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A morphological cladistic analysis of *Lobostemon* (Boraginaceae)

M.H. Buys

A.P. Goossens Herbarium, Plantkunde, Skool vir Omgewingswetenskappe en -ontwikkeling, Noordwes-Universiteit, Privaatsak X6001, Potchefstroom 2520, South Africa

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Abstract

A cladistic analysis of *Lobostemon* (Boraginaceae) based on morphological data is presented. The data matrix comprises 28 ingroup taxa and *Echiostachys incanus* and *Pontechium maculatum* as the outgroups. 31 vegetative and floral characters are used. The three most parsimonious trees and the strict consensus tree derived from them produces 4 monophyletic groups within *Lobostemon*, corresponding to four sections within the genus. Section *Grandiflori* Levyns is paraphyletic. Medium sized flowers, and the presence of staminal scales and stigma branches are synapomorphies for *Lobostemon*. New hypotheses, include actinomorphic flowers to be derived and Section *Argentei* to be sister to the rest of the genus.

Keywords: Lobostemon; Boraginaceae; Morphology; Cladistics

1. Introduction

Lobostemon Lehm. was last revised 71 years ago by Levyns (1934a). Since then many changes have taken place in systematics, including new techniques and concepts such as cladistics and monophyly which can now be applied for the first time to the genus.

The history of *Lobostemon* Lehm. begins with its description by Lehmann (1830), based on a plant grown in the Botanical Gardens at Hamburg, Germany. Lehmann stressed the presence of staminal scales in *Lobostemon* in distinguishing it from *Echium* L. From the outset there has been no consensus on the taxonomic status of *Lobostemon* in relation to *Echium*. Buek (1837) transferred 33 species, most of which had been formerly included in *Echium*, to *Lobostemon* by extending Lehmann's generic concept to include those taxa in which the staminal scales are reduced or absent, and distinguished *Echium* from *Lobostemon* through the former possessing glabrous (and slightly thickened) stamen bases. De Candolle (1846) followed Lehmann's narrow definition of *Lobostemon* and transferred back to *Echium* those taxa lacking definite staminal scales. Gürke (1897) once again transferred a number of *Echium* taxa back to *Lobostemon*, this time citing the bilobed stigmas of the latter and the bifid stigmas of the former as the main difference between the two. Wright (1904), being oblivious of Gürke (1897), independently moved *Echium* taxa without clear staminal scales, but with hairy stamen bases, back to *Lobostemon*. For one reason or another, Wright did not return *E. formosum* Pers. to *Lobostemon*. Johnston (1924), being guided by Wright's (1904) suggestion that *Echium* (in the form of *E. formosum*) occurred naturally in the Cape, initially concluded that the presence of staminal scales as well as Gürke's (1897) distinction in the stigma morphology could not distinguish *Lobostemon* from *Echium*. However, Johnston (1953) separated the two genera on the position of the staminal hairs. Levyns (1934a) recognised *Lobostemon* as separate from *Echium*. In terms of *Lobostemon* systematics, her contribution was fourfold: (1) her recognition of a myriad of synonyms and the publication of eight new species (Levyns, 1934a,b); (2) the description of *Echiostachys* Levyns, which was in effect a re-ranking of *Echium* L. Section *Trichobasis* DC.; (3) the delimitation of five sections based on floral characters (Table 1); and (4) presenting a branching diagram to elucidate relationships within the genus (Fig. 1).

This paper reports on a cladistic analysis of morphological data with the aim of answering the following questions: (1) Is *Lobostemon* monophyletic and if so, what characters support it? (2) Are the sections within *Lobostemon* monophyletic and if so what characters support them? (3) Can existing hypotheses

E-mail address: buysmh@puk.ac.za.

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Table 1
Diagnostic characters for the sections in *Lobostemon sensu* Levyns (1934a)

Characters	Sections				
	Lobostemon I	*Trichotomi* II	*Argentei* III	*Fruticosi* IV	*Grandiflori* V
Inflorescence	Cincinnus — appearing capitate	Cincinnus — appearing as a compound cyme	Cincinnus — appearing as a pseudo-spike	Cincinnus — appearing as a compound cyme	Cincinnus — appearing as a compound cyme
Flowers shape	Rotate	Infundibular	Infundibular	Infundibular	Tubular
Flower symmetry	Actinomorphic	Zygomorphic	Zygomorphic	Zygomorphic	Actinomorphic
Abaxial petal surface	Hairy	Glabrous	Glabrous	Hairy	Hairy
Staminal scales	Well developed	Well developed	Reduced to ridges	Reduced to ridges	Reduced to swellings
Staminal lateral lobes	Present	Present	Absent	Absent	Absent

regarding inter-specific relationships sensu Levyns (1934a) be falsified?

2. Material and methods

2.1. Ingroup

Although Levyns (1934a,b) recognised 29 taxa in *Lobostemon*, 28 were included as terminals (Table 2) because three species have been synonymised–*L. horridus* Levyns, *L. inconspicuus* Levyns, *L. bolusii* Levyns (Buys and Van der Walt, 1997; Buys, 1997)–and two new species have been described—*L. belliformis* M.H. Buys and *L. daltonii* M.H. Buys (Buys and Van der Walt, 1996, 1999).

2.2. Outgroups

The absence of a family wide cladistic analysis makes the choice of a suitable outgroup problematic. *Pontechium maculatum* (L.) Böhle and Hilger was chosen to root the cladograms because Hilger and Böhle (2000) indicate *P. maculatum* to be sister to *Echium*, *Lobostemon* and *Echiostachys* based on *trnL* intron, *trnL-F* spacer and ITS1 sequence data. However, both *Pontechium* and *Echiostachys* could form part of the ingroup in a wider analysis. The character states pertaining to the outgroup were obtained from Klotz (1959) as well as Hilger and Böhle (2000). In addition, *Echiostachys incanus* (Thunb.) Levyns was also included in the analysis to test the monophyly of *Lobostemon* in relation to the former.

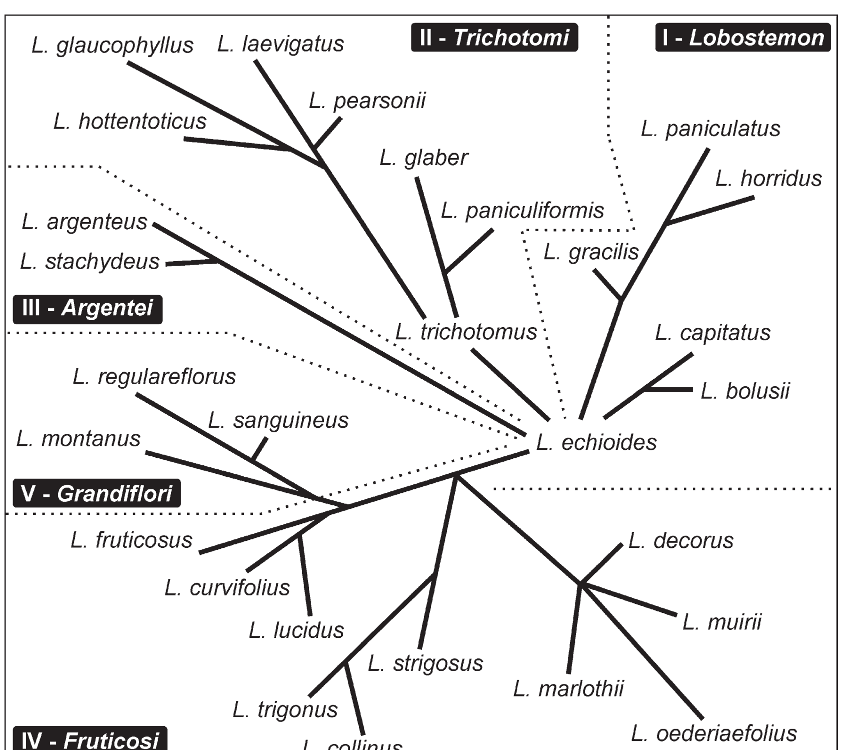

Fig. 1. Modified branching diagram as depicted in Levyns (1934a) to illustrate the inter-specific and sectional relationships in *Lobostemon*.

Table 2
Terminal taxa studied and voucher specimens where applicable

Taxa	Vouchers
Lobostemon argenteus	MHB 426
Lobostemon belliformis	MHB 432
Lobostemon capitatus	MHB 380
Lobostemon collinus	MHB 505
Lobostemon curvifolius	MHB 392
Lobostemon daltonii	MHB 501
Lobostemon decorus	MHB 422
Lobostemon echioides	MHB 414
Lobostemon fruticosus	MHB 386
Lobostemon glaber	MHB 397
Lobostemon glaucophyllus	MHB 384
Lobostemon gracilis	MHB 443
Lobostemon hottentoticus	MHB 379
Lobostemon laevigatus	MHB 400
Lobostemon lucidus	MHB 446
Lobostemon marlothii	MHB 419
Lobostemon montanus	MHB 381
Lobostemon muirii	MHB 413
Lobostemon oederiaefolius	MHB 396
Lobostemon paniculatus	MHB 421
Lobostemon paniculiformis	MHB 365
Lobostemon pearsonii	MHB 515
Lobostemon regulareflorus	MHB 439
Lobostemon sanguineus	MHB 447
Lobostemon stachydeus	MHB 465
Lobostemon strigosus	MHB 412
Lobostemon trichotomus	MHB 507
Lobostemon trigonus	MHB 391
Echiostachys incanum	MHB 430
Pontechium maculatum	ex lit.

MHB = MH Buys specimens housed in NBG.

2.3. Characters

All the states of the ingroup were obtained from personal research based on fresh, pickled (FAA) and herbarium material. The following 31 informative characters were used:

0 Branch pubescence: hairy (0); glabrous (1).
1 Leaf texture: herbaceous (0); coriaceous (1).
2 Leaf apex: acuminate (0); acute (1); obtuse (2).
3 Leaf trichome texture: protuberances absent (0); protuberances smooth (1); protuberances undulate (2).

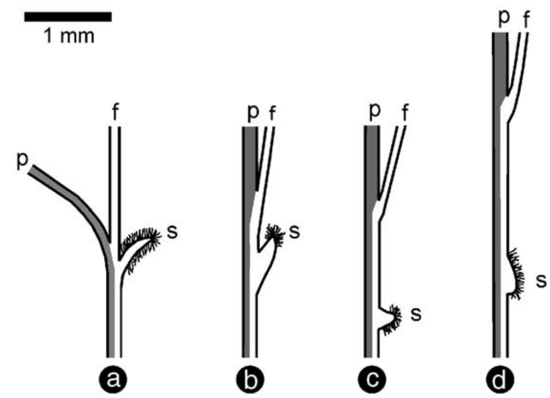

Fig. 3. General structure of staminal scales in *Lobostemon*. (a) Well-developed staminal scales confined to the throat of the corolla tube with filaments free above the scales; (b) well-developed staminal scales situated well below the throat of the corolla tube with filaments adnate above the scales; (c) ridges situated well below the throat of the corolla tube with filaments adnate above the scales; (d) swellings situated well below the throat of the corolla tube with filaments adnate above the scales. p = petals; f = filament; s = staminal scales.

4 Abundance of hair on adaxial leaf surfaces: sparse (0); copious (1).
5 Distribution of hair on sparsely hairy adaxial leaf surfaces: evenly spread (0); unevenly spread (1).
6 Confinement of hair on adaxial leaf surfaces to: margin, midvein and apex (0); margin and apex (1); margin and midvein (2).
7 Abundance of hair on abaxial leaf surfaces: sparse (0); conspicuous (1).
8 Distribution of hair on sparsely hairy abaxial leaf surfaces: evenly spread (0); unevenly spread (1).
9 Hair length: similar (0); dissimilar (1).
10 Inflorescence shape: compact, branched (0); cylindrical, unbranched (1).
11 Flower size: small (0); medium (1); large (2).
12 Flower symmetry: actinomorphic (0); zygomorphic (1).
13 Flower shape: rotate (0); infundibular (1); tubular (2).
14 Sepals fusion: free (0); variously fused (1).
15 Sepal apices shape: incurved (0); aplanate (1); recurved (2).
16 Sepal length in relation to petals: less than half (0); half (1); more than half (2).

Fig. 2. Three main flower shapes in *Lobostemon*. (a) Rotate flowers exemplified by *Lobostemon echioides*; (b) infundibular flowers exemplified by *Lobostemon curvifolius*; (c) tubular flowers exemplified by *Lobostemon regulareflorus*.

17 Posterior sepal length: 0–4.5 mm (0); 4.6–8.5 mm (1); 8.6–12.5 mm (2); 12.6–20 mm (3); more than 20 mm (4).
18 Abundance of hair on abaxial sepal surface: sparse (0); copious (1).
19 Petals abaxially: glabrous (0); hairy (1).
20 Posterior petal lobe size: 0–3.4 mm (0); 3.5 mm or longer (1).
21 Stamen lengths: similar (0); dissimilar (1).
22 Extent of longest stamen filament adnation above staminal scales: free (0); short (1); long (2).
23 Staminal scales: absent (0); present (1).
24 Staminal scales position: entrance of corolla tube (0); well below the throat of the corolla tube (1).
25 Staminal scales development: well-developed (0); ridges (1); swellings (2).
26 Lateral lobes on staminal scales: absent (0); present (1).
27 Staminal scales shape: triangular (0); rounded (1).
28 Inter-scale area pubescence: glabrous (0); hairy (1).
29 Stigmatic region consisting of: stigma branches (0); style branches shorter than 50 μm (1); style branches ± 100 μm long (2).
30 Style pubescence: glabrous (0); hairy (1).

Indumentum characters, inflorescence characters and stigma and style characters are elucidated in Buys (2005), Buys and Hilger (2003) and Buys (2001) respectively. Three general flower shapes were recognised. In rotate flowers the base of the corolla forms a short tube and at a point about half-way up the flower, the free lobes suddenly expand horizontally outwards (Fig. 2a). In infundibular flowers the corolla widens gradually from a narrow base and the lobes rarely attain a horizontal position (Fig. 2b). Tubular flowers are reminiscent of rotate flowers except that the flowers are larger in all aspects and the corolla tube has lengthened to a great degree (Fig. 2c). A few words on the symmetry of flowers in *Lobostemon* are necessary. The meaning of actinomorphic and zygomorphic is open to interpretation (Weberling, 1989). I have taken into account solely the arrangement of the perianth and the size of the corresponding parts. Staminal scales have played an integral part in the historical development of *Lobostemon* systematics. Staminal scales either occur at the entrance of (Fig. 3a), or well below the throat of the corolla tube (Fig. 3b–d). Staminal scales are well-developed (Fig. 3a and b) or reduced to ridges (Fig. 3c) or swellings (Fig. 3d). Staminal scales are rounded or triangular in shape and may also possess lateral lobes (Fig. 4). Stamen filaments are free (Fig. 3a), shortly adnate (<5 mm) or markedly adnate (>5 mm) above the staminal scales (Fig. 3b–c and d respectively). In the majority of species with stamens dissimilar in length, the shortest stamen is usually free and the remaining stamens are variously short adnate. Where relevant, the longest stamen is coded independently in each species.

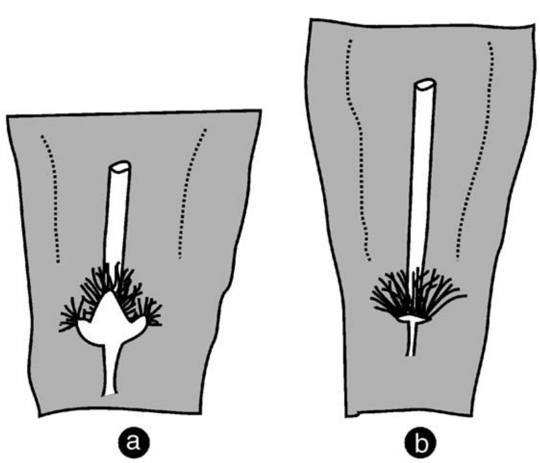

Fig. 4. Shape of staminal scales and presence of lateral lobes in *Lobostemon*. (a) Triangular staminal scales with lateral lobes as exemplified by *Lobostemon glaber*; (b) rounded staminal scales without lateral lobes as exemplified by *Lobostemon fruticosus*.

2.4. Excluded characters

Apart from those already mentioned, an additional 89 characters were investigated but not included in the analysis because of large amounts of inter- and infraspecific polymorphism.

2.5. Cladistic analyses

Character states for *Lobostemon* were initially transformed from a Delta character list (Dallwitz et al., 1993 onwards) via the TOHEN directive into a data matrix for use in Nona (Goloboff, 1996) via Winclada (Nixon, 1999).

Eleven of the 31 characters (2, 3, 6, 11, 13, 15, 16, 17, 22, 25 and 29) are multistate (Table 3). Of these, characters 15, 16, 17 and 29 were treated as additive. Characters states that were not available, or for which coding was uncertain were assigned a question mark. Polymorphic multistate characters were encoded as a subset where applicable.

The data matrix was analysed using Winclada applying the following search parameters for Nona's heuristic search: maximum trees to keep (hold) = 10000, number of replications (mult**N*) = 100, starting trees per rep (hold/) = 10. A multiple tree bisection–reconnection (TBR) plus TBR (mult*max*) search strategy was employed. All the characters were weighted equally. A consensus tree was calculated using the strict consensus option in Winclada. Jackknife support values (Lanyon, 1985) for nodes were calculated with 1000 replicates, 30 search replicates (mult*30), and three starting trees per replication (hold/3) without TBR branch swapping and maximum number of trees set to 10000.

3. Results

When *P. maculatum* was used to root the cladograms, the analysis yielded 3 parsimonious trees, each with 85 steps, a CI = 49 and a RI = 77. The three initial trees and the strict consensus tree (Fig. 5) derived from them support the monophyletic status of *Lobostemon* based on medium sized flowers, the presence of staminal scales and stigma branches as synapomorphies.

The four resulting trees produce 4 monophyletic groups within *Lobostemon*. Clade A, with a Jackknife support value of

Table 3
Data matrix used in the cladistic analysis of *Lobostemon*

Taxon	Characters																													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Pontechium maculatum	0	0	1	?	1	–	–	1	–	1	1	0	1	1	0	0	?	1	?	1	?	1	–	0	–	–	–	–	–	1	1
L. argenteus	0	0	1	1	1	–	–	1	–	1	1	1	1	1	0	0	0	1	[01]	0	0	1	1	1	1	1	0	1	1	0	1
L. belliformis	0	0	0	2	1	–	–	1	–	0	0	2	1	2	1	1	1	4	1	1	1	[01]	2	1	1	2	0	1	0	0	1
L. capitatus	0	0	1	1	0	0	–	1	–	0	0	0	0	0	0	0	[01]	0	1	0	0	0	0	1	0	0	1	0	1	0	0
L. collinus	0	1	2	1	0	1	0	0	1	0	0	1	1	1	0	0	2	1	[01]	1	1	1	1	1	1	1	0	1	1	0	1
L. curvifolius	0	0	[01]	1	1	–	–	1	–	0	0	1	1	1	0	0	[12]	3	1	1	1	1	1	1	1	1	0	1	1	0	1
L. daltonii	0	1	[12]	1	[01]	1	0	[01]	1	0	0	1	1	1	0	2	[12]	2	1	1	1	1	1	1	1	1	0	?	1	0	1
L. decorus	0	0	1	[01]	0	0	–	0	0	0	0	1	1	1	0	0	[12]	2	0	1	1	1	1	1	1	1	0	1	1	0	1
L. echioides	0	0	[12]	1	[01]	1	2	1	–	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0
L. fruticosus	0	0	[12]	1	1	–	–	1	–	1	0	1	1	1	0	0	1	2	1	1	1	1	1	1	1	1	0	1	1	0	1
L. glaber	0	0	1	1	[01]	0	–	1	–	1	0	1	1	1	0	1	0	1	1	0	[01]	1	0	1	1	0	1	0	1	0	1
L. glaucophyllus	1	0	1	1	0	1	1	0	[01]	0	0	1	1	1	0	1	[01]	1	0	0	0	1	0	1	1	0	1	1	1	0	1
L. gracilis	0	0	1	1	1	–	–	1	–	1	0	0	1	0	0	0	0	0	1	1	0	[01]	0	1	0	0	1	0	1	0	[01]
L. hottentoticus	1	0	1	1	0	1	1	[01]	1	0	0	1	1	1	0	1	0	1	0	0	1	1	0	1	1	1	1	1	1	0	1
L. laevigatus	1	0	1	1	0	1	1	0	1	0	0	1	1	1	0	1	[01]	1	0	0	0	1	0	1	1	0	1	0	1	0	1
L. lucidus	0	0	1	1	[01]	0	–	[01]	?	0	0	1	1	1	0	0	1	3	1	1	1	1	1	1	1	1	0	1	1	0	1
L. marlothii	0	0	[12]	[01]	[01]	0	–	[01]	0	0	0	1	1	1	0	0	[01]	2	1	1	1	1	1	1	1	1	0	1	1	0	1
L. montanus	0	0	[12]	1	1	–	–	1	–	0	0	1	1	2	0	0	2	1	1	1	1	[01]	1	1	1	1	0	1	1	0	1
L. muirii	0	0	1	0	0	0	–	0	0	0	0	1	1	2	0	0	2	2	0	0	0	1	1	1	1	0	0	1	1	0	1
L. oederiaefolius	0	0	1	0	1	–	–	1	–	0	0	1	1	1	0	0	1	2	0	1	1	1	1	1	1	1	0	1	1	0	1
L. paniculatus	0	0	1	1	0	0	–	1	–	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0
L. paniculiformis	0	0	2	1	0	0	–	1	–	0	0	1	1	1	0	1	[01]	1	1	0	0	1	0	1	1	0	1	0	1	0	1
L. pearsonii	1	0	1	1	0	1	2	0	1	0	0	1	1	1	0	1	0	1	0	0	0	1	0	1	1	1	1	0	1	0	1
L. regulareflorus	1	0	0	0	0	?	–	–	–	0	0	2	1	2	1	1	2	4	0	1	1	[01]	2	1	1	2	0	1	0	0	1
L. sanguineus	0	1	1	0	0	0	–	0	1	0	0	1	1	2	0	1	2	1	0	1	0	1	2	1	1	1	0	1	1	0	1
L. stachydeus	0	0	1	1	1	–	–	1	–	1	1	1	1	1	1	0	0	1	1	0	0	1	1	1	1	1	0	1	1	0	1
L. strigosus	0	0	2	1	1	–	–	1	–	0	0	1	1	1	0	0	1	2	1	1	1	1	1	1	1	1	0	1	1	0	1
L. trichotomus	0	0	1	1	[01]	0	–	1	–	1	0	1	1	1	0	1	[012]	1	1	0	0	1	0	1	1	0	1	0	1	0	[01]
L. trigonus	0	0	2	1	[01]	0	–	[01]	0	0	0	1	1	1	0	0	[01]	1	1	1	1	1	1	1	1	1	0	1	1	0	1
Echiostachys incanus	0	0	1	?	1	–	–	1	0	0	1	0	1	1	1	1	[012]	1	1	1	0	1	1	0	–	–	–	–	–	2	1

less than 50, is supported by a single homoplasious character state—petals with a glabrous abaxial surface. This state also occurs in *L. capitatus* in Clade B, Clade C and in *L. muirii* in Clade D. The three remaining clades possess compact branched inflorescences. The clade containing B and C is supported by three synapomorphies—stamen filaments free from the petals,

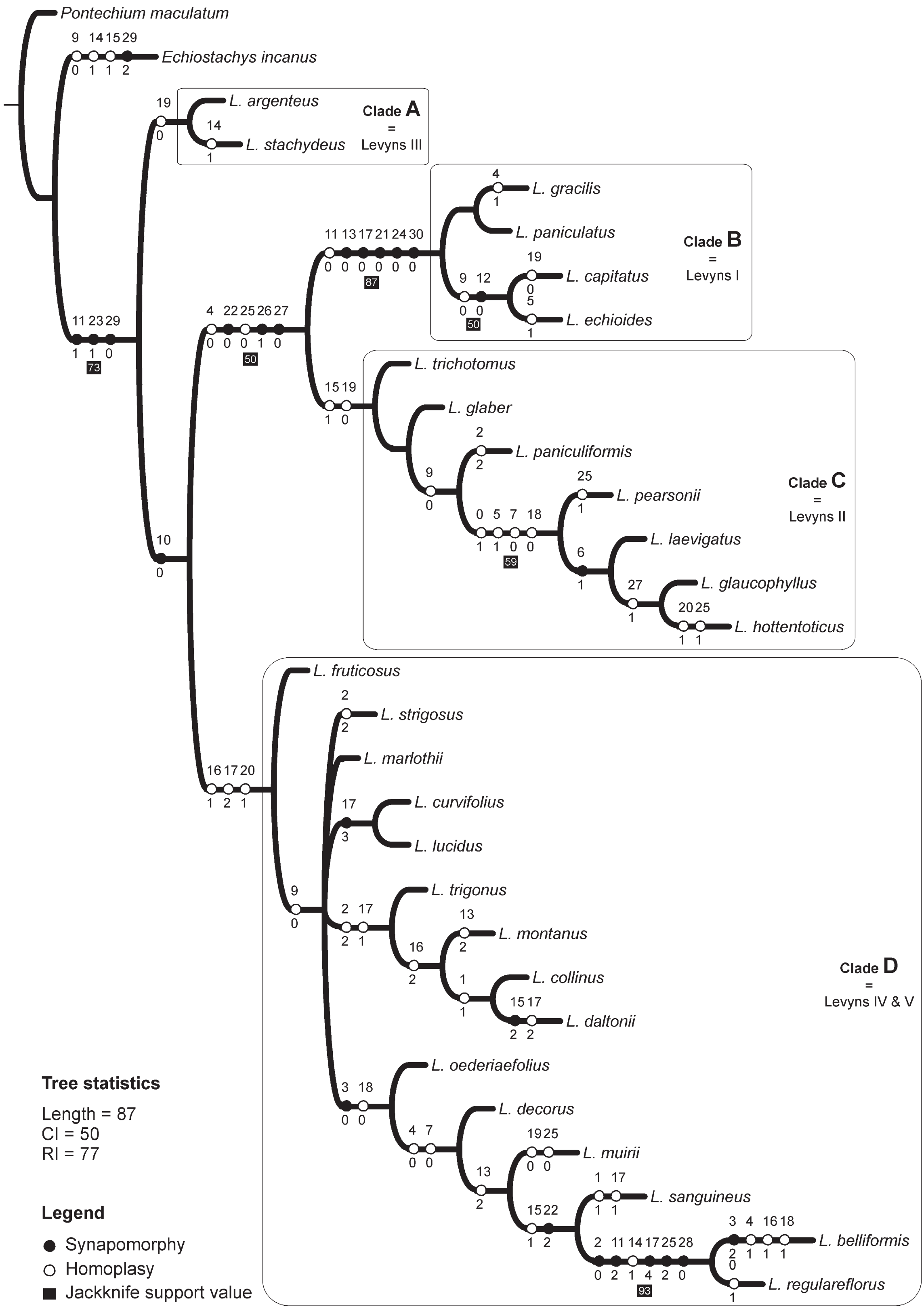

Fig. 5. Strict consensus tree of the three most-parsimonious trees obtained from a cladistic analysis of *Lobostemon*. Character and state numbers refer to those listed in the text. Only Jackknife support values greater than 50 are shown.

staminal scales with lateral lobes and staminal scales triangular. In addition, there are two homoplasious character states at this node—adaxial leaf surface sparsely hairy and staminal scales well developed. Clade B possesses rotate flowers, posterior sepals 4.5 mm or shorter, stamens similar in length, staminal scales positioned at the entrance of the corolla tube and glabrous styles. In addition this clade is characterised by small flowers, an apparent reversal. Only one synapomorphic character state occurs in Clade C, viz. hairs confined to the margin and apex of adaxial leaf surfaces. The only polytomy occurs in Clade D. The most stable node in this clade is that supporting *L. belliformis* and *L. regulareflorus* (Ker-Gawl.) M.H. Buys. Synapomorphic character states present here are leaf apices acuminate, flowers large, posterior sepals more than 20 mm long, staminal scales reduced to swellings and the inter-scale area glabrous. The three initial most parsimonious trees differ only in the placement of *L. marlothii* Levyns, *L. strigosus* (Lehm.) H. Buek, *L. curvifolius* H. Buek and *L. lucidus* (Lehm.) H. Buek (Fig. 6). The latter two however, always group. All attempts to resolve the polytomy in Clade D via successive weighting failed.

Support for the consensus tree is weak. Only six clades received Jackknife support values greater than 50 with the highest support of 93 going to the node supporting *L. regulareflorus* and *L. belliformis*.

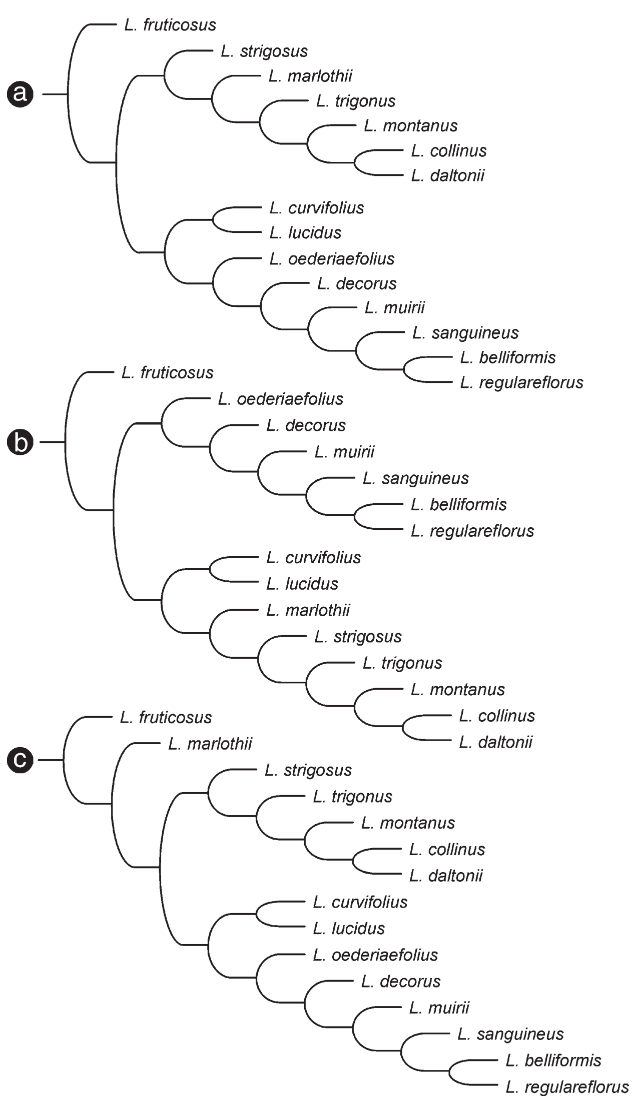

Fig. 6. Three most parsimonious cladograms for Section *Fruticosi* obtained from a cladistic analysis of *Lobostemon*.

4. Discussion and conclusions

The poor Jackknife support values were expected considering the amount of homoplasy in the data matrix.

4.1. Relationships and classification: comparison of results to Levyns (1934a)

Levyns (1934a) recognised five sections in *Lobostemon* (Fig. 1). This cladistic analysis reveals four major clades that can be ranked as sections. Levyns' Sections *Fruticosi* (Fig. 1, IV) and *Grandiflori* (Fig. 1, V) are integrated and cannot be supported from a cladistic point of view (Fig. 5). The remaining three clades (Fig. 5, Clade A–C) correspond to Levyn's Sections *Argentei* (III), *Lobostemon* (I) and *Trichotomi* (II) respectively.

Another major departure from Levyns' classification is that Section *Argentei* (Fig. 5, Clade A) is sister to the rest of the genus. Levyns was of the opinion that *L. echioides* Lehm. and Section *Lobostemon* (Fig. 1) are basal. Levyns (1934a: 396) was no doubt influenced by the Besseyan dicta into thinking that actinomorphic flowers are plesiomorphic: "The family Boraginaceae, as a whole, is characterised by regular flowers... and it is therefore legitimate to assume that where zygomorphism occurs... we are dealing with advanced forms." When determining the floral symmetry as I have done, *E. incanus* and *P. maculatum* are coded as zygomorphic. Actinomorphic flowers are confined to *L. echiodes* and *L. capitatus* (L.) H. Buek. and are hypothesised to be derived in the context of this analysis.

The possession of small flowers in Section *Lobostemon* (Fig. 5, Clade B) is hypothesised to be a reversal, accompanied by the development of a rotate floral morphology as well as stamens becoming equal in length and a glabrous style.

The hypothesised inter-specific relationships in the three most parsimonious trees support Levyns' (1934a) view to an extent, but a number have been falsified. The following hypotheses are novel: (1) *L. paniculiformis* DC. is now viewed to be sister to *L. pearsonii* Levyns and the rest of the clade and not to *L. glaber* (Vahl) H. Buek; (2) Section *Grandiflori* is considered paraphyletic because *L. montanus* H. Buek is more closely related to *L. daltonii* and *L. collinus* C.H. Wright than to *L. sanguineus* Schltr. and *L. regulareflorus*; (3) Furthermore, Levyns (1934a) grouped *L. decorus* Levyns *and L. muirii* Levyns with *L. oederiaefolius* DC. and *L. marlothii*. This analysis hypothesises that *L. decorus and L. muirii* are sister taxa to *L. sanguineus*, *L. belliformis* and *L. regulareflorus*.

Biogeographically, it is noteworthy that the *L. trigonus*–*L. daltonii* lineage is confined to the coastal plains south of the mountain ranges running west to east in the southern Cape.

Similarly, the majority of taxa in the proposed *L. oederiaefolius–L. regulareflorus* lineage are confined to, or found north of these mountain ranges. The two exceptions are *L. sanguineus* and *L. belliformis* which are prime candidates for molecular analyses to test homology of the characters used in this analysis.

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