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**Review of the systematics of Scrophulariaceae s.l.
and their current disposition**

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Abstract. Recent molecular phylogenetic studies in Lamiales have shown that the large group traditionally recognised as Scrophulariaceae is not monophyletic. Efforts to reconstruct the phylogeny of this large clade and to revise its classification to reflect that phylogeny have resulted in seven monophyletic groups, comprised mostly of members of Scrophulariaceae s.l., recognised as families in recent angiosperm classifications. These are Scrophulariaceae s.s., Orobanchaceae, Veronicaceae (cf. Plantaginaceae), Phrymaceae, Calceolariaceae, Linderniaceae, and Stilbaceae. Sampling completeness at the genus level varies from group to group, but is quite good for many. A few individual genera formerly assigned to Scrophulariaceae do not fit into any existing clade recognised at family rank and are left, at present, unassigned to family. In addition to the recognition of several clades comprised primarily of former members of Scrophulariaceae s.l., several groups previously recognised as families are now included within some of these clades. For example, Scrophulariaceae s.s. includes Buddlejaceae and Myoporaceae, and Veronicaceae includes Callitrichaceae, Globulariaceae, Hippuridaceae, and Plantaginaceae. The clades now recognised as families often are not easily diagnosed, but in many cases are more consistent with certain functional traits and geographical patterns. Examples include Orobanchaceae, which comprises all of the parasitic plants (hemiparasites and holoparasites) and Scrophulariaceae s.s., which is predominantly a southern hemisphere group.

Introduction

Any discussion of Scrophulariaceae *sensu lato* (s.l.) necessarily includes a discussion of the Lamiales. Lamiales represent the largest order of the Lamiid clade, comprising nearly 18 000 species and at least 23 families (Bremer *et al.* 2002; Angiosperm Phylogeny Group (APG) II 2003; Judd and Olmstead 2004). The monophyly of the Lamiales (Olmstead *et al.* 1993, 2001; Oxelman *et al.* 1999; Backlund *et al.* 2000; Soltis *et al.* 2000; Albach *et al.* 2001; Bremer *et al.* 2002; Hilu *et al.* 2003) and many of the families comprising the order are well established (Scotland *et al.* 1995; Smith *et al.* 1997a; Wagstaff and Olmstead 1997; McDade and Moody 1999; Spangler and Olmstead 1999; Wallander and Albert 2000; Müller *et al.* 2004; Oxelman *et al.* 2005; Rahmanzadeh *et al.* 2005). Despite these studies, relationships among the major lineages of Lamiales are still unclear, and the phylogenetic affinities of many taxa comprising Scrophulariaceae s.l., remain obscure, although a phylogenetic framework is emerging.

Scrophulariaceae, as traditionally described, were the largest family in Lamiales and appeared to be an easily

recognised group. However, molecular phylogenetic studies have suggested that it is not the presence of a suite of uniquely derived characteristics that allows for an easily recognisable Scrophulariaceae s.l., but rather, the absence in Scrophulariaceae of the synapomorphies that characterise closely related families. Two independent studies (Olmstead and Reeves 1995; dePamphilis *et al.* 1997) first identified the polyphyletic nature of the traditional Scrophulariaceae and corroborated previous speculations (e.g. Thieret 1967) that Scrophulariaceae s.l. may not be a natural group. Subsequent studies have substantiated the polyphyly of the traditional scrophs (e.g. Young *et al.* 1999; Backlund *et al.* 2000; Olmstead *et al.* 2000, 2001; Albach *et al.* 2001; Bremer *et al.* 2001, 2002; Beardsley and Olmstead 2002; Müller *et al.* 2004; Oxelman *et al.* 2005; Rahmanzadeh *et al.* 2005).

The widely differing circumscriptions of Scrophulariaceae in traditional classifications (e.g. Bentham 1876; Wettstein 1891; Hallier 1903; Cronquist 1981) seem to reflect the conclusion of a polyphyletic Scrophulariaceae s.l. Most classifications of Scrophulariaceae, following Wettstein (1891), reflect the segregation of what were

believed to be distinct families including Callitrichaceae, Globulariaceae, Hippuridaceae, Orobanchaceae and Plantaginaceae. Some of these families were acknowledged to be closely related to Scrophulariaceae by some authors (e.g. Orobanchaceae and Plantaginaceae, Cronquist 1981). Likewise, intrafamilial classifications of Scrophulariaceae have been based on a variety of characters, including floral aestivation (Bentham 1846, 1876; Wettstein 1891; Pennell 1935), stamen morphology (e.g. Van Tieghem 1903) and nectary morphology and the parasitic habit (e.g. Bellini 1907), indicating a disagreement over what characteristics are important for recognising natural groups in Scrophulariaceae s.l. (Olmstead and Reeves 1995; Olmstead *et al.* 2001).

Suggestions that Scrophulariaceae s.l. were not monophyletic were commonplace for many years before the molecular systematics revolution (e.g. Cronquist 1981). However, the first molecular phylogenetic evidence for this came when *Callitriche* was found to be closer to *Digitalis* than either was to *Antirrhinum* (Olmstead *et al.* 1993). Though aquatic plants (e.g. *Callitriche*) often have been difficult to classify due to reduction in a suite of reproductive and vegetative traits, various suggestions for the placement of *Callitriche* (e.g. Cronquist 1981; Takhtajan 1997) had not included Scrophulariaceae. A follow-up study intended to document the phylogenetic placement of three aquatic plant families, Callitrichaceae, Hippuridaceae and Hydrostachyaceae (each consisting of a single genus), lumped together by Cronquist (1981) into an artificial order for convenience only, resulted in the discovery that two of these (Callitrichaceae and Hippuridaceae) formed a clade that was nested within a group of genera assigned to Scrophulariaceae (Olmstead and Reeves 1995) and the third, Hydrostachyaceae, belonged elsewhere, near Hydrangeaceae and Loasaceae (Hempel *et al.* 1995). Furthermore, the study of Olmstead and Reeves (1995) found two distinct clades typically classified together in Scrophulariaceae. These were labelled 'scroph I,' containing *Scrophularia* and several other genera, including *Buddleja* (traditionally Buddlejaceae), and 'scroph II,' containing *Antirrhinum*, *Digitalis*, *Veronica*, *Callitriche*, *Hippuris* and *Plantago* (traditionally Plantaginaceae). *Myoporum* was included in this study and was sister to the group labelled 'scroph I'. Two other genera (*Paulownia* and *Schlegelia*), which had been assigned either to Scrophulariaceae or Bignoniaceae, were included as well and were not found to fit with either of the two strongly supported Scrophulariaceae clades. Subsequently, *Paulownia* and *Schlegelia* were also shown to be distinct from Bignoniaceae (Spangler and Olmstead 1999).

Contemporaneous with the above studies, molecular phylogenetic research on the parasitic plant family Orobanchaceae was undertaken to understand the origin of parasitism in Scrophulariaceae. Sampling included both the

holoparasitic plants traditionally assigned to Orobanchaceae and the hemiparasites (containing chlorophyll and capable of photosynthesis, but also forming parasitic haustorial connections to host plants) assigned to Scrophulariaceae (dePamphilis *et al.* 1997; Wolfe and dePamphilis 1998; Young *et al.* 1999). These studies found that the hemi- and holoparasites formed a third clade apparently distinct from either of those identified by Olmstead and Reeves (1995).

Following on these findings, the authors of the aforementioned studies collaborated to more fully address the question of Scrophulariaceae polyphyly (Olmstead *et al.* 2001). Their study was based on three plastid genes (*rbcL*, *ndhF*, and *rps2*) and a sampling of 39 genera representing c. 24 tribes commonly assigned to Scrophulariaceae s.l. plus representatives of 15 other families in Lamiales. Their results identified five distinct lineages comprised primarily of taxa traditionally placed in Scrophulariaceae s.l. The clades identified by Olmstead *et al.* (2001) as Scrophulariaceae *sensu stricto* (s.s.) and Veronicaceae [Plantaginaceae *sensu* APG II (2003)] corresponded to the 'scroph I' and 'scroph II' clades, respectively, of Olmstead and Reeves (1995), but with a significantly larger sampling for each of these clades. Scrophulariaceae s.s. was expanded to include Myoporaceae, and Veronicaceae was expanded to include Globulariaceae [excluding Selaginaceae, which had been placed previously in Globulariaceae by Cronquist (1981) but which now belongs in Scrophulariaceae s.s.]. The third clade, Orobanchaceae, originally identified by dePamphilis *et al.* (1997), comprised the holoparasitic and hemiparasitic lineages and the non-parasitic genus *Lindenbergia*, which was resolved as the sister group to the rest of the Orobanchaceae. The fourth and fifth clades described by Olmstead *et al.* (2001) were Calceolariaceae, comprising the traditional scroph tribe Calceolarieae, and Stilbaceae, which included the small family Stilbaceae s.s. plus the traditional scroph genus *Halleria*. The genus *Mimulus*, traditionally placed in the Gratioleae of Scrophulariaceae (Bentham 1876; Wettstein 1891), was left unassigned to any more inclusive clade at the rank of family pending more detailed studies (Olmstead *et al.* 2001). Subsequent analyses of *Mimulus* and other closely related genera identified a sixth clade and, in the process, redefined and vastly expanded Phrymaceae (Beardsley and Olmstead 2002). As in previous studies, *Paulownia* and *Schlegelia* occupied isolated positions in Lamiales and were treated as the distinct families Paulowniaceae (Nakai 1949) and Schlegeliaceae (Reveal 1996), respectively.

A seventh clade composed of taxa belonging to tribe Lindernieae (*sensu* Fischer 2004) was identified by Rahmzadeh *et al.* (2005) and reassigned to the rank of family. In their study, tribe Gratioleae also were identified as a clade distinct from Veronicaceae, where they had been found previously (Olmstead *et al.* 2001), and recognised

at the rank of family (Gratiolaceae Martynov). However, subsequent and more detailed studies (Albach *et al.* 2005a; Oxelman *et al.* 2005) confirmed the placement of Gratiolaceae in Veronicaceae. A series of recent studies have expanded upon the sampling of several of the segregate clades of Scrophulariaceae s.l. (Kornhall *et al.* 2001; Beardsley *et al.* 2004; Albach *et al.* 2005a; Oxelman *et al.* 2005; Wolfe *et al.* 2005; P Kornhall, B Bremer unpubl. data). One of these (Oxelman *et al.* 2005) identified a small clade comprising the Asian genera *Mazus* and *Lancea* as distinct from Phrymaceae, with which they had been included in an earlier study (Beardsley and Olmstead 2002), and *Rehmannia* weakly associated with it. As more studies explore the phylogeny of former members of Scrophulariaceae s.l., the number of unsampled taxa is becoming smaller and the likelihood of identifying additional distinct clades is decreasing.

The career and contributions of Lawrie Johnson, to whom this review series is dedicated, spanned a time in the evolution of our discipline from which the phylogenetic age of plant systematics has emerged. Following his retirement in 1985, he continued to be actively engaged in collaborative research, and recognised the integral role that molecular systematics would play in enhancing our understanding of plant phylogeny and evolution (Briggs 2001). Our modern concept of Scrophulariaceae offers one such example of how dramatically molecular systematics can alter our views of traditional plant families. In this paper, we summarise the disposition of what was once the family Scrophulariaceae s.l. and provide a summary of the major lineages comprised primarily of taxa once placed in the Scrophulariaceae s.l. based on the last decade of molecular systematic studies. In addition, we will briefly discuss the placement of some problematic taxa that are not encompassed by any of these clades.

The disintegrated Scrophulariaceae s.l.

Figure 1 presents a summary of the current view of phylogenetic relationships in the Lamiales. All of the segregate lineages comprised in part or in total by previous members of Scrophulariaceae s.l. (designated in bold in Fig. 1) belong to the core Lamiales clade (*sensu* Judd and Olmstead 2004). Although the individual lineages of the Lamiales generally are well supported, relationships among these groups are poorly understood and should be the subject of future research.

Since the polyphyletic nature of Scrophulariaceae s.l. was revealed by molecular systematic studies (Olmstead and Reeves 1995; dePamphilis *et al.* 1997; Olmstead *et al.* 2001), several researchers have investigated the phylogenetic placement of taxa traditionally found in Scrophulariaceae s.l. (Steiner 1996; Wolfe *et al.* 1997, 2002; Oxelman *et al.* 1999, 2005; Young *et al.* 1999; Ghebrehiwet *et al.* 2000; Kornhall *et al.* 2001; Olmstead *et al.* 2001; Beardsley and Olmstead 2002; Kelchner 2003; Kornhall and Bremer 2004;

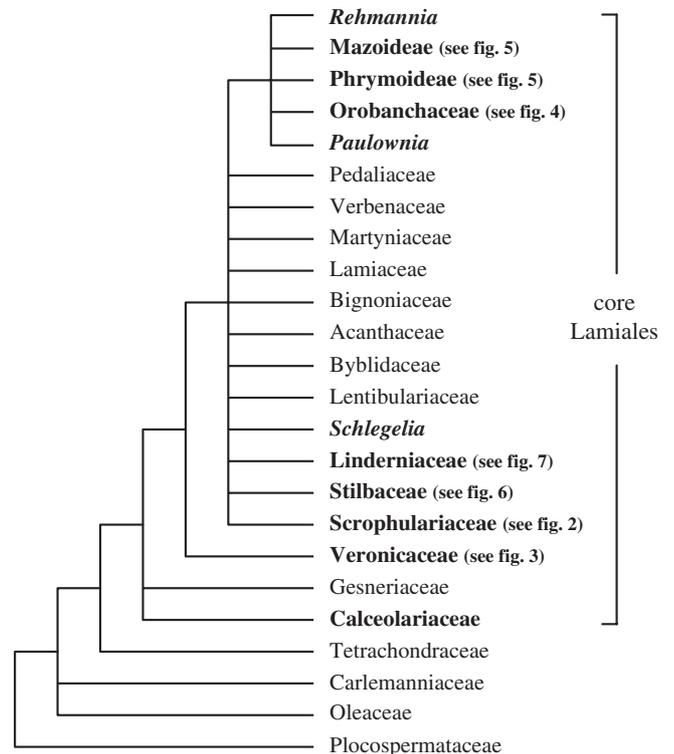


Fig. 1. Summary of phylogenetic relationships in the Lamiales compiled from multiple molecular systematic studies of cpDNA and nuclear rDNA (Backlund *et al.* 2000; Albach *et al.* 2001, 2005a; Olmstead *et al.* 2001; Bremer *et al.* 2002; Müller *et al.* 2004; Oxelman *et al.* 2005; Rahmanzadeh *et al.* 2005). Only those relationships that are well supported by multiple studies are depicted as resolved. The core Lamiales is delimited *sensu* Judd and Olmstead (2004). Taxa in bold are those that are entirely or partially comprised of species that are traditionally included in Scrophulariaceae s.l.

Albach *et al.* 2005a; Beardsley and Barker 2005; Rahmanzadeh *et al.* 2005; P Kornhall, B Bremer unpubl. data). Most of these studies were focused on clarifying the breadth of taxa that belong to a specific clade and, as a result, a phylogenetic framework is emerging for many of the genera traditionally comprising Scrophulariaceae s.l. In the following sections we discuss the current systematic disposition of Scrophulariaceae s.s., Veronicaceae [= Plantaginaceae in Angiosperm Phylogeny Group II (2003)], Orobanchaceae, Phrymaceae, Stilbaceae, Linderniaceae and Calceolariaceae. For a synoptical classification of Lamiales to genus that reflects the results of the recent phylogenetic literature for the major lineages of scrophs reviewed below see <http://depts.washington.edu/phylo/classifications/Lamiales.html> (verified 4 January 2006).

Paulownia, Rehmannia and Schlegelia

In addition to the seven distinct lineages that have emerged from phylogenetic studies of Scrophulariaceae s.l., a few

taxa have been identified that do not belong to a more inclusive clade given the current status of phylogenetic relationships in the Lamiales (Fig. 1). Among these, the two small genera *Paulownia* and *Schlegelia* are not resolved in any distinct Lamiales lineage, and have been treated as families Paulowniaceae and Schlegeliaceae (including *Exarata*, *Gibsoniothamnus* and *Synopsis*), respectively (*sensu* Olmstead *et al.* 2001; APG II 2003). *Paulownia* appears to belong in a clade with Orobanchaceae and Phrymaceae, a placement confirmed by several studies (Olmstead *et al.* 2001; Beardsley and Olmstead 2002; Bremer *et al.* 2002; Müller *et al.* 2004; Oxelman *et al.* 2005; Rahmzadeh *et al.* 2005). In contrast, the phylogenetic placement of *Schlegelia* within the Lamiales is less certain. Olmstead *et al.* (2001) found weak support for *Schlegelia* as the sister group to Bignoniaceae (44% bootstrap support); Bremer *et al.* (2002) showed moderate support for a sister group relationship between *Schlegelia* and Acanthaceae (71% jackknife support); and Oxelman *et al.* (2005) recovered a largely unresolved position for *Schlegelia* with respect to the majority of the core Lamiales. Further studies are necessary to determine the phylogenetic affinities of the problematic genus *Schlegelia*.

Rehmannia was placed traditionally in tribe Digitalideae (Bentham 1846, 1876; Wettstein 1891; Solereder 1909; Li 1948; Hong *et al.* 1998) along with other non-parasitic members of subfamily Rhinanthoideae. However, the familial placement of *Rehmannia* has been controversial, having been treated variously in both the Scrophulariaceae and Gesneriaceae. The two genera *Titanotrichum* and *Triaenophora* were segregated from within *Rehmannia* by Solereder (1909), who retained *Rehmannia* and *Triaenophora* in the Digitalideae, and moved *Titanotrichum* to Gesneriaceae. Molecular systematic studies confirm the placement of *Titanotrichum* in Gesneriaceae (Smith *et al.* 1997a, 1997b; Albach *et al.* 2001; Wang *et al.* 2004).

Phylogenetic analyses of three plastid regions, *ndhF*, *trnL/F* and *rps16* (Oxelmann *et al.* 2005), place *Rehmannia* in a clade containing the Phrymoideae and Mazoideae (Phrymaceae *sensu* Beardsley and Olmstead 2002), *Paulownia* and Orobanchaceae, but unresolved with respect to these other groups (Fig. 1). Comparative studies of floral development suggest a close relationship between *Rehmannia* and *Titanotrichum* (Pan *et al.* 2002); however, the phylogenetic utility of the identified floral developmental characteristics is not clear. *Triaenophora* remains unsampled by molecular phylogenetic studies.

Scrophulariaceae sensu stricto

Scrophulariaceae s.s. (Olmstead *et al.* 2001; Angiosperm Phylogeny Group II 2003) were first recognised as a distinct clade by Olmstead and Reeves (1995) based on the comparative analysis of chloroplast DNA sequences.

Since then, a series of phylogenetic analyses have recovered this clade (Oxelmann *et al.* 1999, 2005; Kornhall *et al.* 2001; Olmstead *et al.* 2001; Bremer *et al.* 2002; Kornhall and Bremer 2004). These studies featured increased taxon sampling and the addition of several new datasets, greatly enhancing the resolution of member lineages within Scrophulariaceae.

The investigations above have taken different approaches to resolving relationships within Scrophulariaceae, mainly due to the different hierarchical level investigated in each study. Targeting large-scale resolution of the asterids, Bremer *et al.* (2002) used sequence data from six cpDNA regions, but with few Scrophulariaceae taxa included in the analysis. In contrast, Oxelman *et al.* (2005) sought a more complete taxonomic sampling of the Scrophulariaceae s.l., including 68 representatives of Scrophulariaceae s.s. for three chloroplast regions, not all of which were sequenced for each taxon in the analysis. Olmstead *et al.* (2001) provided an intermediate between the two approaches, using complete sequence data from three cpDNA regions for an intermediate number of taxa representing Scrophulariaceae s.l. Despite their differing aims, datasets, and sampling regimes, all of these studies resolved a monophyletic Scrophulariaceae s.s., as well as several of their lineages. For this reason, and the relatively high bootstrap support for the clade in each molecular study, APG II (2003) has adopted Scrophulariaceae *sensu* Olmstead *et al.* (2001).

Even though this clade is the namesake of the once much larger family, there are a couple of dramatic differences relative to the former concept of this group (apart from its much smaller size). First, this clade is predominantly southern hemisphere in its distribution. Four of its eight tribes are almost entirely distributed in southern Africa and a fifth, the former Myoporaceae, are predominantly Australian. Of the remaining three, only Scrophulariaceae appear to have radiated significantly in the northern hemisphere, with *Scrophularia* and *Verbascum* accounting for 400–500 species. The temperate North American flora (north of Mexico) is left with only three genera, *Scrophularia*, *Capraria* and *Leucophyllum*, with the latter two only just reaching the southern USA. Second, contrary to the typical bilateral corolla symmetry that characterises most core Lamiales, most Scrophulariaceae exhibit examples of sub-radial corolla symmetry. The large genera *Scrophularia* and *Eremophila* are the most notable exceptions within this clade.

Additional studies have expanded the sampling within this clade to better circumscribe the group and understand relationships within it (Kornhall *et al.* 2001; Kelchner 2003; Kornhall and Bremer 2004; Archibald *et al.* 2005). The present concept of Scrophulariaceae s.s. includes at least eight major lineages recognised by Oxelman *et al.* (2005) as tribes: Aptosimeae, Buddlejaceae, Hemimerideae, Leucophylleae, Limoselleae, Myoporeae, Scrophulariaceae

and Teedieae. A few genera fall outside of any recognised tribe (e.g. *Androya*, *Camptoloma* and *Phygelius*). Relationships among these groups are fairly well established (Fig. 2). We provide a synopsis of each tribe, including a list of genera that have been included in the published molecular phylogenies.

Aptosimeae Benth & Hook.f

The present treatment of Aptosimeae agrees with the circumscription of Bentham (1846) and represents one of the few groups of Scrophulariaceae that has remained stable in classification. The lineage is characterised by alternate leaves and dilated corolla tubes. Most species are endemic to Africa; some members of *Anticharis* occur in Malesia. Based on cpDNA sequences, Aptosimeae are most closely related to a clade containing Myoporeae (Myoporaceae), Leucophylleae, and *Androya* (previously Loganiaceae). Genera included in molecular phylogenetic studies include *Anticharis*, *Aptosimum* and *Peliostomum*.

Buddlejeae Benth

Buddlejeae (Buddlejaceae) are consistently recovered as a strongly supported clade in phylogenetic analyses of cpDNA sequence data (Oxelman *et al.* 1999, 2005). *Buddleja* itself is likely to be paraphyletic (Oxelman *et al.* 2005). Buddlejeae, Teedieae, *Camptoloma* and *Phygelius* belong to a lineage that is sister to the Scrophularieae–Limoselleae clade (Fig. 2). Like Teedieae, Buddlejeae are largely comprised of woody taxa. *Buddleja* is worldwide in distribution, including temperate and tropical regions of Africa, Asia, and the New World. Its close relatives (Teedieae, *Camptoloma* and

Phygelius) are predominantly southern African. Genera included in molecular phylogenetic studies include *Buddleja*, *Emorya*, *Gomphostigma* and *Nicodemia*.

Hemimerideae Benth

The present circumscription matches that of Steiner (1996) with the addition of *Colpias*, which was included on the basis of cpDNA evidence (Oxelman *et al.* 2005). Oxelman *et al.* (2005) suggested that nuclear genome sequences should be investigated to test the inclusion of *Colpias*, which shares such characters as a tubular corolla, a staminode in position of a fifth stamen, and a base chromosome number of $x = 20$ with the group Bowkerieae (Stilbaceae). In a study investigating the circumscription of the Stilbaceae that included sequences of the nuclear ribosomal ITS region for a limited sampling of Scrophulariaceae, *Colpias* was resolved as the sister to all other Scrophulariaceae s.s. (P Kornhall, B Bremer unpubl. data), suggesting that its inclusion in the Hemimerideae should be further investigated. The tribe, as described here, is largely South African. Members of *Alonsoa* in South America may form a monophyletic group united by the absence of oil secretion and $2n = 56$ chromosomes (Steiner 1996; Oxelman *et al.* 2005). Genera included in molecular phylogenetic studies include *Alonsoa*, *Colpias*, *Diascia*, *Diclis*, *Hemimeris* and *Nemesia*.

Leucophylleae Miers

Chloroplast DNA phylogenies of Olmstead *et al.* (2001) and Oxelman *et al.* (2005) and molecular and morphological analyses by Kelchner (2003) all show a strongly supported sister relationship between Leucophylleae and Myoporeae (Myoporaceae, Fig. 1). Considerable morphological evidence unites Leucophylleae and Myoporeae, including the presence of tricolpate, diorate pollen (also in *Androya*, Neizgoda and Tomb 1975), xeromorphic wood anatomy (Carlquist and Hoekman 1986), and the presence of spherical, epithelium-lined secretory cavities in vegetative tissues (Lersten and Beaman 1998; Lersten and Curtis 2001). Unlike Myoporeae, the fruit of Leucophylleae are capsules. The lineage is endemic to Central America; *Capraria* has the broadest distribution, ranging from southern United States through Central America, the Caribbean islands, and northern South America. Genera included in molecular phylogenetic studies include *Capraria* and *Leucophyllum*.

Limoselleae Dumort

Limoselleae, as described here, include the former tribes Selagineae and Manuleeae (Kornhall *et al.* 2001; Archibald *et al.* 2005; Oxelman *et al.* 2005). The close relationship between Selagineae (placed in Globulariaceae by Cronquist 1981) and Manuleeae was confirmed by cpDNA analysis (Kornhall *et al.* 2001; Olmstead *et al.* 2001). The earlier name Manuleeae was adopted for this

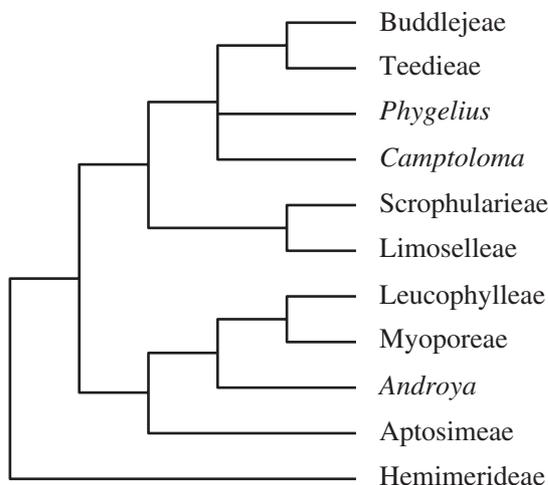


Fig. 2. Summary of the phylogenetic relationships among the tribes of Scrophulariaceae s.s., as delimited by Oxelman *et al.* (2005), including those genera not resolved as a part of any of the tribal lineages. Based on results presented by Oxelman *et al.* (2005).

group (Kornhall *et al.* 2001) until the inclusion of *Limosella* (formerly Gratiolaceae, Hallier 1903) was demonstrated in a subsequent study (Kornhall and Bremer 2004). The name Limoselleae has nomenclatural priority over Manuleeae. The tribe includes a diverse array of genera, most of which contain few species and are endemic to southern Africa, but also includes the globally distributed *Limosella*. Two of the larger genera, *Manulea* and *Sutera*, form a clade with *Manulea* nested within *Sutera*; this has led to the promotion of *Sutera* sect. *Chaetostoma* (46 of the 49 *Sutera* species) to generic status (as *Chaetostoma*), thereby reducing the number of *Sutera* species to three (Kornhall and Bremer 2004). In addition, *Reyemia* was found to be nested within *Zaluzianskya* (Kornhall *et al.* 2001; Archibald *et al.* 2005). Genera included in molecular phylogenetic studies include *Barthlottia*, *Chaetostoma*, *Chenopodiopsis*, *Cromidon*, *Dischisma*, *Glekia*, *Glumicalyx*, *Hebenstretia*, *Jamesbrittenia*, *Limosella*, *Lyperia*, *Manulea*, *Manuleopsis*, *Melanospermum*, *Microdon*, *Phyllopodium*, *Polycarena*, *Pseudoselago*, *Reyemia*, *Selago*, *Sutera*, *Tetraselago*, *Trieenea* and *Zaluzianskya*.

Myoporeae Rchb

Historically treated as a distinct family (Myoporaceae), Myoporeae are now known to be embedded deeply within Scrophulariaceae s.s. (Olmstead *et al.* 2001). A detailed phylogenetic analysis by Kelchner (2003) demonstrated the monophyly of Myoporeae and included all genera circumscribed in Myoporaceae (RJ Chinnock pers. comm.). Inclusion of *Offtia* and *Ranopisoa* in Myoporaceae were not supported by Kelchner (2003). Myoporeae are distinguished by alternate leaves, fleshy 'drupaceous' fruit, and an abundance of spherical resin cavities in the vegetative and reproductive tissues of the plants. Like Leucophylleae, Myoporeae occur predominantly in arid, semi-arid, and coastal environments, although 95% of its ~250 species are endemic to Australia. The sister relationship between Myoporeae (Australian) and Leucophylleae (Central American) poses an interesting biogeographic puzzle, as does the disjunct distribution of *Bontia* in the West Indies, which belongs to a clade of Australian endemic Myoporeae. The possible development of these disjunctions is addressed by Kelchner (2003). Genera included in molecular phylogenetic studies include *Bontia*, *Eremophila* and *Myoporum* (including *Diocirea*, *Calamphoreus*, *Glycocystis* and *Pentacoeilium*).

Scrophularieae Dumort

Scrophularieae form a strongly supported clade in the analysis of Oxelman *et al.* (2005), who added the genera *Antherothamnus* and *Oreosolen* to the previously identified cpDNA clade of *Scrophularia* and *Verbascum* (Olmstead *et al.* 2001). In the context of their sampling, Oxelman *et al.* (2005) revealed a sister-group relationship between

Scrophularia and the Himalayan genus *Oreosolen*, which they report as sharing similar floral morphology and leaf architecture. These genera are sister to *Verbascum*, together comprising a clade that is predominantly north temperate in distribution, unlike most other lineages in Scrophulariaceae. *Antherothamnus*, a monotypic African genus, is sister to the remaining Scrophularieae, although a set of morphological synapomorphies that unite these taxa is not readily apparent. Genera included in molecular phylogenetic studies include *Antherothamnus*, *Oreosolen*, *Scrophularia* and *Verbascum* (including *Celsia*).

Teedieae Benth

Teedieae comprise a lineage of South African shrubs belonging to at least four species-poor genera. Oxelman *et al.* (2005) mention leafy inflorescences as a possible morphological synapomorphy for the clade. Teedieae, Buddlejaceae, Scrophularieae, Limoselleae, *Camptoloma* and *Phygelius* form a well supported clade based on cpDNA analyses (Fig. 2). Genera included in molecular phylogenetic studies include *Dermatobotrys*, *Freylinia*, *Offtia* and *Teedia*.

Veronicaceae Durande (*Plantaginaceae* Durande sensu APG II)

Veronicaceae (recognised by Olmstead and Reeves 1995 as 'scroph II') are the largest of the major lineages to emerge from the former Scrophulariaceae. With increased taxon sampling, Olmstead *et al.* (2001) recognised Veronicaceae as including part or all of Bentham's (1876) tribes Digitalideae, Antirrhineae, Cheloneae and Gratiolaceae, Angelonieae (*sensu* Pennell 1919, a segregate from Hemimerideae), Globularieae (*sensu* Barringer 1993) and the families Callitrichaceae, Hippuridaceae and Plantaginaceae. In that study, support for Veronicaceae was quite low (48% bootstrap support), but subsequent analyses of multiple cpDNA and nuclear rDNA regions have solidified support for this clade (Albach *et al.* 2005a; Oxelman *et al.* 2005). In all of the above studies, a clade comprising Angelonieae, Gratiolaceae, *Melosperma* and *Ourisia* was recovered with modest support and was sister to the rest of Veronicaceae. In contrast, based on sequences of the cpDNA *trnK* intron and intervening *matK* gene (*trnK-matK*), Rahmanzadeh *et al.* (2005) did not recover a monophyletic Veronicaceae, instead finding Gratiolaceae separate from the rest of Veronicaceae in an unresolved position with respect to it and two other clades. On this basis they resurrected the family Gratiolaceae Martynov. However, in light of the more convincing results cited above, the results of Rahmanzadeh *et al.* (2005) are possibly an artefact of limited taxonomic sampling of the large, diverse Gratiolaceae clade, and their use of only one cpDNA region.

Both Olmstead and Reeves (1995) and Olmstead *et al.* (2001) suggested a sister group relationship between

Veronicaceae and the majority of the core Lamiales (excluding Gesneriaceae and Calceolariaceae; Fig. 1), but neither analysis provided strong support for this assertion. The studies of Bremer *et al.* (2002) and Oxelman *et al.* (2005) both recovered this relationship with increasing levels of support.

Although this clade is recognised by the Angiosperm Phylogeny Group as the family Plantaginaceae (APG II 2003), the oldest valid family name associated with taxa found to belong to this clade is Veronicaceae (Olmstead *et al.* 2001). However, Plantaginaceae is a conserved name and, therefore, under the International Code of Botanical Nomenclature, has precedence over Veronicaceae. As it is traditionally recognised, the family Plantaginaceae is a small, easily characterised monophyletic group. However, in the circumscription accepted by APG II (2003) the majority of species do not resemble taxa that most botanists recognise as Plantaginaceae. Even specialists in taxa of the traditional Plantaginaceae still consider 'Plantaginaceae' as a distinct lineage within the clade Veronicaceae (e.g. Hoggard *et al.* 2003). It is clear that the conserved name of Plantaginaceae for this much larger, and more heterogeneous, assemblage of taxa has been, and will continue to be, confusing. Therefore, we follow Olmstead *et al.* (2001) in their use of the name Veronicaceae for this clade.

Since the discovery of the 'scroph II' clade (Olmstead and Reeves 1995; Olmstead *et al.* 2001), this lineage has received considerable attention from molecular systematists (Wolfe *et al.* 1997, 2002; Ghebrehiwet *et al.* 2000; Albach and Chase 2001, 2004; Bello *et al.* 2002; Rønsted *et al.* 2002; Hoggard *et al.* 2003; Albach *et al.* 2004a, 2004b, 2005a, 2005b; Oyama and Baum 2004; Oxelman *et al.* 2005; Rahmanzadeh *et al.* 2005). From these studies, the present concept of Veronicaceae includes ~90 genera and ~2000 species. The most detailed study of Veronicaceae to date is that of Albach *et al.* (2005a) who proposed the groups listed below (Fig. 3). A synopsis is provided in the following sections, with a list of genera for which representative taxa have been included in molecular phylogenetic studies.

Angelonieae Pennell

Angelonieae are a predominantly South American clade including *Angelonia*, *Basistemon*, *Melosperma*, *Monttea* and possibly *Ourisia*, and is recovered by phylogenetic analyses of the nuclear rDNA ITS region and multiple cpDNA regions (Albach *et al.* 2005a; Oxelman *et al.* 2005). A close relationship of *Angelonia*, *Basistemon*, *Melosperma* and *Monttea* was hypothesised by Barringer (1983) and, according to Albach *et al.* (2005a), the shrubby habit, reduced seed number and the presence of oil as a pollinator reward (at least in *Angelonia*, *Basistemon* and *Monttea*) are the most apparent similarities shared between the genera. The inclusion of *Ourisia* (a genus of

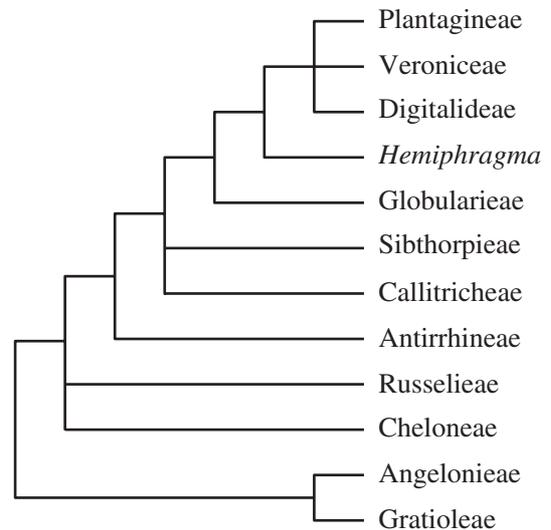


Fig. 3. Summary of the phylogenetic relationships among the tribes of Veronicaceae, as delimited by Albach *et al.* (2005a). Based on results presented by Albach *et al.* (2005a).

c. 30 species distributed in New Zealand, Tasmania and South America) in Angelonieae is more tenuous, making further studies necessary. Although *Ourisia* is resolved as the sister group to the remainder of the tribe by both Oxelman *et al.* (2005) and Albach *et al.* (2005a), this relationship is not well supported. Rossow (1985) erected a separate tribe for *Melosperma* and *Monttea*, a classification that also is consistent with the phylogeny, if *Ourisia* is left unassigned to tribe. Genera included in molecular phylogenetic studies include *Angelonia*, *Basistemon*, *Melosperma*, *Monttea* and *Ourisia*.

Antirrhineae Dumort

Antirrhineae are one of the most stable groups of former scrophs, and the monophyly of the tribe has rarely been questioned. The group is characterised by having unique poricidal capsules, zygomorphic flowers often with a prominent palate, and the presence of a unique form of iridoids, the antirrhinosides (Ghebrehiwet *et al.* 2000). The last detailed revision was done by Sutton (1988), who included 27 genera in the tribe; only 18 of these have been included in molecular studies.

Ghebrehiwet *et al.* (2000) identified four well supported clades: the 'Anarrhinum clade' (*Anarrhinum* and *Kickxia*) as the sister group to the remainder of the tribe, the 'Maurandya clade' (*Asarina*, *Cymbalaria*, *Maurandella*, *Maurandya* and *Rhodochiton*), the 'Gambelia clade' (*Gambelia* and *Galvezia*) and the 'Antirrhinum clade' (*Antirrhinum*, *Chaenorhinum*, *Howelliella*, *Linaria*, *Misopates*, *Mohavea* and *Schweinfurthia*). Relationships within each of these clades were mostly resolved; however, relationships among the last three were unclear. A subsequent study of New World

Antirrhinum (Oyama and Baum 2004) found *Mohavea*, distinctive in Antirrhineae by having only two stamens, to be nested within *Antirrhinum*.

Albach *et al.* (2005a) recovered the same overall relationships with many fewer taxa of the Antirrhineae sampled. In addition, Albach *et al.* (2005a) place the genus *Lafuentea* sister to the 'core' Antirrhineae. *Lafuentea*, a small genus of two species native to southern Spain and Morocco (Mabberley 1997), is traditionally placed in the Digitalideae (Bentham 1876; Wettstein 1891). Although this sister group relationship is strongly supported in their analyses, Albach *et al.* (2005a) suggested that future studies of Antirrhineae that include *Lafuentea* will help clarify potential synapomorphies for this expanded view of the clade. Genera included in molecular phylogenetic studies include *Anarrhinum*, *Antirrhinum*, *Asarina*, *Chaenorhinum*, *Cymbalaria*, *Galvezia*, *Gambelia*, *Howelliella*, *Kickxia*, *Lafuentea*, *Linaria*, *Lophospermum*, *Maurandella*, *Maurandya*, *Misopates*, *Mohavea*, *Rhodochiton* and *Schweinfurthia*.

Callitricheae Dumort

The two aquatic genera *Callitriche* (c. 40 spp.) and *Hippuris* (1 sp.) are placed traditionally in monogeneric families. The reproductive morphology of the two genera is extremely reduced and highly modified for their aquatic habit. This has led to confusion over their taxonomic placement in the Asterids, where Cronquist (1981) placed the two families, along with the unrelated Hydrostachyaceae, in his Callitrichales. Early phylogenetic analyses of the plastid gene *rbcL* revealed a relationship between *Antirrhinum* and *Callitriche* (Olmstead *et al.* 1992). From the first report of the polyphyletic origin of the Scrophulariaceae s.l. (Olmstead and Reeves 1995), *Callitriche* and *Hippuris* have consistently been recovered in the Veronicaceae clade with strong support (Olmstead *et al.* 2001; Bello *et al.* 2002; Albach *et al.* 2005a). Reduction of the androecium to one stamen and the loss of one perianth whorl supports the sister group relationship of the two genera (Reeves and Olmstead 1998). Genera included in molecular phylogenetic studies include *Callitriche* and *Hippuris*.

Cheloneae Benth

In the traditional sense, Cheloneae are a diverse assortment of genera loosely connected by the shared characteristic of a cymose inflorescence (Bentham 1846, 1876; Wettstein 1891). This character has been recognised by numerous authors as largely artificial, resulting in the movement of taxa to other tribes within Scrophulariaceae s.l., as well as to other families in the Lamiales (summarised in Wolfe *et al.* 1997). Wolfe *et al.* (1997) revealed a well supported sister group relationship between the tribes Collinsieae (*Collinsia* and *Tonella*) and Cheloneae. Subsequent analyses have confirmed this close relationship (Olmstead *et al.* 2001;

Wolfe *et al.* 2002; Albach *et al.* 2005a; Oxelman *et al.* 2005). *Pennellianthus*, a monotypic genus segregated from *Penstemon* (Crosswhite and Kawano 1970), and the only Old World member of Cheloneae sampled, has been shown to be the sister group to a clade comprised of the traditional Collinsieae and Cheloneae, resulting in the merger of the two tribes (Wolfe *et al.* 2002). Wolfe *et al.* (2002) proposed that cymose inflorescences, staminodes (or vestigial structure present in development), simple hairs and stems with a pith are synapomorphies for Cheloneae. Genera included in molecular phylogenetic studies include *Chelone*, *Chionophila*, *Collinsia*, *Keckiella*, *Nothochelone*, *Pennellianthus*, *Penstemon* and *Tonella*.

Digitalideae Dumort

Digitalideae have been viewed by some as an unnatural tribe, especially with regards to the inclusion of both *Veronica* and *Digitalis*. Most revisions of tribal delineations (e.g. Bellini 1907; Rouy 1909; Pennell 1921, 1935; Melchior 1964) have separated Digitalideae into three tribes, Veroniceae for those genera with affinities to *Veronica*, Hemiphragmeae and Digitalideae (or Rehmanniae *sensu* Rouy 1909). Therefore, it is no surprise that most of the genera included in Digitalideae *sensu* Wettstein (1891) have been shown to belong either in another clade within Veronicaceae (e.g. *Veronica*), or elsewhere in the Lamiales (e.g. *Rehmannia*). As it remains, Digitalideae now comprise only *Digitalis* (c. 18 spp.), *Erinus* (2 spp.), and *Isoplexis* (2 spp.). Furthermore, based on the study of Albach *et al.* (2005a), and an unpublished manuscript cited therein, *Isoplexis* is derived from within *Digitalis*. Albach *et al.* (2005a) suggested that the phylogenetic position of the small genus *Erinus* as the sister group to the larger, more widespread Eurasian *Digitalis* is consistent with the hypothesis that the current distribution of *Erinus* (restricted to northern Africa, the Pyrenees, and the Alps; Mabberley 1997) is a relict of a once widespread distribution throughout the mountains of the Mediterranean. Genera included in molecular phylogenetic studies include *Digitalis* (including *Isoplexis*) and *Erinus*.

Globularieae Rchb

Bentham (1876) combined *Globularia* and *Poskea* with members of the tribe Selagineae in Selaginaceae, while Wettstein (1891) recognised them as a distinct family (Globulariaceae). Hallier (1903) was the first to include Globulariaceae and Selaginaceae in Scrophulariaceae, however, most recent traditional classifications recognise Globulariaceae as a distinct family (Cronquist 1981; Takhtajan 1997). Barringer (1993) erected the tribe Globularieae for these two genera, and suggested a close relationship of Globularieae with the tribes Manuleeae and Selagineae, based on the dense inflorescence architecture and reduced number of ovules shared between these groups.

However, several studies (Olmstead *et al.* 2001; Albach *et al.* 2005a; Oxelman *et al.* 2005) now indicate that Globularieae are nested in Veroniceae, and the tribes Selagineae and Manuleeae belong to the Scrophulariaceae s.s. (see above). Olmstead *et al.* (2001) revealed a sister group relationship of *Globularia* to a well supported clade containing *Digitalis*, *Hemiphragma*, *Plantago* and *Veronica* (i.e. tribes Digitalideae and Veroniceae plus Plantaginaceae s.s.), and these results are supported by Oxelman *et al.* (2005) and Albach *et al.* (2005a), who both included *Poskea* in their analyses. In addition, both of the latter studies resolved the genus *Campylanthus* as the sister group to the *Globularia*–*Poskea* clade. *Campylanthus* is traditionally placed in the Digitalideae (Bentham 1876; Wettstein 1891), but was unusual in its placement there. Although there are no apparent morphological synapomorphies uniting *Campylanthus* with *Globularia* and *Poskea*, Albach *et al.* (2005a) helped explain this unexpected relationship by reconciling the biogeographic patterns in light of this well supported relationship. Genera included in molecular phylogenetic studies include *Campylanthus*, *Globularia* and *Poskea*.

Gratiroleae Benth

Gratiroleae are one of the least understood tribes of the Veroniceae. Several genera traditionally placed in Gratiroleae have been shown to belong to other clades in the Lamiales (e.g. Mazoideae – *Lancea* and *Mazus*; Phrymoideae – *Elacholoma*, *Glossostigma*, *Microcarpaea*, *Mimulus* and *Peplidium*; Angelonieae – *Melosperma* and *Monttea*; Linderniaceae – *Artanema*, *Craterostigma*, *Crepidorhopalon*, *Lindernia*, *Micranthemum*, *Picria*, *Stemodiopsis* and *Torenia*; Scrophulariaceae s.s. – *Capraria* and *Limosella*; Orobanchaceae – *Lindenbergia*), and only seven of the ~25 remaining genera thought to comprise Gratiroleae have been sampled in molecular systematic studies (Olmstead *et al.* 2001; Albach *et al.* 2005a; Oxelman *et al.* 2005; Rahmanzadeh *et al.* 2005). Little can be said about the intergeneric relationships and potential synapomorphies in Gratiroleae until more extensive sampling is included in phylogenetic analyses. Despite the depauperate taxon sampling of current studies, Gratiroleae are well supported in the above studies. Genera included in molecular phylogenetic studies include *Amphianthus*, *Bacopa*, *Gratiola*, *Mecardonia*, *Otacanthus*, *Scoparia* and *Stemodia*.

Hemiphragmeae Wall

The monotypic genus *Hemiphragma* was often placed in the Digitalideae (Bentham 1876; Wettstein 1891); however, Digitalideae have been split up, with Rouy (1909) recognising tribe Hemiphragmeae, which included *Capraria*, *Scoparia*, *Sibthorpia* and *Hemiphragma*. Phylogenetic analyses place the other three genera elsewhere (Scrophularieae, Gratiroleae,

and Sibthorpieae, respectively), thus leaving *Hemiphragma* by itself. Molecular systematic studies have recovered a well supported clade including *Hemiphragma*, Digitalideae, Veroniceae and Plantagineae (Olmstead *et al.* 2001; Bello *et al.* 2002; Albach *et al.* 2005a). Both Olmstead *et al.* (2001) and Bello *et al.* (2002) recovered *Digitalis* and *Hemiphragma* as successive sister groups to a Veroniceae–Plantagineae clade, but with marginal bootstrap support. In contrast, the more detailed study of Albach *et al.* (2005a) recovered *Hemiphragma* as the sister group to a well supported Digitalideae–Veroniceae–Plantagineae clade. Figure 3 depicts this relationship, but future studies are necessary to understand the uncharacteristic morphology of *Hemiphragma* in light of its phylogenetic position in Veroniceae.

Plantagineae Dumort

Plantagineae, as described here, comprise the genera *Aragoa*, *Littorella* and *Plantago*. The specialised morphology of Plantaginaceae s.s. (i.e. *Plantago* and *Littorella*) has resulted in its segregation from Scrophulariaceae s.l. in most traditional taxonomic treatments (e.g. Bentham 1846, 1876; Wettstein 1891; Bellini 1907; Dahlgren 1975; Cronquist 1981; Takhtajan 1997). However, the derived nature of this group of wind-pollinated plants relative to Scrophulariaceae s.l. was recognised by Hallier (1903) and Melchior (1964), who both suggested a close relationship of *Plantago* and *Veronica*, based on their shared tetramerous corolla, reduced stamen number and seed morphology. This close relationship has been substantiated by molecular systematic studies (Olmstead and Reeves 1995; Olmstead *et al.* 2001; Bello *et al.* 2002; Albach *et al.* 2005a); however, the relationship between Plantagineae and Veroniceae is unresolved with respect to Digitalideae (Fig. 3).

As they are defined traditionally, Plantaginaceae comprise the three genera *Plantago*, *Littorella* and *Bougueria*, and phylogenetic analyses of both morphological and molecular data support the monophyly of this traditional family (Rahn 1996; Hoggard *et al.* 2003; Rønsted *et al.* 2002). Based on morphological cladistic analyses, Rahn (1996) included both *Bougueria* and *Littorella* as subgenera within *Plantago*. Molecular phylogenetic studies (Bello *et al.* 2002; Rønsted *et al.* 2002) support the inclusion of *Bougueria* in *Plantago*, but place *Littorella* as the sister group to *Plantago* and, thus, its inclusion in *Plantago* is equivocal (see Hoggard *et al.* 2003 for arguments against inclusion of *Littorella* in *Plantago*). Bello *et al.* (2002) recovered a sister group relationship between *Aragoa*, a shrubby genus endemic to the South American páramo, and the clade of *Littorella* and *Plantago*. This unexpected relationship has been corroborated by Albach *et al.* (2005a). The taxonomic history of *Aragoa* is quite complex, but, because of its actinomorphic, tetramerous corolla, it has been treated most commonly in Veroniceae (Bello *et al.* 2002). In light

of this relationship, Bello *et al.* (2002) suggest pollen exine morphology and similarities in seed morphology as possible synapomorphies for Plantagineae, and Rønsted *et al.* (2003) identified a suite of phytochemical properties shared between *Aragoa* and *Plantago*. Genera included in molecular phylogenetic studies include *Aragoa*, *Littorella* and *Plantago* (including *Bougueria*).

Russeliae Pennell

Russelia comprises 52 species distributed from Cuba and Mexico to South America. Wettstein (1891), following Bentham (1876), placed *Russelia* in the Cheloneae, but subsequent revisions have recognised the unique fruit morphology as a distinctive characteristic warranting the placement of *Russelia* in its own tribe (Pennell 1935; Thieret 1967). A close relationship between *Tetranema* (two species distributed in Mexico and Central America; Mabberley 1997), also traditionally placed in Cheloneae, and *Russelia* was proposed by Wolfe *et al.* (2002) based on ITS and *matK* sequences and confirmed by additional multigene analyses (Albach *et al.* 2005a; Oxelman *et al.* 2005). Although the two genera share a Central American distribution, there are no apparent synapomorphies uniting the shrubby genus *Russelia* with the herbaceous *Tetranema* (Wolfe *et al.* 2002). A sister group relationship between Cheloneae and Russeliae has been recovered in nearly all analyses that have included representatives of the two tribes (Olmstead *et al.* 2001; Wolfe *et al.* 2002; Oxelman *et al.* 2005); however, never with strong support. Wolfe *et al.* (2002) noted that the small genus *Uroskinnera* (four species distributed in Mexico and Central America; Mabberley 1997), which has yet to be included in a molecular systematic study, shares some morphological characters with both Cheloneae and Russeliae, and may be integral to clarifying the relationship between these two tribes. Genera included in molecular phylogenetic studies include *Russelia* and *Tetranema*.

Sibthorpieae Benth

Sibthorpieae comprise the two small genera *Sibthorpia* and *Ellisiophyllum*. *Sibthorpia* consists of five species disjunctly distributed in tropical and montane Africa, along the Atlantic coast through western Europe, and in Central and South America (Mabberley 1997). The genus has been enigmatic in its taxonomic placement, and variously placed in Digitalideae (Bentham 1876; Wettstein 1891), Hemiphragmeae (Rouy 1909) and Veroniceae (Thieret 1955). Prior to the detailed study of Veroniceae by Albach *et al.* (2005a), *Sibthorpia* had only been sampled in studies investigating the relationships among *Veronica* and its putative relatives (Albach and Chase 2001; Bello *et al.* 2002) and was placed outside Veroniceae. The monotypic genus *Ellisiophyllum* has been suggested to be closely related to *Sibthorpia* (Bentham 1846; Hedberg 1955), and the results of Albach *et al.* (2005a) support this relationship. The two

genera share a unique type of endosperm development not seen in other Veroniceae, and also lack the iridoids typical of Lamiales (Albach *et al.* 2005a). Genera included in molecular phylogenetic studies include *Ellisiophyllum* and *Sibthorpia*.

Veroniceae Duby

As noted above, all of the genera considered here as Veroniceae were treated by Wettstein (1891) in tribe Digitalideae. However, the artificial nature of the Digitalideae has been demonstrated by the results of molecular phylogenetic studies (Olmstead *et al.* 2001; Albach and Chase 2004; Albach *et al.* 2004a, 2004b, 2005a; Oxelman *et al.* 2005). The majority of taxonomic changes in Veroniceae have focused on splitting segregate genera out of *Veronica* (*Besseyia*, *Chionohebe*, *Cochlidiosperma*, *Derwentia*, *Hebe*, *Hebejeebie*, *Heliohebe*, *Leonohebe*, *Oligospermum*, *Parahebe*, *Paederota*, *Pseudolysimachion*, *Synthyris* and *Veronicastrum*) and on circumscription of generic boundaries for the rest of the genera (summarised in Albach *et al.* 2004b). Detailed molecular phylogenetic analyses of Veroniceae (Albach and Chase 2001, 2004; Wagstaff *et al.* 2002; Albach *et al.* 2004a, 2005b; Hufford and McMahon 2004) have revealed complex relationships of *Veronica* and its relatives, with as many as ten genera derived from within *Veronica*. These results have led to a substantial revision of the boundaries of *Veronica* and a new infrageneric classification (Albach *et al.* 2004b). The expanded *Veronica* is derived from a grade of the remaining genera of Veroniceae, including *Lagotis*, *Paederota*, *Picrorhiza*, *Veronicastrum*, *Wulfenia* and *Wulfeniopsis* (the 'wulfenoid grade' *sensu* Albach and Chase 2004). *Paederota* is supported as the sister lineage to *Veronica* in most analyses, but relationships among the genera of the wulfenoid grade are not well understood (see Albach and Chase 2004). The two monotypic genera *Scrofella* and *Kashmiria* are the only two genera of Veroniceae that have not been included in any molecular phylogenetic studies. *Scrofella* has been included previously in *Veronicastrum*, and *Kashmiria* has been treated in *Wulfenia* (Albach *et al.* 2004b, 2005a); therefore, it is likely that these genera will add additional taxa to the wulfenoid grade. Genera included in molecular phylogenetic studies include *Lagotis*, *Paederota*, *Picrorhiza*, *Veronica* (including *Besseyia*, *Derwentia*, *Pseudolysimachion*, *Synthyris*, *Hebe* and its relatives), *Veronicastrum*, *Wulfenia* and *Wulfeniopsis*.

Orobanchaceae Vent

On the basis of recent studies, Orobanchaceae have been defined as 'the least inclusive clade that contains *Orobanche uniflora*, *Schwalbea americana* and *Lindenbergia philippinensis*' (Young *et al.* 1999). These studies (dePamphilis *et al.* 1997; Nickrent *et al.* 1998; Wolfe and dePamphilis 1998) recovered a well supported lineage

that included the holoparasitic members traditionally treated in Orobanchaceae and the hemiparasitic taxa previously treated under Scrophulariaceae. Sister to the parasitic clade, and also included in the expanded Orobanchaceae, is the non-parasitic genus *Lindenbergia* (Gratiroleae in Bentham 1846; Wettstein 1891). Although *Lindenbergia* is not known to be parasitic, the placement of the genus as the sister lineage to the remainder of Orobanchaceae is justified by other characteristics such as similar phytochemical properties, stomatal morphology and floral aestivation (Olmstead *et al.* 2001; Wolfe *et al.* 2005). Brühl (1920) viewed *Lindenbergia* as a link between the hemiparasitic tribe Buchnereae and the non-parasitic tribe Gratiroleae.

The results of this research indicate that parasitism in the Lamiales evolved once and that the holoparasitic plants are not monophyletic, signifying that holoparasitism may have evolved as many as five times independently (Young *et al.* 1999; Wolfe *et al.* 2005). This pattern suggests that the evolution of a haustorial connection to a host plant is a rare event, but once achieved, evolution of obligate parasitism can occur more readily, perhaps through little more than a mutation to one of the many genes critical to photosynthesis. Boeshore (1920) argued for an evolutionary transition series leading from the photosynthetic hemiparasites (e.g. *Castilleja*, *Euphrasia*, *Pedicularis*) through a progressive reduction (e.g. *Harveya*, *Hyobanche*, *Lathraea*) ending in the holoparasitic habit (e.g. *Conopholis*, *Epifagus*, *Orobanche*). The results of molecular phylogenetic studies (dePamphilis *et al.* 1997; Young *et al.* 1999; Nickrent *et al.* 1998; Olmstead *et al.* 2001; Wolfe *et al.* 2005) do not support a transition series from hemi- to holoparasitism.

The new circumscription of Orobanchaceae, including the hemiparasitic genera, comprises *c.* 90 genera and 1700 species (Wolfe *et al.* 2005). Young *et al.* (1999) included 29 genera in their study, but the relationships within and among the major clades that were recovered in their analyses were poorly supported or unresolved. Wolfe *et al.* (2005) have increased the sampling of genera in this clade, and include sequence data from the more variable ITS region in an attempt to better resolve relationships within Orobanchaceae. A parallel study based on sequences of the nuclear gene encoding phytochrome A (PHYA) has been completed, and provides additional insight into these relationships (Bennett and Mathews 2006).

A summary of relationships in Orobanchaceae based on sequence data from cpDNA (Young *et al.* 1999), ITS (Wolfe *et al.* 2005), and PHYA (Bennett and Mathews 2006) is presented in Fig. 4. In phylogenies based on cpDNA sequences (Young *et al.* 1999), *Lindenbergia* was resolved as the sister group to the remaining Orobanchaceae with high bootstrap support for both the monophyly of Orobanchaceae and of the parasitic clade (Orobanchaceae without *Lindenbergia*). However, phylogenies based on

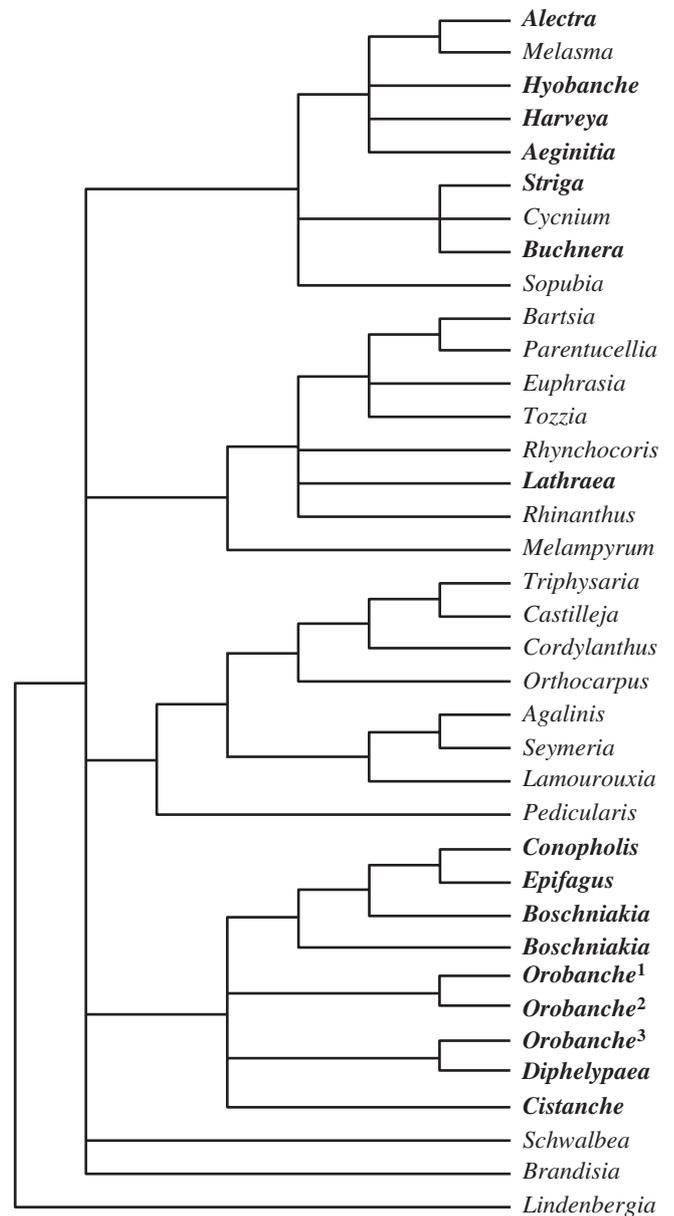


Fig. 4. Summary of the phylogenetic relationships of Orobanchaceae based on results presented by Young *et al.* (1999), Schneeweiss *et al.* (2004), Wolfe *et al.* (2005), and Bennett and Mathews (2006). Genera in bold are those that are either entirely holoparasitic, or comprise both holo- and hemiparasitic species. ¹*Orobanche* sections *Myzorrhiza* and *Gymnocaulis*, ²*Orobanche* section *Trionychon*, ³*Orobanche* section *Orobanche*.

nuclear DNA sequences (ITS, Wolfe *et al.* 2005; PHYA, Bennett and Mathews 2006) have identified a lineage of hemiparasites including *Schwalbea* and related genera that also occurs at or very near the base of the clade.

Relationships among taxa of Orobanchaceae inferred from analyses of cpDNA (Young *et al.* 1999), ITS region (Wolfe *et al.* 2005), and PHYA (Bennett and Mathews 2006)

agree on the presence of four major clades. However, relationships among these major lineages of Orobanchaceae are not consistent among these studies, due to differences in sampling and the limited power of one or more datasets to resolve relationships among parasitic plants, where molecular phylogenetic inference often is problematic (Nickrent *et al.* 1998; Stefanovic and Olmstead 2004). In Fig. 4, only those relationships that are well supported and recovered in more than one molecular phylogenetic analysis are presented.

A major clade recovered in all of the analyses includes taxa distributed in Africa and south-western Asia (the *Alectra*–*Sopubia* clade; Fig. 4). With the exception of *Aeginetia*, these genera are traditionally treated in Scrophulariaceae s.l., although many genera have both holo- and hemiparasitic species. Evidence from cpDNA and nuclear DNA suggests that *Asepalum* and *Cyclocheilon* (Cyclocheilaceae) and *Nesogenes* (Nesogenaceae) also belong to this clade (Bremer *et al.* 2002; Oxelman *et al.* 2005; Bennett and Mathews 2006; DC Tank and RG Olmstead unpubl. data). All three genera have been treated variously in the Verbenaceae s.l., or their own small families, and neither has been previously suggested to be parasitic.

The second major clade comprises taxa that are mostly green hemiparasites distributed primarily in Europe (the *Bartsia*–*Melampyrum* clade; Fig. 4). Although *Bartsia* does have at least three European species, the majority of the genus is endemic to Andean South America (Mabberley 1997), and relationships within the genus have not been studied. Also included in this clade is the holoparasitic genus *Lathraea*, which has been treated historically in either Scrophulariaceae s.l. or Orobanchaceae.

The third major clade is composed exclusively of hemiparasitic plants distributed primarily in North and South America (the *Castilleja*–*Pedicularis* clade; Fig. 4), with the exception of *Pedicularis* (the largest genus in Orobanchaceae, with c. 300 species distributed throughout the northern hemisphere), which is the sister group to the remainder of the clade.

The fourth major group of taxa belonging to Orobanchaceae includes holoparasitic members of the traditional Orobanchaceae (*Boschniakia*, *Cistanche*, *Conopholis*, *Diphelypaea*, *Epifagus* and *Orobanche*; Fig. 4). There was weak support for the monophyly of this group based on cpDNA (Young *et al.* 1999) and ITS sequences (Wolfe *et al.* 2005) were not able to resolve relationships among these genera. Phylogenetic analyses of the PHYA gene, however, agree with the cpDNA results, and recover a well supported monophyletic grouping of these taxa (Bennett and Mathews 2006). In this clade, *Orobanche* is not monophyletic; the North American sections *Myzorrhiza* and *Gymnocaulis* form a clade sister to the European section *Trionychon*, while relationships among section *Orobanche* and other genera remain unresolved

(Schneeweiss *et al.* 2004). Schneeweiss *et al.* (2004) sampled Australian specimens of two species (*O. cernua* var. *australiana* and *O. mutellii*) and found both to be indistinguishable at the DNA level from European conspecifics, suggesting recent, probably human-mediated, colonisation of Australia. *Brandisia*, traditionally placed in Cheloneae (Bentham 1846, 1876; Wettstein 1891), belongs in Orobanchaceae based on cpDNA (Oxelman *et al.* 2005) and PHYA (Bennett and Mathews 2006). *Brandisia* is distributed primarily in China and subtropical eastern Asia and is known to be parasitic in some instances (Hong *et al.* 1998).

Relationships among major groups of Orobanchaceae still need more detailed molecular systematic study. However, our understanding of the composition of the family and relationships between genera has improved greatly. A current study in progress combining sequence data from multiple gene regions, including the nuclear rDNA ITS region and multiple paralogs of the phytochrome gene family, for a large sampling of taxa, is likely to produce a well resolved, family level phylogeny for Orobanchaceae (S Mathews pers. comm.).

Phrymaceae Schauer in DC

Olmstead *et al.* (2001) sampled only one species of *Mimulus* and its familial placement was left unresolved. Subsequently, studies of *Mimulus* and genera putatively related to it (Beardsley and Olmstead 2002; Beardsley and Barker 2005) identified a distinct clade within the Lamiales containing several of these genera and *Phryma*, placed by some previous classifications in the monotypic Phrymaceae. This clade now forms the much-enlarged family Phrymaceae (APG II 2003).

Studies in Phrymaceae have resulted in a reconsideration of taxonomic boundaries within *Mimulus* and related genera (Fig. 5). Phylogenetic analyses of chloroplast and nuclear DNA (Beardsley and Olmstead 2002; Beardsley *et al.* 2004; Beardsley and Barker 2005) support the hypothesis that at least eight genera (*Berendtiella*, *Elacholoma*, *Glossostigma*, *Hemichaena*, *Leucocarpus*, *Microcarpaea*, *Peplidium* and *Phryma*) are derived from within *Mimulus*. The clade containing these genera was recognised as Phrymoideae by Beardsley and Olmstead (2002). The inclusion of *Phryma* was especially surprising. *Phryma* is monotypic with its single species having a disjunct distribution between eastern North America and eastern Asia (Nie *et al.* 2006). *Phryma* has a pseudomonomerous gynoeceum, which develops into a one-seeded fruit (Chadwell *et al.* 1992). *Phryma* has most often been alternatively placed in either the Verbenaceae (e.g. Cronquist 1981) or its own family Phrymaceae (Schauer 1846; Moldenke 1971; Lu 1990; Takhtajan 1997). The molecular data suggest that generic boundaries in this clade need to be redrawn to reconcile the paraphyly of *Mimulus* with respect to the other genera in Phrymoideae (Fig. 5).

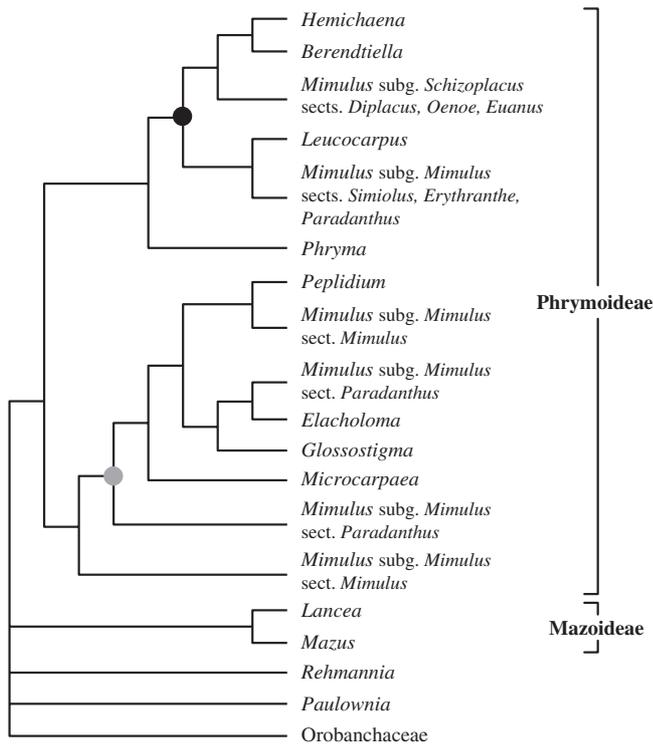


Fig. 5. Summary of the phylogenetic relationships within the clade containing Phrymaceae as defined by Beardsley and Olmstead (2002). Based on results presented by Beardsley and Barker (2005), Beardsley and Olmstead (2002), and Oxelman *et al.* (2005). The clades corresponding to species distributed in western North America and Australia are indicated by black and grey circles, respectively.

Mazus and *Lancea* form a primarily east and south-east Asian clade recognised as the Mazoideae (Beardsley and Olmstead 2002). Beardsley and Olmstead (2002) recognised Phrymaceae as containing both Phrymoideae and Mazoideae on the basis of support from the molecular data (albeit weak) and a series of putative morphological synapomorphies shared by both groups. Specifically, Phrymaceae were based on the following synapomorphies: (1) tubular, toothed calyces, (2) loculicidal capsules and (3) bilamellate stigmas that are receptive only on the inner surface and close together upon contact. Analyses of molecular data reveal strong support for both Phrymoideae and Mazoideae. However, the sister group relationship of Phrymoideae and Mazoideae was not supported in an additional study that included more cpDNA sequence data and a much broader sampling within the Lamiales (Oxelman *et al.* 2005). Relationships of Phrymaceae to other families in the Lamiales requires further attention. Oxelman *et al.* (2005) recovered a clade that contained Orobanchaceae, Paulowniaceae, Phrymoideae, Mazoideae and *Rehmannia*, though support was weak, and the relationships among these groups were not strongly resolved.

Though not all the relationships were resolved, the identification of the potential sister groups to Phrymoideae and Mazoideae permits the re-evaluation of the characters used to define Phrymaceae. (1) All of the species in Orobanchaceae, Paulowniaceae, Phrymoideae, Mazoideae and *Rehmannia* have fused calyces; the major distinction between the groups is the relative length of the calyx lobes. Most members of Phrymoideae have relatively short calyx lobes (less than one-third of the length of the calyx), whereas *Paulownia*, Orobanchaceae and *Rehmannia* typically have calyces fused for less than half their length. *Mazus* is variable for this trait. Thus, as a character to define Phrymaceae, a highly fused calyx is not diagnostic, though it may serve as a synapomorphy for Phrymoideae (with a small percentage of species not conforming to this condition). (2) With the exception of the small genera *Lancea* and *Leucocarpus*, which have berry-like fruits, all the other plants in Orobanchaceae, Paulowniaceae, Phrymoideae, Mazoideae and *Rehmannia* have loculicidal capsules, limiting the usefulness of this character in defining Phrymaceae. (3) Plants in Paulowniaceae, Phrymoideae, Mazoideae and *Rehmannia* have bilamellate stigmas, though only those in the proposed Phrymaceae are reported to be receptive on the inner surface and close together after contact. Stigma morphology in the Australian genera *Glossostigma*, *Peplidium* and *Elacholoma* apparently is derived from *Mimulus*-like ancestors (Barker 1982; Beardsley and Barker 2005). This character needs further investigation in Mazoideae on living plants before it can be shown to be diagnostic of Phrymaceae. More research is needed to better resolve relationships among Phrymoideae, Mazoideae and their relatives and to decide if Mazoideae should be included in Phrymaceae.

Regardless of whether or not Mazoideae is included in Phrymaceae, recent data have improved our understanding of biogeographic patterns in *Mimulus* and its close relatives. The genus *Mimulus* was traditionally considered to be limited almost entirely in distribution to western North America, having only a few species on other continents. Morphological studies (Barker 1982) and molecular analyses (Beardsley and Olmstead 2002; Beardsley *et al.* 2004; Beardsley and Barker 2005) now indicate that within Phrymoideae there are two centres of diversity, one in western North America and one in Australia (Fig. 5). Many of the taxa that are most likely to be closely related to Phrymoideae are primarily Asian in distribution: Paulowniaceae, *Rehmannia*, Mazoideae and *Lindenbergia* (sister to other Orobanchaceae), thus suggesting an Asian ancestry for this group.

Stilbaceae Kunth

In their traditional circumscription, Stilbaceae were a family composed of six small genera (*Stilbe*, *Campylostachys*, *Euthystachys*, *Eurylobium*, *Thesmosphora* and *Xeroplana*), all of which are heath-like shrubs distributed predominately

in South Africa (Rourke 2000). In a realignment of generic boundaries in Stilbaceae, Rourke (2000) included both *Eurylobium* and *Xeroplana* in *Stilbe*, and established *Kogelbergia* for two species previously assigned to *Stilbe*. Like many of the lineages of Lamiales, the affinities of Stilbaceae to other closely related groups has been contested and, thus, Stilbaceae have been variously treated as a distinct family, or as a part of Verbenaceae (Dahlgren 1975; Cronquist 1981). Based on similarities in wood anatomy (Carlquist 1986), the monotypic genus *Retzia* (traditionally assigned to Loganiaceae, Buddlejaceae or Retziaceae) was argued to belong to Stilbaceae and subsequent molecular systematic studies confirmed this relationship (Bremer *et al.* 1994; Oxelman *et al.* 1999). Next, Oxelman *et al.* (1999) determined that *Nuxia*, also formerly of Loganiaceae or Buddlejaceae, belonged to Stilbaceae; Olmstead *et al.* (2001) added *Halleria* (formerly Scrophulariaceae s.l.) and Oxelman *et al.* (2005) added *Bowkeria*, *Ixianthes* and *Anastrabe* (tribe Bowkerieae *sensu* Barringer 1993), and the rare monotypic genus *Charadrophila*.

In this broader Stilbaceae, all of their members have a primarily South African distribution, with the exception of *Nuxia*, which extends north into tropical Africa and Arabia (Mabberley 1997). P Kornhall and B Bremer (unpubl. data) have proposed the following tribal designations: Stilbeae, Bowkerieae and Hallerieae. Relationships among these groups are well supported, with Hallerieae sister to a clade comprised of the other two groups (Fig. 6). The rare South African monotypic genus *Thesmosphora*, historically treated in the traditional Stilbaceae (Rourke 1993), has yet to be sampled.

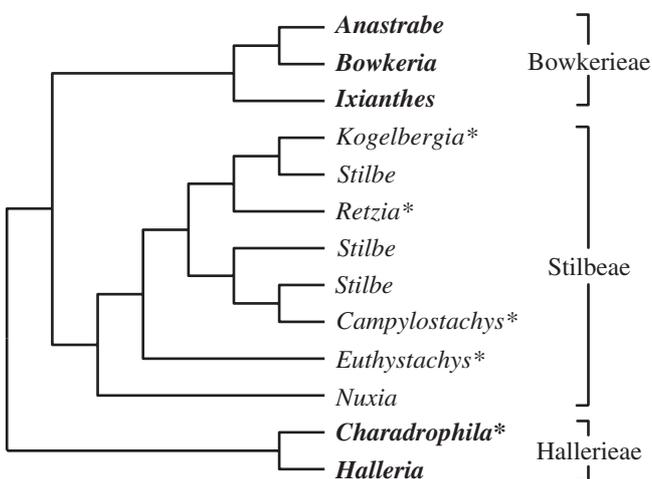


Fig. 6. Summary of intergeneric relationships in Stilbaceae based on results presented by P Kornhall and B Bremer (unpubl. data) and Oxelman *et al.* (2005). Tribal delineations are noted, as described by P Kornhall and B Bremer (unpubl. data). Genera in bold are those that are traditionally included in Scrophulariaceae s.l. An asterisk denotes those genera comprised of only one or two species.

Bowkerieae Barringer

Bowkerieae were originally segregated from the tribe Cheloneae by Barringer (1993) and form a well supported clade in molecular phylogenetic studies (P Kornhall, B Bremer unpubl. data; Oxelman *et al.* 2005). The inclusion of *Colpias* in Bowkerieae (Steiner 1996; Steiner and Whitehead 2002) is not supported by either cpDNA or ITS sequences (Oxelmann *et al.* 2005; P Kornhall, B Bremer unpubl. data) and belongs with Scrophulariaceae s.s. (see above). Genera included in molecular phylogenetic studies include *Anastrabe*, *Bowkeria* and *Ixianthes*.

Hallerieae G Don.

Halleria is a small genus of four African species, and has been assigned variously to the tribes Hallerieae (Don 1838), Cheloneae (Bentham 1846, 1876), and Teedieae (Barringer 1993). In addition to *Halleria*, *Charadrophila capensis*, a rare endemic known only from a few waterfalls in the Cape Province of South Africa, is included in Hallerieae. Most authors have agreed with Marloth's (1898) placement of *Charadrophila* in Scrophulariaceae s.l. (e.g. Burt 1962; Weber 1989). However, in a note accompanying the original description, Engler placed it in Gesneriaceae (see Oxelman *et al.* 2005; P Kornhall, B Bremer unpubl. data). In their analyses, Oxelman *et al.* (2005) place *Charadrophila* with *Halleria*, but with weak support (Fig. 6). P Kornhall and B Bremer (unpubl. data) provide additional support for the clade corresponding to Hallerieae and its placement as the sister group to the remainder of Stilbaceae. However, the monophyly of Hallerieae remains uncertain and the designation of this as a distinct lineage in Stilbaceae warrants further consideration. Genera included in molecular phylogenetic studies include *Charadrophila* and *Halleria*.

Stilbeae Hogg

Analysis of three plastid genes (Oxelmann *et al.* 2005) recovered a weakly supported clade corresponding to the tribe Stilbeae. However, adding ITS sequences to the cpDNA sequences and increasing taxon sampling (including multiple species of *Stilbe* and the addition of *Kogelbergia*) resulted in the recovery of an unambiguous Stilbeae (P Kornhall, B Bremer unpubl. data). *Stilbe* is not monophyletic, and falls into two clades (Fig. 6), one with affinities to *Retzia* and *Kogelbergia*, and the other with the monotypic genus *Campylostachys*. Sister to these two clades is the monotypic genus *Euthystachys*. To reconcile the taxonomy with the phylogeny, P Kornhall and B Bremer (unpubl. data) propose expanding *Stilbe* to include *Campylostachys*, *Euthystachys*, *Kogelbergia* and *Retzia*, which creates a morphologically cohesive group recognised by synapomorphies characteristic of the traditional Stilbaceae (Fig. 6). Genera included in molecular phylogenetic studies

include *Nuxia*, *Stilbe*, *Campylostachys*, *Euthystachys*, *Kogelbergia* and *Retzia*.

Linderniaceae (Rchb.) Borsch, K. Müller, & Eb. Fisch

Wettstein (1891) and most subsequent treatments included *Lindernia* and *Craterostigma* in the tribe Gratioleae. Bentham's original treatment (1846) included Lindernieae within Gratioleae as a subtribe, but, most recently, Fischer (1992, 2004) treated Lindernieae as a tribe distinct from Gratioleae. Molecular systematic studies of Scrophulariaceae s.l. (e.g. Albach *et al.* 2005a; Oxelman *et al.* 2005; Rahmzadeh *et al.* 2005) confirm that Lindernieae are distinct from Gratioleae and, furthermore, identify Lindernieae as yet another distinct lineage of Scrophulariaceae s.l. Lindernieae lack the iridoid compounds and the type of protein bodies typically found in Veronicaceae (Albach *et al.* 2005a). Due to their limited sampling, neither Albach *et al.* (2005a) nor Oxelman *et al.* (2005) proposed a formal name for this clade. However, Rahmzadeh *et al.* (2005) included a larger sampling of taxa and proposed recognition at the rank of family as Linderniaceae.

Plants included in Linderniaceae are recognised by their conspicuous geniculate, curved, or spurred abaxial filaments (Fischer 1992, 2004). The sampling of Rahmzadeh *et al.* (2005) included representatives throughout the Lamiales, with an emphasis on Lindernieae, where they sampled five of 13 genera (*Artanema*, *Craterostigma*, *Crepidorhopalon*, *Lindernia* and *Torenia*) in the tribe (*sensu* Fischer 1992, 2004). Otherwise, however, their sampling of Gratioleae was limited and, therefore, their circumscription of Linderniaceae included only those genera previously assigned to Lindernieae. In contrast, Albach *et al.* (2005a) and Oxelman *et al.* (2005) sampled more genera in Gratioleae and, as a result, discovered that *Micranthemum* and *Stemodiopsis* (both traditionally treated in Gratioleae) belong in this clade, as well. Oxelman *et al.* (2005) also included *Picria*, which is traditionally included in Lindernieae. Due to a lack of overlap in the taxon sampling of these three independent studies, the relative positions of *Micranthemum*, *Stemodiopsis* and *Picria* within Linderniaceae are not clear (Fig. 7). Both *Micranthemum* and *Stemodiopsis* possess geniculate or curved abaxial filaments or staminodes (Oxelman *et al.* 2005), supporting this character as a potential synapomorphy for Linderniaceae as suggested by Rahmzadeh *et al.* (2005). Within Linderniaceae, *Lindernia*, the largest genus of the family, is polyphyletic (Rahmzadeh *et al.* 2005).

Linderniaceae (*sensu* Rahmzadeh *et al.* 2005) include genera with centers of diversity in tropical Africa and south-east Asia (including northern Australia). *Stemodiopsis* also is distributed in tropical Africa; however, *Micranthemum* has a New World distribution from the southern United States to Argentina (Mabberley 1997). A small group of *Lindernia* species (12 of the c. 100 species; not sampled in their study)

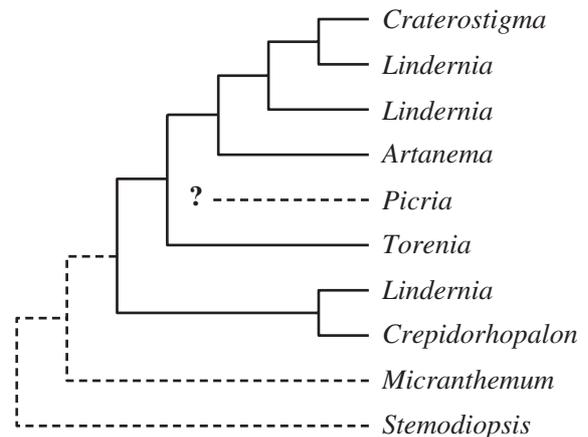


Fig. 7. Summary of intergeneric relationships in Linderniaceae based on results presented by Albach *et al.* (2005a), Oxelman *et al.* (2005), and Rahmzadeh *et al.* (2005). Dashed branches indicate the uncertain position of those genera due to a lack of taxon overlap between the multiple studies.

is also distributed from the southern United States to South America (Rahmzadeh *et al.* 2005). More detailed studies of Linderniaceae will be necessary to reconcile their phylogeny and geographic distributions.

Calceolariaceae (D. Don) Olmstead

Calceolariaceae have been recognised as a distinct family only since its removal from Scrophulariaceae s.l. by Olmstead *et al.* (2001). Prior to this treatment, the three genera comprising the family, *Calceolaria*, *Jovellana* and *Parodittia*, had been treated in tribe Calceolarieae (Bentham 1846, 1876; Wettstein 1891). Olmstead *et al.* (2001) included one species each of *Calceolaria* and *Jovellana* and found them to be one of the most distinct and isolated groups of former scrophs. Along with Gesneriaceae, Calceolariaceae are found at the base of the core Lamiales (Fig. 1), far removed from the remainder of the segregate scroph lineages (Olmstead *et al.* 2001; Rahmzadeh *et al.* 2005).

Calceolaria is the largest genus in the family with c. 270 species distributed throughout the New World from Mexico to Chile; *Jovellana* comprises four or five species distributed in Chile and New Zealand, and *Parodittia* is a monotypic genus restricted to Peru (Molau 1988). Calceolariaceae can be recognised by the distinctive combination of a two-lobed corolla and the reduction of the androecium to two stamens (Molau 1988; Olmstead *et al.* 2001). Furthermore, *Calceolaria* is one of the few genera among Scrophulariaceae s.l. to produce oil as a pollinator reward. The elaiophores in *Calceolaria* are restricted to a dense patch of glandular hairs located in an inward fold of the lower corolla lobe. Other genera with oil-producing flowers in Scrophulariaceae s.l. are found in the tribes Bowkerieae (Stilbaceae), Angelonieae (Veronicaceae) and Hemimerideae

(Scrophulariaceae s.s.), indicating that this unusual trait has evolved at least four times independently among plants formerly classified as Scrophulariaceae s.l. (Vogel 1974; Albach *et al.* 2005a).

Conclusions

Given the turbulent taxonomic history of Scrophulariaceae s.l., both in terms of relationships within the family and circumscribing the limits of the family, it should not have been surprising that the traditional circumscription did not comprise a natural group. The family was a repository for taxa whose placement in Lamiales was clear, but that did not fit in any of the more clearly defined lineages (e.g. Acanthaceae, Bignoniaceae, Gesneriaceae, Lamiaceae). As is borne out by numerous molecular systematic studies, many genera were treated as scrophs based on the presence of a few shared characteristics that may have persisted from a common ancestor throughout the diversification of the order. Despite the large amount of effort that has been invested in resolving these relationships, the backbone phylogeny of Lamiales is largely unresolved. Without a firm understanding of these relationships, it is difficult to determine morphological synapomorphies that can be used to define these new lineages and many of them remain difficult to diagnose morphologically. However, these phylogenetic studies allow us to begin to identify some characteristics that should not be used to define these natural groups (e.g. Bentham's floral aestivation), and point us towards the informative traits that were overlooked or understudied by previous taxonomists (e.g. nuclear protein bodies, phytochemistry). Once relationships among Lamiales are better resolved, the evolution of characteristics ranging from the origin of carnivory (e.g. Müller *et al.* 2004) to the molecular basis of floral development (e.g. Reeves and Olmstead 2003) can be viewed in a comparative framework and begin to shed light on the processes involved in the diversification of Lamiales into the many lineages once recognised as 'Scrophulariaceae.' Without the tools of molecular systematics, the identification of many of these natural groups of former scrophs would not have been possible. As the scale of molecular phylogenetic studies continues to grow and more taxa and sequence data are included, it is possible that additional independent lineages of Lamiales will emerge from the remnants of Scrophulariaceae s.l.

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