms were generated by using the computer software package Hennig 86 (Farris 1988). Character states were polarized using the method of outgroup comparison. The "mhennig*", "bb*" and "ie" algorithms were applied to produce trees of minimal length. Autapomorphies have been excluded from the analyses as they serve no purpose as grouping characters.

Four separate analyses of relationships were carried out (Tables 2–5; Figs. 9, 10). In the first analysis, the *Mirbelieae*, *Crotalarieae* and an hypothetical ancestor were used as outgroups, due to the perplexity regarding the affinity of

Table 2. Characters and character states used for the cladistic analysis of the genera of the *Podalyrieae* and *Liparieae*, with the *Mirbelieae*, *Crotalarieae*, *Cadia* and an hypothetical ancestor as outgroups. The fully resolved cladogram generated from this data set is shown in Fig. 9

Genera	Character states					
Hypothetical Ancestor	00000	00000	00000	00000	00000	00
Mirbelieae	1?000	00000	00001	01100	00000	00
Crotalarieae	11100	00000	00101	01100	10000	01
Cadia	00000	00000	00000	000?0	10110	01
Calpurnia	00000	10101	01101	01110	11110	11
Cyclopia	11100	00101	01101	01110	00000	01
Podalyria	11100	00101	01101	01110	10010	11
Stirtonanthus	11100	00101	01101	01110	10110	11
Virgilia	00000	10101	01001	01110	11110	01
Amphithalea	11111	01110	10111	11111	00001	01
Coelidium	11111	01110	10111	11111	00001	01
Hypocalyptus	10100	00001	01100	00000	00000	00
Liparia	11110	00101	01101	01110	10011	01
Xiphotheca	11111	01100	10101	01111	01000	01

Characters

1. Habit: trees (0); shrubs (1).
2. Secondary xylem: vessels arranged in small tangential and/or radial groups (0); vessels arranged in large confluent groups (1).
3. Leaf type: pinnate (0); digitate or simple (1).
4. Petiole: present (0); strongly reduced or absent (1).
5. Stipules: present (0); strongly reduced or absent (1).
6. Hairy filaments: absent (0); at least sometimes present (1).
7. Inflorescence type: not geminate (0); geminate (1).
8. Bracteoles: present and conspicuous in most taxa (0); inconspicuous or absent in most taxa (1).
9. Hypanthium: not prominent (0); prominent (1).
10. Calyx base: not intrusive (0); intrusive (1).
11. Wing petals: not lobed towards the inside (0); thickly lobed towards the inside (1).
12. Keel apex: obtuse (0); rostrate or beaked (1).
13. Stamen fusion: totally free (0); fused (1).
14. Ovule number: several ovules (0); 1 or 2 ovules (1).
15. Seed aril: continuous around hilum (0); interrupted at micropylar end (1).
16. Seed aril shape: aril not extended towards the lens (0); aril extended towards the lens (1).
17. Seed micropyle type: ypsaloid (0); punctate (1).
18. Seed micropyle position: outside the hilum (0); inside the hilum or on the rim (1).
19. Antipodals: not persistent (0); persistent (1). [Giant antipodals as in some *Mirbelieae* (Cameron & Prakash 1990) is considered to be a separate development.]
20. Piperidyl alkaloids: low concentrations or absent (0); present as major compounds in most taxa (1).
21. Tetracyclic quinolizidine alkaloids: absent (0); present (1).
22. Bicyclic quinolizidine alkaloids: absent (0); present (1).
23. Carboxylic acid esters of alkaloids: absent (0); present (1).
24. Esterification of monohydroxylated lupanines: absent (0); present (1).
25. Ammodendrine: absent (0); present as a major compound in at least some taxa (1).
26. Esterification of polyhydroxylated lupanines: absent (0); present (1).
27. Canavanine: present (0); absent (1).

Table 3. Characters and character states used for the cladistic analysis of the genera of the *Podalyrieae*, using the *Mirbelieae* as an outgroup. The fully resolved cladogram generated from this data set is shown in Fig. 10A

Genera	Character states						
Mirbelieae	1?000	00000	00000	00000	00000	00000	000
Calpurnia	00000	00000	01001	11000	01010	11110	111
Cyclopia	11100	10111	01011	01011	00000	00100	010
Podalyria	11100	10101	01011	01011	00000	10110	110
Stirtonanthus	11100	10101	01011	01011	01010	11110	110
Virgilia	00000	00101	01011	11011	01010	11110	011
Amphithalea	11111	11001	10100	00100	10101	00101	010
Coelidium	11111	11001	10100	00100	10101	00101	010
Liparia	11110	10111	01011	01111	00000	10111	010
Xiphotheca	11111	11000	00100	00100	00001	00100	011

Characters

1. Habit: trees (0); shrubs (1).
2. Secondary xylem: vessels arranged in small tangential and/or radial groups (0); vessels arranged in large confluent groups (1).
3. Leaf type: pinnate (0); digitate or simple (1).
4. Petiole: present (0); strongly reduced or absent (1).
5. Stipules: present (0); strongly reduced or absent (1).
6. Inflorescence position: not axillary (0); axillary (1).
7. Inflorescence type: racemose (0); geminate (1).
8. Bracts: not sheathing (0); sheathing (1).
9. Sterile bracts: absent (0); present (1).
10. Bracteoles: present (0); absent (1).
11. Hypanthium: not prominent (0); prominent (1).
12. Calyx base: not intrusive (0); at least sometimes intrusive (1).
13. Wing petals: not lobed towards the inside (0); thickly lobed towards the inside (1).
14. Corolla: not firmly textured (0); firmly textured (1).
15. Keel apex: obtuse (0); rostrate or beaked (1).
16. Filaments: not hairy (0); at least sometimes hairy (1).
17. Filaments: not thickened at base (0); thickened at base (1).
18. Stamen fusion: totally free or slightly fused (0); fused high up (1).
19. Nectar well: upper stamens not modified (0); upper stamens modified to form a circular opening (1).
20. Anthers: not dimorphic or slightly dimorphic (0); strongly dimorphic (1).
21. Ovule number: several ovules (0); 1 or 2 ovules (1).
22. Seed aril: fleshy (0); non-fleshy (1).
23. Seed aril shape: aril not extended towards the lens (0); aril extended towards the lens (1).
24. Seed aril type: collar-like (0); rim-like (1).
25. Piperidyl alkaloids: low concentrations or absent (0); present as major compounds in most taxa (1).
26. Tetracyclic quinolizidine alkaloids: absent (0); present (1).
27. Carboxylic acid esters: absent (0); present (1).
28. Canavanine: present (0); absent (1).
29. Esterification of monohydroxylated lupanines: absent (0); present (1).
30. Ammodendrine: absent (0); present as a major compound in at least some taxa (1).
31. Esterification of polyhydroxylated lupanines: absent (0); present (1).
32. Antipodals: ephemeral or absent (0); persistent (1).
33. Bicyclic quinolizidine alkaloids: absent (0); present (1).

Table 4. Characters and character states used for the cladistic analysis of the genera of the *Podalyrieae*, using the *Crotalarieae* as an outgroup. The fully resolved cladogram generated from this data set is shown in Fig. 10B

Genera	Character states						
Crotalarieae	11100	00000	00000	00000	00000	00000	00
Calpurnia	00000	00000	01001	11100	00011	01111	11
Cyclopia	11100	10111	01011	01110	10101	10010	01
Podalyria	11100	10101	01011	01110	10101	00111	01
Stirtonanthus	11100	10101	01011	01110	00001	01111	01
Virgilia	00000	00101	01011	11110	00011	01110	11
Amphithalea	11111	11001	10100	00001	11100	10000	01
Coelidium	11111	11001	10100	00001	11100	10000	01
Liparia	11110	10111	01011	01010	10101	00100	01
Xiphotheca	11111	11000	00100	00000	10110	10010	11

Characters

1. Habit: trees (0); shrubs (1);
2. Secondary xylem: vessels arranged in small tangential and/or radial groups (0); vessels arranged in large confluent groups (1).
3. Leaf type: pinnate (0); digitate or simple (1).
4. Petiole: present (0); strongly reduced or absent (1).
5. Stipules: present (0); strongly reduced or absent (1).
6. Inflorescence position: not axillary (0); axillary (1).
7. Inflorescence type: racemose (0); geminate (1).
8. Bracts: not sheathing (0); sheathing (1).
9. Sterile bracts: absent (0); present (1).
10. Bracteoles: present (0); absent (1).
11. Hypanthium: not prominent (0); prominent (1).
12. Calyx base: not intrusive (0); intrusive (1).
13. Wing petals: not lobed towards the inside (0); thickly lobed towards the inside (1).
14. Corolla: not firmly textured (0); firmly textured (1).
15. Keel apex: obtuse (0); rostrate or beaked (1).
16. Filaments: not hairy (0); at least sometimes hairy (1).
17. Filaments: not thickened at base (0); thickened at base (1).
18. Stamen fusion: fused high up (0); slightly fused or totally free (1).
19. Nectar well: upper stamens not modified (0) upper stamens modified to form a circular opening (1).
20. Ovule number: several ovules (0); 1 or 2 ovules (1).
21. Seed aril: non-fleshy (0); fleshy (1).
22. Seed aril shape: aril not extended towards the lens (0); aril extended towards the lens (1).
23. Seed aril type: rim-like (0); collar-like (1).
24. Pods: generally inflated (0); compressed (1).
25. Piperidyl alkaloids: present as major compounds in most taxa (0); low concentrations or absent (1).
26. Tetracyclic quinolizidine alkaloids: present (0); absent (1).
27. Carboxylic acid esters: absent (0); present (1).
28. Esterification of monohydroxylated lupanines: absent (0); present (1).
29. Ammodendrine: present as a major compound in at least some taxa (0); absent (1).
30. Esterification of polyhydroxylated lupanines: absent (0); present (1).
31. Bicyclic quinolizidine alkaloids: absent (0); present (1).
32. Antipodals: not persistent (0); persistent (1).

Table 5. Characters and character states used for the cladistic analysis of the genera of the *Podalyrieae*, using the genus *Cadia* as outgroup. The fully resolved cladogram generated from this data set is shown in Fig. 10C

Genera	Character states					
Cadia	00000	10000	00000	00000	00000	0000
Calpurnia	00000	00000	01001	11100	00011	0000
Cyclopia	11100	10111	01101	10111	01011	0110
Podalyria	11100	10101	01101	10111	01011	0010
Stirtonanthus	11100	10101	01101	10111	00011	0000
Virgilia	00000	00101	01101	11011	00011	0000
Amphithalea	11111	11001	10010	00100	11111	1111
Coelidium	11111	11001	10010	00100	11111	1111
Liparia	11110	10111	01101	10111	01011	0011
Xiphotheca	11111	11000	00010	00100	01011	1110

Characters

1. Habit: trees (0); shrubs (1);
2. Secondary xylem: vessels arranged in small tangential and/or radial groups (0); vessels arranged in large confluent groups (1).
3. Leaf type: pinnate (0); digitate or simple (1).
4. Petiole: present (0); strongly reduced or absent (1).
5. Stipules: present (0); strongly reduced or absent (1).
6. Inflorescence position: terminal (0); axillary (1).
7. Inflorescence type: racemose (0); geminate (1).
8. Bracts: not sheathing (0); sheathing (1).
9. Sterile bracts: absent (0); present (1).
10. Bracteoles: present (0); absent (1).
11. Hypanthium: not prominent (0); prominent (1).
12. Calyx base: not intrusive (0); intrusive (1).
13. Corolla: not firmly textured (0); firmly textured (1).
14. Wing petals: not lobed towards the inside (0); thickly lobed towards the inside (1).
15. Keel apex: obtuse (0); rostrate or beaked (1).
16. Filaments: not thickened at base (0); thickened at base (1).
17. Filaments: not hairy (0); hairy (1).
18. Stamen fusion: totally free (0); fused (1).
19. Nectar well: upper stamens not modified (0); upper stamens modified to form a circular opening (1).
20. Anthers: not dimorphic or slightly dimorphic (0); strongly dimorphic (1).
21. Ovule number: several ovules (0); 1 or 2 ovules (1).
22. Seed aril: non-fleshy (0); fleshy (1).
23. Seed aril shape: aril not extended towards the lens (0); aril extended towards the lens (1).
24. Seed aril: not interrupted at micropylar end (0); interrupted (1).
25. Micropyle shape: ypsaloid (0); punctate (1).
26. Piperidyl alkaloids: low concentrations or absent (0); present as major compounds in most taxa (1).
27. Tetracyclic quinolizidine alkaloids: present (0); absent (1).
28. Carboxylic acid esters: present (0); absent (1).
29. Ammodendrine: absent (0); present as a major compound in at least some taxa (1).

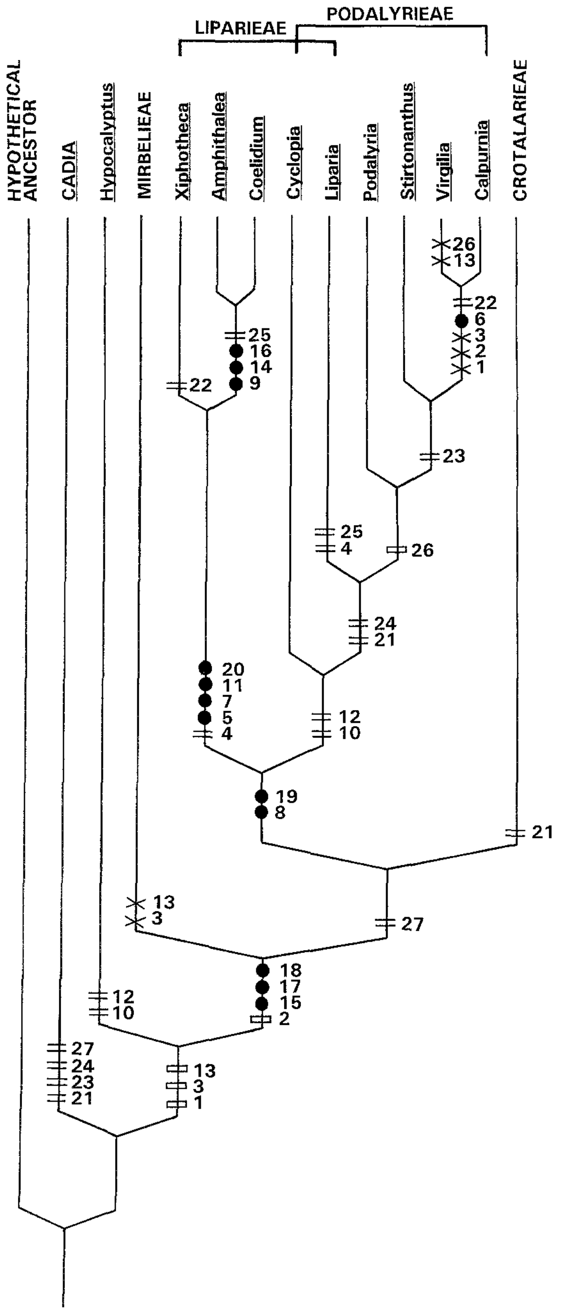

Fig. 9. Fully resolved cladogram of relationships at tribal and generic level, based on Table 2. ● apomorphy without homoplasy; ☐ apomorphy with subsequent reversal; = convergence; x reversal

Hypocalyptus (Table 2). *Cadia* was also included in the investigation to determine whether it should be included in the *Podalyrieae*. Information on the *Crotalarieae* came from Van Wyk & Schutte (1995b). Data for the *Mirbelieae* were taken from Polhill (1976, 1981c) and Crisp & Weston (1987, 1995), whilst Van der Maesen (1970) was consulted for details on the genus *Cadia*. A single fully resolved

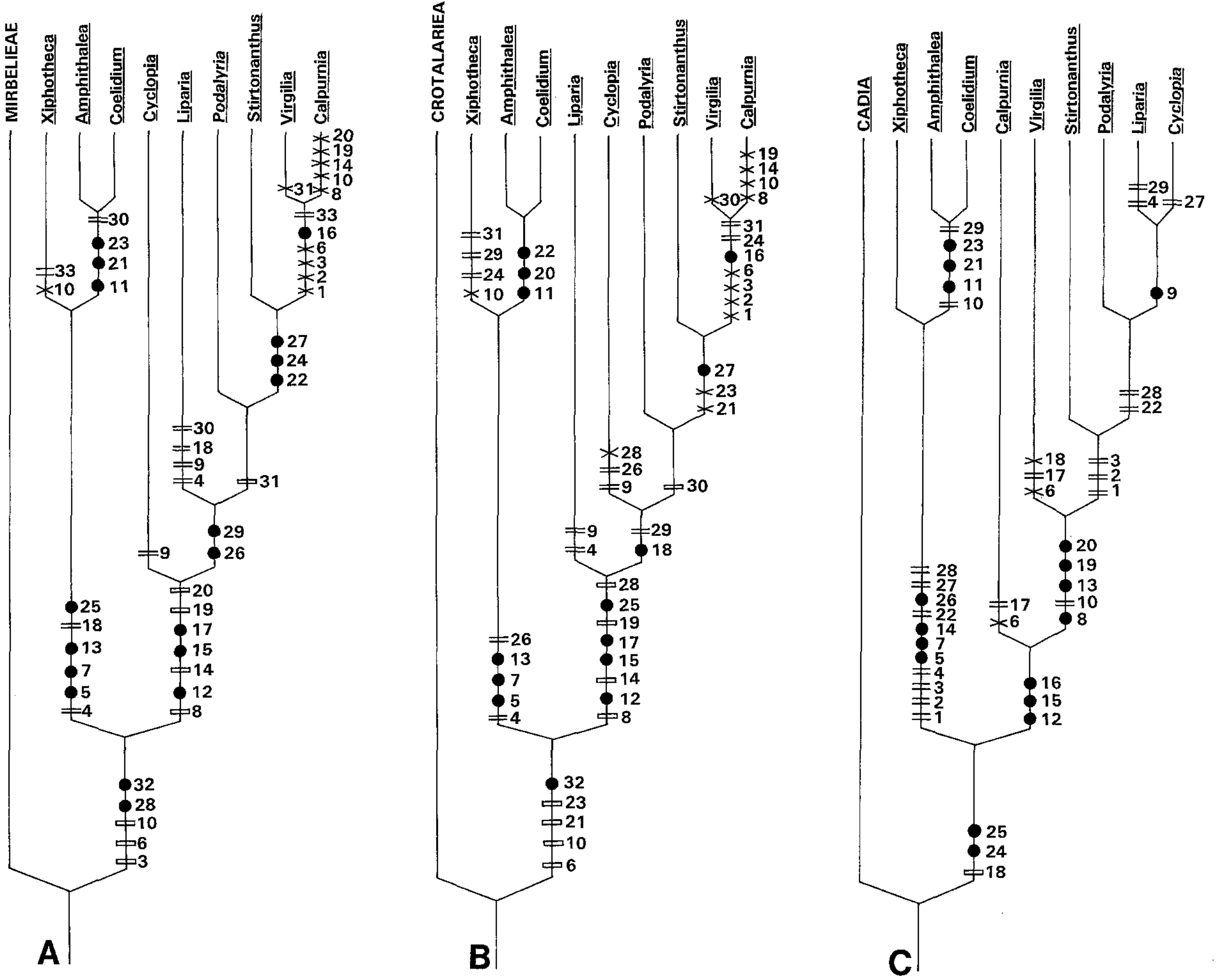

Fig. 10. Fully resolved cladograms of relationships in the *Podalyrieae* and *Liparieae* (excluding *Hypocalyptus*). Topology A is based on Table 3, with the *Mirbelieae* as outgroup. Topology B is based on Table 4, with the *Crotalarieae* as outgroup and topology C on Table 5, with *Cadia* as outgroup. – Symbols as in Fig. 9

cladogram was generated from the data set (Fig. 9; consistency index 61, length 44, retention index 77). The result clearly indicates that the *Podalyrieae* plus *Liparieae* are monophyletic, with at least two apomorphies supporting the clade. Furthermore, it is also evident that *Hypocalyptus* is quite unlike any of the other genera or tribes included in the investigation. *Cadia* does not seem to fit into the *Podalyrieae* either.

In the remaining three analyses, the relationships between the genera of the *Podalyrieae* and *Liparieae* were examined, using the *Mirbelieae*, *Crotalarieae* and *Cadia* as outgroups respectively. The data sets are shown in Tables 3–5. *Hypocalyptus* was omitted from these investigations, since it dropped to a basal position in the previous analysis. Each analysis resulted in one fully resolved topology (Fig. 10 A–C), but with the *Mirbelieae* as outgroup, the cladogram had a consistency index of 70 (length 47, retention index 80), with the *Crotalarieae* as outgroup, a consistency index of 66 (length 48, retention index 78) and with *Cadia* as outgroup, a consistency index of 70 (length 41, retention index 80). Two major clades are apparent in all three the cladograms, each supported by at least three synapomorphies: (1) a *Xiphotheca* clade, with *Amphithalea* and *Coelidium*, and (2) a *Podalyria* clade, with *Cyclopia*, *Liparia*, *Stirtonanthus*, *Virgilia* and *Calpurnia*. In the *Xiphotheca* clade, a sister relationship between *Amphithalea* and *Coelidium* is supported by three shared derived characters. The only obvious difference between topologies A and B, lies in the positions of *Cyclopia* and *Liparia* in the *Podalyria* clade, where *Cyclopia* is basal in cladogram A, and *Liparia* basal in cladogram B. In topology C, however, the sequence of genera in the *Podalyria* clade is completely the reverse of A and B.

Discussion

Convincing evidence for an enlarged *Podalyrieae* (excluding *Hypocalyptus*) is provided by at least two synapomorphies (Fig. 9), namely the strongly reduced or absent bracteoles and the occurrence of persistent antipodals in the female gametophyte. To these may be added the accumulation of esters of anthocyanins in all the pink, purple and orange-flowered species. Other apomorphies include the absence of canavanine in the seed, punctate micropyle and interrupted seed aril, depending on which outgroup is used.

Previously, Van Wyk & Schutte (1995b) also found the two tribes to be monophyletic if *Hypocalyptus* is omitted, but both tribes were monophyletic on their own and it was therefore decided to retain them as separate taxa. In the cladograms presented above, however, *Liparia* grouped with the *Podalyrieae* clade rather than the *Xiphotheca* clade, thereby implicating a stronger relationship with the former than the latter. Based on the available data, the present topology appears to be an improved representation of possible relationships between the tribes. *Liparia* has more characters in common with the *Podalyria* clade, than with the *Xiphotheca* group. In fact, the basal split into these two phylogenetic groups resulted from each analysis, regardless of the choice of outgroup. The two main clades are given subtribal status in an enlarged *Podalyrieae* in the taxonomic treatment below.

This provides sound evidence for earlier suggestions (Polhill 1976, 1981d, e; Van Wyk & Schutte 1995b) that the *Podalyrieae* and *Liparieae* should be amalgamated. The primary reason for the separation between the two tribes has been weighting of the stamen character. Traditionally free stamens have been used as the essential feature of the *Podalyrieae*, but in recent years it has been recorded to segregate some natural groups. For instance, a diadelphous stamen arrangement has excluded *Calpurnia* from the *Podalyrieae*. Van Wyk & Schutte (1995b) proved that this character is over-shadowed by at least four synapomorphies, indicating a strong sister relationship between *Virgilia* and *Calpurnia*. Moreover, it has been found that the stamen character breaks down in some genera, e.g. *Podalyria*, where they are often strictly diadelphous (Schutte, pers. obs.).

The three cladograms in Fig. 10 A–C are identical, except for variation in the sequence of branching in the *Podalyria* clade. Topologies A and B differ only in the positions of *Liparia* and *Cyclopia*. In topology A, *Cyclopia* is basal to the clade, with *Liparia*, *Podalyria*, *Stirtonanthus*, *Virgilia* and *Calpurnia* forming a monophyletic group, supported by two synapomorphies (i.e. presence of tetracyclic quinolizidine alkaloids and esterification of monohydroxylated lupanines). In this tree, *Liparia* is well-separated from the *Xiphotheca* clade and the uniqueness of *Cyclopia* seems to stand out. Topology B has *Liparia* basal to the clade, thereby reflecting its affinity with the *Xiphotheca* group. Apart from its strong relationship with the *Podalyria* group, *Liparia* also has a number of characters in common with *Xiphotheca*, *Amphithalea* and *Coelidium* (e.g. strongly reduced or absent petioles and accumulation of ammodendrine). In this clade, *Cyclopia* forms a natural group with *Podalyria*, *Stirtonanthus*, *Virgilia* and *Calpurnia*, which is subtended by two apomorphies (i.e. slightly fused or free stamens and absence of ammodendrine).

The sequence of branching of the *Podalyria* clade in topology C is precisely the reverse of the other two topologies. From a biogeographical point of view, this sequence is probably the most reasonable hypothesis of evolutionary relationships, in terms of a progression from a widespread to a reduced distribution area. [*Calpurnia* is a widespread summer rainfall genus, occurring from the southern Cape region in South Africa, northwards along the highlands of Africa to India. All the other genera are restricted to the winter rainfall Cape Floristic Region of South Africa (SCHUTTE & VLOK, unpubl.).] Yet in this case, *Cadia* was used as outgroup, which in the first analysis proved not to be closely related to the *Podalyrieae*. The taxonomic significance of additional chemical and genetic characters is currently under investigation (i.e. electrophoretic, flavonoid and DNA studies). It is not impossible that these or other future studies may indicate that *Cadia* should be moved to a position closer to the *Podalyrieae*.

According to the results, the *Podalyrieae* appear to be well-placed between the African *Crotalarieae* and the Australian clade. There is no valid evidence to support a direct connection between the *Podalyrieae* and the Australian tribes, as has been proposed by CRISP & WESTON (1987). However, little doubt exists about the affinity between the African *Podalyrieae* and *Crotalarieae* (VAN WYK & SCHUTTE 1995b). We therefore favour topology B, where the *Crotalarieae* were used as outgroup. In this cladogram, *Liparia* is basal to the *Podalyria* clade and not far removed from the *Xiphotheca* group, with which it also shares a number of characters.

Hypocalyptus remains a problem as far as its taxonomic position is concerned. It evidently does not fit into any of the tribes included in this study. A paper dealing with its position and status within subfam. *Papilionoideae* will be published elsewhere (SCHUTTE & VAN WYK 1997).

Taxonomic treatment

Tribe *Podalyrieae* BENTH. emend. A. L. SCHUTTE emend. nov., BENTH. Comm. Leg. Gen., 1 (1837); BENTH. in Ann. Wien. Mus. **2**: 65 (1839); HARV. in HARV. & SOND., Fl. Cap. **2**: 2 (1862); HUTCH., Gen. Fl. Pl. **1**: 336 (1964); POLHILL in POLHILL & RAVEN, Adv. Leg. Syst. **1**: 396 (1981); YAKOVLEV, Bobovye Zemnogo

Shara, 85 (1991); Van Wyk & Schutte in Crisp & Doyle, Adv. Leg. Syst. **7**: 304 (1995).

Loteae DC. subtribe *Lipariinae* Benth. in Hook., London J. Bot. **2**: 441 (1843), as '*Liparieae*'.

Genisteae Benth. subtribe *Lipariinae* (Benth.) Benth. in Benth. & Hook. f., Gen. Pl. **1**: 439 (1865), as '*Liparieae*'.

Liparieae (Benth.) Harv. in Harv. & Sond., Fl. Cap. **2**: 2 (1862) syn. nov.; Hutch., Gen. Fl. Pl. **1**: 346 (1964); Polhill in Bot. Syst. **1**: 313 (1976) p. p.; Polhill in Polhill & Raven, Adv. Leg. Syst. **1**: 398 (1981) p. p.; Van Wyk & Schutte in Crisp & Doyle, Adv. Leg. Syst. **7**: 304 (1995).

Liparieae (Benth.) Harv. subtribe *Lipariinae* (Benth.) Benth., Yakovlev, Bobovye Zemnogo Shara, 87 (1991) syn. nov.

Trees, shrubs or subshrubs. Leaves imparipinnate, digitately trifoliolate or simple; petiole present or reduced to a pulvinus only; leaf bases ± prominent; stipules present, sometimes strongly reduced. Inflorescences axillary racemes or terminal panicles, 1-several -flowered; peduncles present or absent; bracts small or enlarged, often sheathing at the base, sometimes brightly coloured; bracteoles rarely present. Pedicels present or absent. Calyx with base intrusive or with a prominent hypanthium; two upper lobes fused higher up than lower three; carinal lobe as large as or sometimes much larger than the others. Corolla yellow, pink, mauve, white or reddish-orange, totally glabrous. Bracteoles strongly reduced or absent. Standard thickly textured with strongly reflexed claw or thinly textured with slightly reflexed claw; base sometimes auriculate; apex emarginate. Wing petals sometimes auriculate and pocketed; petal sculpturing sometimes present. Keel petals obtuse, shortly or strongly beaked, sometimes auriculate; pocket present or absent. Stamens 10, free, monadelphous or diadelphous; anthers subequal to dimorphic, alternately short dorsifixed, long basifixed or subbasifixed. Pistil sessile; ovary 1–22 -ovuled; style curved upwards with base often hairy. Pods coriaceous, dehiscent, mostly inflated, sometimes compressed between the seeds. Seeds reniform, with a small radicular lobe; micropyle punctate; aril fleshy collar-like or non-fleshy rim. Chromosome number $2n = 18, 36, 54, \pm 126$. Nine genera, all restricted to the Cape, except *Calpurnia* which extends through Africa to India.

Key to the genera

1\. Leaves imparipinnate, leaflets several 2
1\. Leaves digitate or simple, leaflets 1 or 3 3
2\. Flowers pink, purple or white; stamens free . . . . 8. *Virgilia*
2\. Flowers yellow; stamens fused . . . . 9. *Calpurnia*
3\. Leaves digitately 3-foliolate; bracts paired . . . . 5. *Cyclopia*
3\. Leaves simple; bracts single 4
4\. Stamens free almost to the base 5
4\. Stamens diadelphous or monadelphous 6
5\. Flowers yellow, decussate (arranged in opposite pairs of 2, 4 or 6 flowers); seeds with a non-fleshy rim-aril . . . . 7. *Stirtonanthus*

5. Flowers pink, mauve or white, racemose (1–5 flowers per raceme); seeds with a fleshy collar-like aril . . . . 6. *Podalyria*
6. Calyx with base intrusive; carinal lobe of calyx usually longer than the upper 4 lobes; leaves sessile, 3- or more-veined from the base; inflorescences 4- many-flowered (rarely 2-flowered); bracts often leaf-like . . . . 4. *Liparia*
6. Calyx with base gradually narrowing to the pedicel; carinal lobe of calyx usually as long as the upper 4 lobes; leaves usually petiolate or at least with a pulvinus, single veined from the base; inflorescences 1- or 2-flowered; bracts not leaf-like 7
7. Flowers yellow, fading to brown with age; bracteoles often present; aril not extended towards the lens; pods compressed between the seeds . . . 1. *Xiphotheca*
7. Flowers mostly pink, mauve or white (if rarely yellow, then less than 10 mm long and not fading to brown with age); bracteoles totally absent; aril extended towards the lens; pods not compressed between the seeds 8
8. Vexillary filament fused with other filaments . . . . 3. *Coelidium*
8. Vexillary filament free down to hypanthium. . . . . 2. *Amphithalea*

Subtribe *Xiphothecinae* A. L. SCHUTTE subtribus nova; subtribus Podalyriinis affinis, a qua basis calycis non intrusis et apicibus carinis obtusis differt.

Type: *Xiphotheca* ECKL. & ZEYH.

This subtribe is recognized by its non-intrusive calyx base, obtuse keel apex, reduced number of ovules and the wing petals, which have a thickened lobe on the abaxial surface. Three genera constitute the subtribe.

1. *Xiphotheca* ECKL. & ZEYH., Enum. Pl. Afric. Austral. **2**: 166 (1836); SCHUTTE & VAN WYK in Taxon **42**: 45 (1993); VAN WYK & SCHUTTE in CRISP & DOYLE, Adv. Leg. Syst. **7**: 305 (1995); SCHUTTE in Ann. Missouri Bot. Gard. **84**: 93 (1997). Nine species.

2. *Amphithalea* ECKL. & ZEYH., Enum. **2**: 167 (1836); BENTH. in HOOK., London J. Bot. **2**: 442 & 449 (1843); HARV. in HARV. & SOND., Fl. Cap. **2**: 21 (1862); HUTCH., Gen. Fl. Pl. **1**: 347 (1964); DYER, Gen. **1**: 247 (1975); POLHILL in Bot. Syst. **1**: 316 (1976); POLHILL in POLHILL & RAVEN, Adv. Leg. Syst. **1**: 398 (1981); GRANBY in Opera Bot. **80**: 12 (1985); VAN WYK & SCHUTTE in CRISP & DOYLE, Adv. Leg. Syst. **7**: 305 (1995). Twenty-one species.

3. *Coelidium* VOGEL ex WALP. in Linnaea **13**: 472 (1839).; BENTH. in HOOK., London J. Bot. **2**: 442 & 453 (1843); HARV. in HARV. & SOND., Fl. Cap. **2**: 24 (1862); HUTCH., Gen. Fl. Pl. **1**: 350 (1964); DYER, Gen. **1**: 248 (1975); POLHILL in Bot. Syst. **1**: 316 (1976); GRANBY in Opera Bot. **54**: 12 (1980); POLHILL in POLHILL & RAVEN, Adv. Leg. Syst. **1**: 398 (1981); VAN WYK & SCHUTTE in CRISP & DOYLE, Adv. Leg. Syst. **7**: 305 (1995). Twenty-one species.

Subtribe *Podalyriinae*

Subtribe *Podalyriinae* has an intrusive calyx base and a beaked keel tip. It consists of six genera.

4. *Liparia* L., Mant. **2**: 156 (1771); DC., Prodr. **2**: 121 (1825); BENTH. in HOOK., London J. Bot. **2**: 442 (1843); HARV. in HARV. & SOND., Fl. Cap. **2**: 14 (1862); HUTCH., Gen. Fl. Pl. **1**: 347 (1964); Bos in J. S. Afr. Bot. **33**: 272 (1967); DYER, Gen. **1**: 246 (1975); POLHILL in Bot. Syst. **1**: 315 (1976); POLHILL in POLHILL &

RAVEN, Adv. Leg. Syst. **1**: 397 (1981); SCHUTTE & VAN WYK in Taxon **43**: 577 (1994); VAN WYK & SCHUTTE in CRISP & DOYLE, Adv. Leg. Syst. **7**: 305 (1995); SCHUTTE in Nordic J. Bot. **17** (1): (1997c). Twenty species.

5. *Cyclopia* VENT., Dec. Gen. Nov., 8 (1808); DC., Prodr. **2**: 101 (1825), Mém. Lég., 167 (1826); BENTH. in Ann. Wien. Mus. **2**: 67 (1839); BENTH. in HOOK., London J. Bot. **2**: 432 (1843); HARV. in HARV. & SOND., Fl. Cap. **2**: 6 (1862); HOFMEYR & E. PHILLIPS in Bothalia **1**: 106 (1922); KIES in Bothalia **6**: 162 (1951); HUTCH., Gen. Fl. Pl. **1**: 343 (1964); DYER, Gen. **1**: 246 (1975); POLHILL in POLHILL & RAVEN, Adv. Leg. Syst. **1**: 397 (1981); VAN WYK & SCHUTTE in CRISP & DOYLE, Adv. Leg. Syst. **7**: 304 (1995); SCHUTTE in Edinburgh J. Bot. **54** (2): (1997d). 23 species.

6. *Podalyria* LAM., Illustr. **2**: 454, t. 327, f. 3 (1793); DC., Prodr. **2**: 101 (1825); ECKL. & ZEYH., Enum. **2**: 155 (1836); E. MEY., Comm. **1**: 4 (1836); BENTH. in Ann. Wien. Mus. **2**: 67 (1839); BENTH. in Hook., London J. Bot. **2**: 435 (1843); HARV. in HARV. & SOND., Fl. Cap. **2**: 9 (1862); HUTCH., Gen. Fl. Pl. **1**: 339 (1964); DYER, Gen. **1**: 246 (1975); POLHILL in POLHILL & RAVEN, Adv. Leg. Syst. **1**: 397 (1981); VAN WYK & SCHUTTE in CRISP & DOYLE, Adv. Leg. Syst. **7**: 304 (1995). Nineteen species.

7. *Stirtonanthus* B.-E. VAN WYK & A. L. SCHUTTE in Nordic J. Bot. **15**: 67 (1995). Three species.

8. *Virgilia* POIR., Encycl. **8**: 677 (1808); DC., Prodr. **2**: 98 (1825); E. MEY., Comm. **1**: 1 (1836); HARV. in HARV. & SOND., Fl. Cap. **2**: 2: 266 (1862); HUTCH., Gen. Fl. Pl. **1**: 323 (1964); YAKOVLEV in Bot. Zhurn. **55**: 837 (1970); PALMER & PITMAN, Trees S. Afr. **2**: 903 (1973); DYER, Gen. **1**: 245 (1975); COATES PALGRAVE, Trees. S. Afr., 301 (1977); POLHILL in POLHILL & RAVEN, Adv. Leg. Syst. **1**: 397 (1981); VAN WYK in S. African J. Bot. **52**: 348 (1986); VAN WYK & SCHUTTE in CRISP & DOYLE, Adv. Leg. Syst. **7**: 304 (1995). Two species.

9. *Calpurnia* E. MEY., Comm. **1**: 2 (1836); BENTH. in Ann. Wien. Mus. **2**: 89 (1839); HARV. in HARV. & SOND., Fl. Cap. **2**: 266 (1862); HUTCH., Gen. Fl. Pl. **1**: 329 (1964); DYER, Gen. **1**: 244 (1975); POLHILL in POLHILL & RAVEN, Adv. Leg. Syst. **1**: 229 (1981); VAN WYK & SCHUTTE in CRISP & DOYLE, Adv. Leg. Syst. **7**: 304 (1995). Seven species.

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