

A phylogenetic analysis of genus *Lomelosia* Rafin. (Dipsacaceae) and allied taxa

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Riassunto. *Analisi filogenetica del genere Lomelosia Rafin. (Dipsacaceae) e dei taxa affini*

È stata effettuata un'indagine filogenetica delle specie del genere *Lomelosia* (Dipsacaceae), insieme con appropriati outgroup. Sono stati impiegati 19 caratteri multistato relativi alla morfologia, alla palinologia e alla cariologia. Gli alberi filogenetici risultanti suggeriscono che nell'evoluzione del genere ci sia stato un passaggio da specie perenni a specie annuali, da specie con tubi dell'epicalice prismatici a specie con tubi campanulati, da specie con i margini dei fiori esterni interi a specie con margini flabellati. La maggior parte dei caratteri mostra omoplasia elevata. Nell'outgroup le specie di *Scabiosa* che si trovano, non risolte, alla base dell'albero, sono probabilmente simili all'ultimo antenato comune di tutto il gruppo in studio.

Key Words: Dipsacaceae, *Lomelosia*, Phylogeny.

INTRODUCTION

Within Dipsacaceae, tribe *Scabioseae* includes the greatest diversity in terms of evolutionary novelties and morphology of single taxa. This tribe, as presently circumscribed (MAYER & EHRENDORFER, 1999) includes the genera *Lomelosia* Rafin. (= *Scabiosa* sect. *Trochocephalus* Mert. & Koch), *Pterocephalus* (Vaill.) Adans. pro parte, *Pycnocomon* Hoffmans. & Link, *Scabiosa* L. sensu stricto (= *Scabiosa* sect. *Scabiosa*), *Sixalix* Rafin. (= *Scabiosa* sect. *Cyrtostemma* Mert. & Koch). The other taxa which were formerly included in the tribe, i.e., *Pseudoscabiosa* Devesa (= *Scabiosa* sect. *Asterothrix* Font Quer), the Himalayan species of genus *Pterocephalus* (now *Pterocephalodes* V. Mayer & Ehrend.), *Pterocephalidium* G. López, *Succisa* Necker, and *Succisella* Beck have been excluded from the tribe on the basis of the anatomy of the diaspores (MAYER & EHRENDORFER, 1999; 2000). Tribe *Scabioseae*, as presently circumscribed, is composed of taxa whose epicalyx (a

rigid structure, synapomorphic for the family, which encases the ovary) is radially symmetrical and roughly prismatic. This structure is differentiated in a tube which ends in the majority of the taxa with a membranous expansion called corona. Almost all taxa show a diaphragma which contributes to keep the ovary, and later the achene, in place. The area of the epicalyx tube above the diaphragma, until the interface with the corona, is differentiated in a region which varies in dependence with the various taxa and is named epidiaphragma (MAYER & EHRENDORFER, 1999).

Relationships among the genera of Dipsacaceae have been the object of various past studies (VERLÀQUE, 1977a,b; 1984a,b; 1985a,b; 1986a,b; CAPUTO & COZZOLINO, 1994). These contributions indicated slightly different hypotheses of descent for the taxa which belong to the "Scabiosa" morphotype (i.e., taxa whose involucre shows a wide corona and five calyx bristles). In particular, according to VERLÀQUE (1986b), *Scabiosa* s.s. was closely related to *Pterocephalus*, whereas the other taxa (*Lomelosia*, *Sixalix* and *Pycnocomon*) formed a closely knit unit. CAPUTO & COZZOLINO (1994) suggested that the whole group of genera made a monophyletic unit, with *Scabiosa* s.s. at the base, as a sister group to a clade composed of *Lomelosia*, *Sixalix* and *Pycnocomon* (the latter two in a sister group relationship).

However, recently MAYER & EHRENDORFER (1999) provided another hypothesis, indicating a sister group relationship between *Lomelosia* and *Pycnocomon*, as well as between *Scabiosa* and *Sixalix*. However, all the above mentioned contributions dealt with phylogeny at genus level and no attempt has been made to resolve relationships below that level in the genera of *Scabioseae*, regardless of the fact that some genera show evolutionary tendencies which have been variously treated for the past as parallelisms or synapomorphies (e.g., production of pits at the distal end of the epicalyx tube, shape of the diaphragma and epidiaphragma, heterocarpy).

This paper deals with a cladistic analysis of genus *Lomelosia* based on morphological, karyological and palynological characters. *Lomelosia*, which can be distinguished from the other related genera

for the presence of eight pits on the epicalyx tube, includes over 50 perennial and annual species, diffused around the Mediterranean sea, with the greatest diversity concentrated in the eastern Mediterranean and Middle East, and outliers reaching China and Japan.

MATERIAL AND METHODS

Taxa examined

In order to reduce the complexity of the investigation, the taxa of genus *Lomelosia* have been fused in various cases in informal groups (several of them corresponding to those of VERLÀQUE, 1986b) which share at least an exclusive synapomorphy.

A list of the investigated species and species groups follows:

L. argentea group [including *L. argentea* (L.) Greuter & Burdet, *L. cosmoides* (Boiss.) Greuter & Burdet and *L. hispidula* (Boiss.) Greuter & Burdet]

L. bicolor (Boiss.) Greuter & Burdet

L. brachiata (Sibth. & Smith) Greuter & Burdet

L. calocephala (Boiss.) Greuter & Burdet

L. camelorum group [including *L. camelorum* (Coss. & Dur.) Greuter & Burdet, *L. kurdica* (Post) Greuter & Burdet, *L. cyprica* (Post) Greuter & Burdet and *L. paucidentata* (Hub.-Mor.) Greuter & Burdet]

L. candollei (Wall. Ex DC.) Soják

L. caucasica group [including *L. caucasica* (M. Bieb.) Greuter & Burdet, *L. sulphurea* (Boiss. & Huet) Greuter & Burdet, *L. balianii* (Diratz.) Greuter & Burdet, *L. alpestris* (Kar. & Kir.) Soják, *L. soongarica* (Schrenk) Soják, *L. speciosa* (Royle) Soják].

L. crenata group [including *L. crenata* (Cyr.) Greuter & Burdet, *L. oberti-manetti* (Pamp.) Greuter & Burdet, *L. pulsatilloides* (Boiss.) Greuter & Burdet, *L. robertii* (Barr.) Greuter & Burdet, *L. isetensis* (L.) Soják]

L. cretica group [including *L. albocincta* (Greuter) Greuter & Burdet, *L. cretica* (L.) Greuter & Burdet, *L. hymettia* (Boiss. &

Spruner) Greuter & Burdet, *L. minoana* (P.H. Davis) Greuter & Burdet, *L. variifolia* (Boiss.) Greuter & Burdet]

Scabiosa deserticola Rech. f. [No name is available under *Lomelosia* as yet (P. Caputo, in prep.); it is informally referred to as *L. deserticola* in the cladogram of Fig. 1].

L. flavida (Boiss. & Hausskn.) Soják

L. graminifolia group [including *L. graminifolia* (L.) Greuter & Burdet, *L. epirota* (Halácsy & Bald.) Greuter & Burdet, *L. hololeuca* (Bornm.) Greuter & Burdet, *L. pseudograminifolia* (Hub. Mor.) Greuter & Burdet, *L. rhodopensis* (Stoj. & Stefanov) Greuter & Burdet]

L. leucactis (Patzak) Soják

L. micrantha group [including *L. divaricata* (Jacq.) Greuter & Burdet, *L. micrantha* (Desf.) Greuter & Burdet]

L. olivieri (Coult.) Soják

L. polykratis (Rech. f.) Greuter & Burdet

L. prolifera (L.) Greuter & Burdet

L. reuteriana (Boiss.) Greuter & Burdet

L. rhodantha (Kar. & Kir.) Soják

L. rotata group [including *L. aucheri* (Boiss.) Greuter & Burdet, *L. palaestina* (L.) Rafin., *L. persica* (Boiss.) Greuter & Burdet, *L. porphyroneura* (Blakelock) Greuter & Burdet, *L. rotata* (M.B.) Greuter & Burdet]

L. rufescens (Freyn & Sint.) Greuter & Burdet

Scabiosa schimperiana Boiss. & Buhse [No name is available under *Lomelosia* as yet (P. Caputo, in prep.); it is informally referred to as *L. schimperiana* in the cladogram of Fig. 1].

L. sphaciotica (Roem. & Schult.) Greuter & Burdet

L. stellata group [including *L. stellata* (L.) Rafin., *L. simplex* (Desf.) Rafin.]

Scabiosa transcaspica Rech. f. [No name is available under *Lomelosia* as yet (P. Caputo, in prep.); it is informally referred to as *L. transcaspica* in the cladogram of Fig. 1].

Outgroups

As outgroups, all species of genera *Pycnocomon* and *Sixalix*, as

well as a selection of species from genus *Scabiosa* have been chosen. The reason of selecting a subsample of species in the latter genus is mainly related to the fact that over thirty names available for segregates of *S. columbaria* L. have been regarded as a single species.

A list of the outgroups follows:

Pycnocomon intermedium (Lag.) Greuter & Burdet

P. rutifolium (Vahl) Hoffmans. & Link

Scabiosa africana L.

S. columbaria L.

S. japonica Miq.

S. parviflora Desf.

S. silenifolia Waldst. & Kit.

S. tenuis Boiss.

Sixalix arenaria (Forssk.) Greuter & Burdet

S. atropurpurea (L.) Greuter & Burdet

S. cartenniana (Pons & Quézel) Greuter & Burdet

S. farinosa (Coss.) Greuter & Burdet

S. lybica (Alavi) Greuter & Burdet

S. parielii (Maire) Greuter & Burdet

S. semipapposa (DC.) Greuter & Burdet

S. thysdrusiana (Le Houérou) Greuter & Burdet

Investigated characters

The employed characters have been assessed on at least one flowering and one fruiting specimen for each of the species listed above. In this context, an extended loan from B and W is gratefully acknowledged. Characters have been double checked with the available literature sources, such as VERLÀQUE (1977b; 1984a; 1985a; 1986a,b), DEVESA (1984), HILGER & HOPPE (1984), CAPUTO & COZZOLINO (1994), RECHINGER (1991), MAYER & EHRENDORFER (1999).

A list of the characters follows:

- 1. Life form.** This is a self-explicative character. A detailed choice of states was preferred over a simple dual choice (i.e.,

perennial vs. annual) because of the fact that in various genera, and notably within *Lomelosia*, a correlation may be found between derivativeness and terophytic life style, whereas the most archaic forms are usually fruticous. **(0) = Scapous hemicryptophyte. (1) = Suffruticous chamaephyte. (2) = Fruticous chamaephyte. (3) = Biennial hemicryptophyte. (4) = Scapous terophyte.**

2. **Radiant capitula.** In the majority of the taxa in study, capitula have zygomorphic external flowers, so that the inflorescence has a radiant appearance. On the contrary, capitula are haemispheric or, however, do not have a radiant appearance in few plesiomorphic species of *Lomelosia*, *Scabiosa* and *Sixalix*. Also some quite derived members of genus *Lomelosia* (e.g., *L. olivieri*) do not have this character. **(0) = Capitula globose. (1) = Capitula radiant.**
3. **Number of flowers in the capitula.** In the inclusive group in study, capitula are multiflowered (i.e., with over 30 flowers each). Only in few members of genus *Lomelosia* (i.e., *L. olivieri* and related annual species of sect. *Olivierianae*) the number of flowers in the capitula is reduced to less than fifteen. **(0) = multiflowered. (1) = pauciflowered.**
4. **Involucral bract connation.** Involucral bracts are free in the majority of *Scabioseae*. Only in the genus *Pycnocomon* they are usually connate (VERLÀQUE, 1977b; 1986a). In *P. rutifolium*, they are connate in their basal half and in *P. intermedium* are connate only at their very base. **(0) = Absent. (1) = Basal.**
5. **Involucral bract length.** In the inclusive group in study, involucral bracts (i.e., the bracts which surround the capitulum in the appearance of a calyx) are either shorter than the radius of the head or, at maximum, equal. They are distinctly

longer only in few species of *Lomelosia* (i.e., in the group of *L. micrantha*). This character has to be observed in fully expanded flowering capitula only, and, for this reason, it is scored as unknown for various taxa which have been observed as herbarium specimens only. **(0) = Shorter than head. (1) = Longer than head.**

6. **External flower margin.** In the taxa in which capitula are radiant, the corolla lobes of the outer flowers are different in shape as compared to the others. The outer margins of these corolla lobes (which contribute the most to the overall shape of the capitulum) may be entire or subentire (e.g., in the majority of the outgroup taxa, in *L. argentea* and *L. graminifolia*) or, in various taxa, crenulated (typically in the group of *L. crenata*, but also in *L. bicolor* and in *L. prolifera*). Rarely, but however in various species of *Lomelosia*, this margin may be visibly flabellate (in *L. calocephala*, *L. leucactis*, *L. schimperiana*). **(0) = (Sub)entire. (1) = Crenate. (2) = Flabellate.**
7. **Epicalyx tube pits.** The epicalyx grooves are usually smooth. The top of the epicalyx tube shows a minute pit in each groove in *Pycnocomon*. In *Lomelosia*, the epicalyx tube is terminated by eight deep cavities below the attachment to the corona. **(0) = Absent. (1) = Shallow depressions at the top of the tube. (2) = Deep round or elliptical cavities at the top of the tube.**
8. **Epicalyx sclerenchyma.** Cross sections of the dipsacaceous epicalyx show that the sclerenchyma is either diffuse or organized in bundles or rings surrounding the vascular bundles. In the investigated species, it is either present in the form of a single ring or as a double, concentric ring (in *Lomelosia* and *Pycnocomon*, MAYER & EHRENDORFER, 1999) **(0) = Single ring. (1) = Double ring**

9. **Involucel tube length.** In the majority of the taxa in study, the involucel tube is vertically developed, i.e., the length is greater than the width. This is the plesiomorphic condition for the whole family and, certainly, also for the taxa taken into consideration here. However, in various taxa of *Lomelosia*, the involucel tube is roundish in appearance, because width is similar to length. This is the case, for example, of *L. brachiata*, *L. micrantha*, *L. olivieri*. The epicalices of several annual species of genus *Sixalix* (i.e., *S. arenaria* and *S. lybica*) also have a roundish appearance but, in that case, the involucel tube prolongs into the erected epidiaphragma region and, taking into consideration the whole of the tube, the involucel is longer than large. **(0) = Longer than large. (1) = as long as large.**

10. **Sulcus between pits.** As already stated, genus *Lomelosia* shows a definite pitting in the distal part of the epicalyx tube. The eight resulting foveoles are separated by thin strands of tissue. These strands may show a central furrow (e.g., in various perennial taxa, as *L. crenata*, *L. cretica*, *L. caucasica* and related species) or not, in the latter case being smooth (e.g., in many annuals, as *L. olivieri*, *L. rhodantha*, as well as in the group of *L. argentea*). The character is not applicable in *Scabiosa* and *Sixalix*. **(0) = Present. (1) = Absent.**

11. **Epicalyx corona.** In all taxa taken into account, i.e., *Lomelosia*, *Pycnocomon*, *Scabiosa* and *Sixalix*, the corona is formed by a membranaceous limb (MAYER & EHRENDORFER, 1999); this interpretation is different from that presented in VERLÀQUE (1985a,b) and CAPUTO & COZZOLINO (1994). Those authors, in fact, suggested that the corona in *Pycnocomon* and *Sixalix* was woody and fenestrated; regardless, MAYER & EHRENDORFER (1999) clearly demonstrated that what the previous authors misconstrued as a corona was indeed part of the involucel tube, and that the corona in *Pycnocomon* and *Sixalix*

has the same nature as in the other mentioned taxa. However, the corona is expanded in *Lomelosia* and *Scabiosa*, but very diminutive in *Pycnocomon* and *Sixalix*. **(0) = Corona wide. (1) = Corona narrow.**

12. **Corona veins.** The corona limb is lined by rigid veins, which allow it to be kept expanded. These veins may merely reach the rim of the membranous expansion (as in *Scabiosa*, *Sixalix*, and various species of *Lomelosia*, notably the groups of *L. cretica*, *L. crenata*, *L. rotata*) or protrude from it in the fashion of an umbrella (as in the group of *L. argentea* and in *L. brachiata*). **(0) = Veins not excurrent. (1) = Veins excurrent.**
13. **Epidiaphragma position.** The studies by MAYER & EHRENDORFER (1999) showed the relevance of the epidiaphragma for the understanding of the reproductive biology and systematics of *Scabioseae*. Such epidiaphragma (which is present also in some taxa not taken into account in the present study) is flat (i.e., horizontal) in *Lomelosia* as well as in the majority of the species of *Scabiosa*, and shows a roughly vertical disposition in *Sixalix*, *Pycnocomon* and *Scabiosa parviflora*. **(0) = Horizontal. (1) = Vertical.**
14. **Epidiaphragma length.** The epidiaphragma is short in *Scabiosa*, *Pycnocomon* and *Sixalix farinosa*, and long, regardless of its position (see char. 13), in both *Lomelosia* and the other species of *Sixalix* (MAYER & EHRENDORFER, 1999).
15. **Bristle position.** In various of the taxa in study, calyx bristles are expanded, so as to give a flat appearance to the calyx; in few of them, and mainly in some species of *Lomelosia*, bristles are erect. **(0) = Erect. (1) = Widening.**
16. **Bristle size.** In various taxa in study, calyx bristles greatly protrude from the corona limb; in various species, however,

bristles are diminutive and so entirely hidden by the membranous corona. **(0) = Hidden. (1) = Evident.**

Tab. 1 - Data matrix for the cladistic analysis. Bracketed states are polymorphic. Question marks indicate unknown states. Dashes indicate inapplicability. Characters are listed as in the text.

Lomelosia_candollei	110000210000011111?
L._argentea_group	[03]100[01]02101010111111
L._bicolor	4[01]0001210[01]01011111?
L._brachiata	41?0?02110010111112
L._calocephala	410002210100011111?
L._camelorum	10010-210000010011?
L._caucasica_group	01000021000[01]0110111
L._crenata_group	[01]100012100000111111
L._cretica_group	2100002100000100111
L._deserticola	40100-211100011111?
L._flavida	411000211100011111?
L._graminifolia_group	1100002100000100111
L._leucactis	410002210101011111?
L._micrantha_group	40001-2110010111111
L._olivieri	40100-2111000111111
L._polykratis	1100[01]021010101111?
L._prolifera	41000121?0000101111
L._reuteriana	4100[01]1210001011111?
L._rhodantha	401000211100011111?
L._rotata_group	4[01]00[01]?21100001[01]111[012]
L._rufescens	40000-21110?011111?
L._schimperiana	310002210?00011111?
L._sphaciotica	11?00?2101010111111
L._stellata_group	4[01]00[01]?21000001[01]111[012]
L._transcapica	411000211100011111?
Pycnocomon_intermedium	01010011[012]-111010111
Pycnocomon_rutifolium	01010011[012]-111010111
Scabiosa_africana	0100?0000-001010000
Sc._columbaria_group	0100?0000-000011000
Sc._japonica	0100?0000-00000000?
Sc._parviflora	40000-000-001000100
Sc._silenifolia	0100??000-000010000
Sc._tenuis	4100??000-000011000
Sixalix_arenaria	410000001-10111100?
Si._atropurpurea	[34]10000000-101111000
Si._cartenniana	1100?0000-10111100?
Si._farinosa	10000-000-001000000
Si._lybica	410000001-10111100?

Si._parielii	1000?-000-101110000
Si._semipapposa	410000000-101111000
Si._thysdrusiana	0100?0000-10111100?

RESULTS

After the cladistic analysis, 27 maximum parsimony cladograms were obtained (length = 55, C.I. = 0.47, R.I. = 0.83), the strict consensus of which is shown in Fig. 1. The tree has been rooted by using *Scabiosa* and *Sixalix*, leaving *Pycnocomon* in the ingroup. The topology of the ingroup shows *Pycnocomon* as sister group to *Lomelosia*. *Pycnocomon* is monophyletic in having connate involucral bracts (char. 4), as well as characters pertaining to the corona and epidiaphragma (chars. 11-13). The latter three characters, however, behave as synapomorphies only locally. *Lomelosia* is monophyletic in having a wide epidiaphragma (char. 14). Such character is, however, only locally synapomorphic, because it develops in the derived members of genus *Sixalix* in a parallel fashion. Topology in genus *Lomelosia* is not entirely resolved (Fig. 1). However, several clades are well defined. The genus has a basal clade made of the group of *L. caucasica*, then a clade composed of *L. camelorum*, and the species of the *L. cretica* and *L. graminifolia* groups. All members of this clade show a reduction of the calyx bristles (char. 15). The more internal clade has a basal, local synapomorphy, also related to calyx (char. 16, widening bristles). This clade shows *L. candollei* basally and then *L. crenata*, the latter sister being group to an inner clade composed (primarily) of annual species (char. 1). The character, however, reverts once in some apomorphic species. The remaining species and species groups, which are of primarily Eastern distribution, are mainly characterized by excurrent corona veins (char. 12, reverting later). In this clade, besides two basal collapses of two central and Eastern Mediterranean species each, two clades are visible, one including the group of *L. argentea*, *L. polykratis*, *L. sphaciotica*, *L. leucactis*, *L. calocephala* and *L. schimperiana* and the other with *L. brachiata* (the only spe-

cies of the genus with ten calyx bristles), the group of *L. micrantha*, the group of *L. rotata* as sister group to the annual Eastern sect. *Olivierianae* (Rech. f.) V. Mayer & Ehrendorfer. This section is composed by small, pauciflowered (char. 3) annuals.

In the outgroup, no synapomorphy keeps genus *Scabiosa* together. Genus *Sixalix*, on the contrary, is characterized by a vertical epidiaphragma (char. 13). It is to be noted that *Scabiosa parviflora* nestes together with one plesiomorphic member of genus *Sixalix* (*S. farinosa*).

DISCUSSION

The phylogenetic analysis of genus *Lomelosia* allows recognition of various evolutionary trends, some of which had already been identified, although on an intuitive basis, in previous literature. The most plesiomorphic species of the genus, for example, are scapous hemicryptophytes (i.e., the group of *L. caucasica*). Several species of the genus then evolved to (sub)fruticous chamaephytes. A definite shrubby habit is present only in the group of *L. cretica*; suffruticous habit, however is rather diffuse in the genus (e.g., *L. camelorum*, *L. crenata*, *L. graminifolia*, *L. polykratis*, *L. sphaciotica*), and probably developed in an independent fashion at least twice. The great majority of the most apomorphic taxa, however, is annual.

Many species, both in genus *Lomelosia* and in the outgroups, have radiant capitula. The occurrence of radiant capitula, which is apomorphic in the family (CAPUTO & COZZOLINO, 1994), is however plesiomorphic in the inclusive group in study. Regardless, globose capitula are present in several taxa and, in particular, in several species of the outgroup (*Scabiosa parviflora*, *Sixalix farinosa*, *Sixalix parielii*) as well as in the plesiomorphic *L. camelorum*. For these taxa the globose capitula seem to have been apomorphically acquired; however, it is difficult to state whether the condition is truly apomorphic or not (it may depend upon our outgroup choice). Globose capitula, however, are also present (in one case the cha-

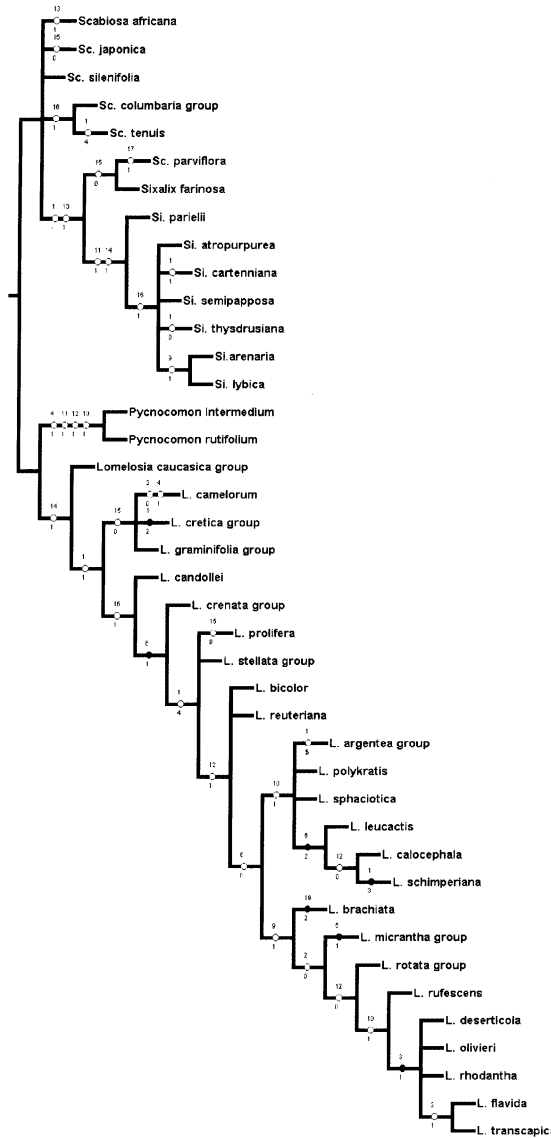


Fig. 1 - Consensus tree for the taxa in study out of 27 maximum parsimony cladograms (length = 55, C.I. = 0.47, R.I. = 0.83). Black dots indicate synapomorphy; white dots indicate homoplasy. Numbers above each dot are the character numbers as indicated in the text and in the matrix. Numbers below dots represent the state at the internode.

racter is polymorphic) in several derived species of *Lomelosia* (the group of *L. micrantha*, the group of *L. rotata*, as well as in *L. rufescens*, *L. deserticola*, *L. olivieri*, *L. rhodantha*). The change in the overall shape of the capitulum may be related to pollinator shifts, in particular for the last mentioned group of species, in several of which a reduction in the number of flowers in the capitulum occurs.

Outer florets margins modify their shape throughout the genus. The most plesiomorphic species have entire flower margins, whereas several independently evolve crenate margins (e.g., the group of *L. crenata* or *L. reuteriana*) or even visibly flabellate margins (*L. leucactis*, *L. calocephala*, *L. schimperiana*). Another character which can be followed throughout the genus is related to the overall proportions of the epicalyx tube, which is roughly cylindrical in most species, but becomes campanulate (i.e., as long as large) in *L. brachiata*, *L. micrantha*, *L. olivieri* and few other species.

As far as the outgroups are concerned, we would like to point out that the lack of synapomorphies within genus *Scabiosa* s.s. is, in our opinion, not an artifact of our analysis. In fact, this genus developed an expanded, membranous corona which, however, is also present in all other genera taken into account (as well as in others which are not present in this investigation). *Scabiosa* probably represents a successful body plan, which has been further exploited in *Lomelosia* and *Sixalix*. From some ancestor which had to be similar to present-day plesiomorphic species of the genus (e.g., *Scabiosa japonica*), *Lomelosia*, *Sixalix*, *Pycnocomon*, as well as the most derived species of *Scabiosa* have probably originated.

A clear artifact of our analysis, on the contrary, is the sister group relationship between *Scabiosa parviflora*, an annual and aberrant species from Sicily, Italy, and *Sixalix farinosa*. The presence of *S. parviflora* within genus *Sixalix* may derive from the fact that some of its autapomorphies are misconstrued as synapomorphies; most likely, however, a deeper investigation would bring also *Sixalix farinosa* to collapse, together with the species of *Scabiosa*, at the base of the tree. *Sixalix farinosa*, in fact, is a very plesiomorphic species, and may represent the ancestor of all the other species of

Sixalix (MAYER & EHRENDORFER, 1999). Eventually, *Pycnocomon*, a genus which was regarded in the past as closely related to *Sixalix* (VERLÀQUE, 1986a; CAPUTO & COZZOLINO, 1994), appears from this analysis as sister taxon of *Lomelosia*. This depends on the reassessment of the homology of the epicalyx parts carried out by MAYER & EHRENDORFER (1999), who showed the close resemblance between the two genera.

The results shown here, in terms of genus-level topology, coincide, to the extent of the taxa in common, with preliminary results based on molecular characters (Caputo et al., in prep.).

In conclusion, genus *Lomelosia*, as well as the related *Scabiosa*, *Sixalix*, and *Pycnocomon*, are taxa beset with parallelisms (as shown by the very low C.I. of the cladograms), which may often obscure true synapomorphy. Various of the tendencies which are observed in one of the genera, develop also in the others in a parallel fashion. This, up to recent times, has prevented a clear understanding of the phylogenetic relationships. Ongoing studies, based on molecular characters, will allow further insights in the relationships of some of the taxa (mainly, *Scabiosa parviflora* and *Sixalix farinosa*, but also all the other species of *Scabiosa*) which have not been elucidated here.

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Abstract. The species of genus *Lomelosia* (Dipsacaceae), as well as an appropriate set of outgroups, were investigated to elucidate their phylogenetic relations-

hips based on 19 multistate morphological, palynological and karyological characters. The resulting phylogenetic trees suggest that evolution in *Lomelosia* proceeded from perennial to annual species, from species with prismatic epicalyx tubes to species with campanulate ones, from species with entire outer flower margins to species with flabellate ones. The majority of the characters show rampant homoplasy in the whole tree. Within the outgroup, the species of genus *Scabiosa*, which collapse at the base of the phylogenetic tree, are interpreted as similar to the last common ancestor of the inclusive group in study.

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