

Lamiales: Introduction and Conspectus

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Lamiales as presented here are a well-supported clade of the Lamiids (Bremer et al. 2002) found in all major, recent molecular studies of the Asterids (APG II 2003; see also Wagenitz 1992). The Lamiids, comprising approximately 23,600 species in 1140 genera, are herbaceous or less commonly woody plants with often opposite leaves. The flowers are sympetalous and mostly 5-merous, often representing zygomorphic lip flowers with a showy corolla and with a single whorl of stamens (the five stamens often reduced to four or two), and a bicarpellate ovary with the two carpels in median position (Endress 1994). Anthers very often have an outgrowth of the connective into the anther locule, known as pollen sac placentoid (Hartl 1964), glandular hairs with a head with only vertical cell walls are often present, and pollen tubes appear to lack callose (Prósperi and Cocucci 1979; Cocucci 1983). Both micropylar and chalazal endosperm haustoria are common (Yamazaki 1974), endosperm formation is cellular, and embryogeny normally is of the Onagrad type (Polygonad in Oleaceae; Albach et al. 2001). Protein bodies in the nuclei are widespread (Speta 1977, 1979; Bigazzi 1984, 1989a, b). Chemically, typical constituents of the order are 6- and/or 8-hydroxylated flavone glycosides (Grayer et al. 1999), verbascosides and cornoside as characteristic caffeic acid derivatives (Mølgaard and Ravn 1988; Jensen 1992), shikimate-derived anthraquinones (Jensen 1992), C11-decarboxylated iridoids (Jensen 1991, 1992), and stachyose or other oligosaccharides as carbon storage compounds (Hegnauer 1989). As will be discussed below, several of the characters listed above, including the zygomorphic lip flowers, originated only within the order (Stevens 2001).

In large part, Lamiales as circumscribed here correspond to the Tubiflorae (Wettstein 1935; Melchior 1964) or Personatae (Drude 1885–1887; Warming and Möbius 1929; Huber 1991) of earlier authors, and to Cronquist's (1981) Lamiales, Callitrichales, Plantaginales and Scrophulariales, to Thorne's (1992) Bignoniales, and to Takhtajan's (1997) Oleales, Scrophulariales, Lamiales, Callitrichales and Hippuridales. In compari-

son to the latter three systems, the Lamiales as circumscribed here differ by the exclusion of Boraginaceae (incl. Lennoaceae), treated as part of Lamiales by Cronquist (1981), and by the inclusion of Byblidaceae (Cronquist 1981: Rosales; Thorne 1992: Pittosporales; Takhtajan 1997: Aralianae-Byblidales), Carlemanniaceae (Cronquist 1981: Dipsacales; Thorne 1992: not recognized; Takhtajan 1997: Rubiales) and Plocospermataceae (Cronquist 1981: Gentianales; Thorne 1992: Gentianales; Takhtajan 1997: Gentianales), treated as belonging elsewhere by Cronquist (1981), Thorne (1992) and Takhtajan (1997). There is good molecular evidence for the inclusion of these three families in Lamiales (Byblidaceae: Hedrén et al. 1995; Bremer et al. 2001; Albach et al. 2001; Carlemanniaceae: Savolainen, Fay et al. 2000; Bremer et al. 2001; Plocospermataceae: Bremer et al. 2001), and other characters in support of this can be found. Thus, Plocospermataceae contain cornoside as a caffeic acid derivative commonly found in the order (Jensen 1996, 2000), the carnivorous Byblidaceae share embryological characters with the equally carnivorous Lentibulariaceae (Lang 1901; Conran 1996), and Carlemanniaceae have flowers with only two stamens which may prove to be morphological support of their sister-group relationship with Oleaceae.

The exact relationships of Lamiales within Lamiids are not finally resolved, but it is clear from molecular evidence (e.g. Downie and Palmer 1992; Olmstead et al. 1992, 1993; Backlund and Bremer 1997; Olmstead et al. 2000; Savolainen, Chase et al. 2000; Savolainen, Fay et al. 2000; Soltis et al. 2000; Albach et al. 2001; Bremer et al. 2001; Olmstead et al. 2001) that they are part of a larger clade containing Boraginaceae/Boraginales, Gentianales, Solanales, Vahliaceae. In some of these analyses (Olmstead et al. 2000; Savolainen, Chase et al. 2000) they are sister to Gentianales. Inclusion of Vahliaceae into Lamiales should be considered (Savolainen, Fay et al. 2000; Albach et al. 2001).

Although the Lamiales clearly represent a monophylum, their division into families in this treatment differs from that proposed by APG II (2003; see Table 1).

Table 1. Families recognized in this volume compared with the APG classification

APG II	FGVP
Acanthaceae	Acanthaceae
Bignoniaceae	Bignoniaceae
= Scrophulariaceae s.str.	Buddlejaceae
Byblidaceae	Byblidaceae
= Plantaginaceae s.l.	Callitrichaceae
Calceolariaceae	Scrophulariaceae s.l.
Carlemanniaceae	Carlemanniaceae
Orobanchaceae	Cyclocheilaceae
Gesneriaceae	Gesneriaceae
= Plantaginaceae s.l.	Globulariaceae
= Plantaginaceae s.l.	Hippuridaceae
Labiatae	Labiatae
Lentibulariaceae	Lentibulariaceae
Martyniaceae	Martyniaceae
= Scrophulariaceae s.str.	Myoporaceae
Orobanchaceae	Nesogenaceae
Oleaceae	Oleaceae
Orobanchaceae	= Scrophulariaceae s.l.
Paulowniaceae	= Scrophulariaceae s.l.
Pedaliaceae	Pedaliaceae
Phrymaceae	Phrymaceae
Plantaginaceae s.l.	Plantaginaceae s.str.
Plocospermataceae	Plocospermataceae
Schlegeliaceae	= Scrophulariaceae s.l.
Scrophulariaceae	Scrophulariaceae
Stilbaceae	Stilbaceae
Tetrachondraceae	Tetrachondraceae
= Pedaliaceae	Trapellaceae
Verbenaceae	Verbenaceae

Apart from the inclusion of Avicenniaceae in Acanthaceae here (Schwarzbach and McDade 2002), in contrast to APG II, and the inclusion of Trapellaceae in Pedaliaceae by APG II, also in contrast to the present work, the major difference between APG II and this FGVP volume lies in the treatment of Scrophulariaceae s.l. and allies.

Following the molecular evidence last summarized and expanded by Olmstead et al. (2001), APG II divide Scrophulariaceae s.l. and allies into Orobanchaceae, Paulowniaceae, Plantaginaceae (incl. Callitrichaceae, Globulariaceae and Hippuridaceae; these are the Veronicaceae of Olmstead et al. 2001), Schlegeliaceae and Scrophulariaceae s.str. (incl. Buddlejaceae and Myoporaceae). Calceolariaceae are recognized as an additional family by Olmstead et al. (2001), and there is increasing evidence that Phrymaceae, containing *Phryma* and several genera mainly (but not only) of Scrophulariaceae-Mimuleae, should be recognized in an expanded circumscription (Beardsley and Olmstead 2002). In contrast, Scrophulariaceae in the present treatment include Calceolariaceae, Orobanchaceae, Paulowniaceae, and Schlegeli-

aceae. Buddlejaceae, Callitrichaceae, Globulariaceae, Hippuridaceae, Plantaginaceae s.str. as well as Myoporaceae are treated as separate families. Also, Phrymaceae here are treated as a monotypic family. Such treatment of Scrophulariaceae s.l. is non-phylogenetic in at least one respect. It is quite clear that Scrophulariaceae s.l. are paraphyletic when Buddlejaceae, Callitrichaceae, Globulariaceae, Hippuridaceae, Myoporaceae and Plantaginaceae, and probably also Phrymaceae are treated as separate families. Buddlejaceae and Myoporaceae group with one part of Scrophulariaceae s.l. with good support (= Scrophulariaceae s.str.: 78%; Olmstead et al. 2001), and Callitrichaceae, Globulariaceae and Hippuridaceae group with another part of Scrophulariaceae s.l., although with only low support (= Plantaginaceae = Veronicaceae: 48%; Olmstead et al. 2001). The recognition of a close relationship between most of the preceding families and Scrophulariaceae is by no means novel and had already been recognized (and partly formalized) by, for example, Hallier (1903) and Hartl (1965–1974). Following Olmstead et al. (2001), recognition of Scrophulariaceae s.l. including Buddlejaceae, Callitrichaceae, Globulariaceae, Hippuridaceae, Myoporaceae and Plantaginaceae s.str. is not significantly less parsimonious than dividing them into the above five families, provided that Calceolariaceae are excluded. This latter family groups quite distant from Scrophulariaceae s.l. Considering this and the comparatively small sample of genera analysed so far, treatment of Scrophulariaceae in a wide circumscription is justifiable, but not when Buddlejaceae, Callitrichaceae, Globulariaceae, Hippuridaceae, Myoporaceae and Plantaginaceae (and probably Phrymaceae) are excluded, and *Calceolaria* and allies are included. However, it is very likely that eventually Calceolariaceae, Orobanchaceae, Paulowniaceae, Plantaginaceae/Veronicaceae (incl. Callitrichaceae, Globulariaceae and Hippuridaceae), Schlegeliaceae, Scrophulariaceae s.str. (incl. Buddlejaceae and Myoporaceae) and an expanded Phrymaceae will have to be recognized because these lineages are, at least partly, more closely related to other families of Lamiales than to each other. Accordingly, the treatment of Scrophulariaceae s.l. (see Fischer, this Vol.) indicates the likely contents of the above lineages.

As regards the treatment of Labiatae/Verbenaceae here and in APG II, in comparison with mainly Cronquist (1981) but partly also Thorne (1992) and Takhtajan (1997), major parts of Verbenaceae as traditionally circumscribed have been transferred to Labiatae, based on sub-

stantial morphological and molecular evidence (Cantino 1992a, b; Wagstaff and Olmstead 1997; Wagstaff et al. 1998), and Tetrachondraceae, treated as part of Labiatae by Cronquist (1981), and Cyclocheilaceae, Nesogenaceae, Phrymaceae and Stilbaceae, treated as part of Verbenaceae by Cronquist (1981; Cyclocheilaceae, Nesogenaceae not mentioned), are treated as separate families here. In terms of this transfer, Verbenaceae can be recognized mainly by their racemose inflorescence, their usually colporate or porate pollen grains and their stigmatic lobes which are apically thickened with stigmatic tissue, and Labiatae by their primarily cymose inflorescence (sometimes racemose through reduction), usually colpate pollen grains and slender stigmatic lobes. The ovules are attached to the sides of the false septa of the ovary in the Labiatae, whereas in the Verbenaceae they are attached to the carpel margins. Verbenaceae and Labiatae do not appear to be closely related to each other (Olmstead and Reeves 1995; Wagstaff and Olmstead 1997; Albach et al. 2001). Of the above five segregate families of Labiatae/Verbenaceae, the Tetrachondraceae, Cyclocheilaceae, Phrymaceae and Stilbaceae were analysed by Wagstaff and Olmstead (1997) and did not group with either Labiatae or Verbenaceae. The same applies to Nesogenaceae (Bremer et al. 2001).

Although family delimitation is reasonably unproblematic apart from Scrophulariaceae s.l., family interrelationships are still largely unclear. It seems likely that Plocospermataceae are sister to the remainder of the order (Oxelmann et al. 1999; Savolainen, Fay et al. 2000), followed by Oleaceae plus Carlemanniaceae as a clade (Savolainen, Fay et al. 2000; Bremer et al. 2001), and Tetrachondraceae (Oxelmann et al. 1999; Olmstead et al. 2000; Savolainen, Fay et al. 2000). There is evidence that, of the remaining and mostly lip-flowered families, Gesneriaceae are sister to the rest (Olmstead et al. 2001; Bremer et al. 2002). Beyond that, there is little statistical support for any relationship which led Savolainen, Fay et al. (2000) to suggest to combine all families (except Carlemanniaceae, Oleaceae and Plocospermataceae; Tetrachondraceae not included) in Scrophulariaceae s.l.

The distribution of the basal lineages Plocospermataceae (New World), Oleaceae (Old World and New World, with an exclusive occurrence of basal lineages in the Old World; Wallander and Albert 2000), Carlemanniaceae (Old World) and Tetrachondraceae (New World and Old World), in combination with the mostly very wide distribution of the remaining families, does not readily suggest where the order might

have originated. The origin of the order dates back at least to the Eocene (Magallón and Sanderson 2001).

The above phylogenetic topology allows to trace the evolution of at least some characters in the order. Most notably, the zygomorphic lip flower with a variable number of petals forming the lower and upper lip (Donoghue et al. 1998; Endress 1999), and with a usually (albeit variably) reduced number of stamens (Endress 1999), appears to have originated only after the divergence of the three basal lineages (Plocospermataceae, Oleaceae + Carlemanniaceae, Tetrachondraceae). Somewhat zygomorphic flowers with only two stamens, however, are also found in Carlemanniaceae, and Oleaceae typically have two stamens only. Within the lip-flowered Lamiales, a reversal to actinomorphic flowers appears to have taken place in Byblidaceae at the family level, but many times within several families (Endress 1994; Donoghue et al. 1998; Endress 1999). Although Lamiales have the second-highest diversification rate among (investigated) angiosperm orders (Magallón and Sanderson 2001), this can not be explained by its lip flowers and associated flower biological diversification because high diversification rates are characteristic of all euasterids (Magallón and Sanderson 2001). Shikimate-derived anthraquinones (acetate-derived in Oleaceae; Jensen 1992), stachyose and other oligosaccharides as carbon storage compounds (mannitol in Oleaceae), 6- and/or 8-hydroxylated flavone glycosides (not present in Oleaceae; Grayer et al. 1999), as well as chalazal endosperm haustoria also appear to be synapomorphies of only the lip-flowered Lamiales (Stevens 2001). Iridoids of the IIa biosynthetic route sensu Jensen (1991) may have originated only after the divergence of Gesneriaceae. No iridoids have been found in Plocospermataceae (Jensen 1992) and Gesneriaceae, and Oleaceae have iridoids originating along a different biosynthetic pathway (Jensen 1991; Albach, Soltis and Soltis 2001). Finally, anatomical evidence (Carlquist 1992) suggests that while woodiness is primary in Oleaceae, it may be secondary at least in some representatives of several of the lip-flowered Lamiales (Acanthaceae, Gesneriaceae, Labiatae, Scrophulariaceae s.l., Stilbaceae, Verbenaceae).

The very close relationship among the different lineages of the lip-flowered Lamiales probably is also reflected in many parallel evolutionary trends in the different families. As summarized by Endress (1994), such trends are found, for example, in petal aestivation (ascending,

descending, quincuncial, contort), stamen number (reduction from 4 to 2, reduction or loss of upper or lower pair; reversal to full complement of 5; Endress 1999), ovary structure (bi- or unilocular through variation of length of synascidiate zone as well as degree of protrusion of placentas), ovule number (reduction from many to few), anther structure and synorganization (monothecal, synthecal) and other characters often closely associated with pollination syndromes (Endress 1994).

The absence of well-supported hypotheses on the phylogenetic relationships among and, in most cases, also within the families of the lip-flowered Lamiales, the difficulties in family delimitation, particularly in Scrophulariaceae s.l., and the often very wide geographical distribution of the above taxa or assemblages make any attempt to explain the evolution of this group in terms of geographical and/or ecological diversification highly speculative. In addition, summary statements about geographical distribution and ecological properties, particularly of the very large families, are far from accurate.

However, a certain degree of geographical and ecological vicariance perhaps can be recognized when the large families or assemblages, i.e. Acanthaceae, Bignoniaceae, Gesneriaceae, Labiatae, Scrophulariaceae s.l. and Verbenaceae, are considered, and the geographical distribution of basal lineages, as far as identified, is accepted as at least an indication of their geographical origin. The possible sister-group relationship of constituent lineages of Scrophulariaceae s.l. to the remaining large families can not be taken into account in the following argument because such relationships are not yet clear.

Of the large families, Scrophulariaceae s.l. and Labiatae have their distribution centres mainly in extratropical zones (or additionally in tropical mountains in the case of Scrophulariaceae) and there often inhabit open habitats. If Viticoideae, Symphorematoideae and Prostantheroideae-Chloantheae of the Labiatae indeed should prove to be basal lineages of the family (Cantino et al. 1992; Wagstaff and Olmstead 1997; Harley et al., this volume), its origin might lie in the Old World

tropics. This may also apply to Gesneriaceae, where the possibly basal lineages are distributed mainly in the Old World (Smith et al. 1997; Burt 1998). In contrast, the geographical distribution of Verbenaceae suggests a New World origin (Atkins, this volume), and Bignoniaceae are distributed mainly in the New World but their origin in either the Old or New World is equivocal, considering the pantropical distribution of the presumably basal Tecomeae (Spangler and Olmstead 1999). The origin of Acanthaceae in the Old or New World is equally unclear because presumably basal lineages of this family (Nelsonioideae: Old and New World, Thunbergioideae: Old World, Mendoncioideae: Old World; Hedrén et al. 1995; Scotland et al. 1995; McDade and Moody 1999; Schwarzbach and McDade 2002) are distributed in both the Old and New World. By containing many lianas and trees, Bignoniaceae could be regarded as ecologically vicarious with the mostly herbaceous Acanthaceae and Gesneriaceae, but not in comparison with the often woody (although commonly shrubby) Verbenaceae. What is most difficult to understand is the wide sympatry of Acanthaceae and Gesneriaceae. Although Gesneriaceae contain a large number of epiphytic taxa in the Neotropics, and Acanthaceae, with their mostly active ejaculation of seeds, are specialized in terms of dispersal ecology, this is not likely to be explanation enough. Possibly their phytochemical differentiation (Gesneriaceae: lack of iridoids; Acanthaceae: calcium oxalate cystoliths), perhaps implying specializations in terms of herbivore and pathogene defence, allows the largely sympatric distribution of these two families. This hypothesis, however, has no observational basis.

When such considerations are extended to the smaller families of the order, Byblidaceae and Lentibulariaceae are distinguished by their carnivory, Stilbaceae by their largely ericoid habit and limitation to the Cape region of South Africa, Trapellaceae by being aquatic (a common condition also in parts of Scrophulariaceae s.l.), and Pedaliaceae and Martyniaceae by their occurrence in arid regions and their very specialized fruit morphology.

Conspectus of families as treated in this volume

1. Ovary with a single ovule
 2. Leaves verticillate, perianth a low collar, flowers with 1 stamen; aquatic, amphibious or rarely terrestrial herbs with drupaceous fruits. 1/1, temperate to boreal parts of both hemispheres **Hippuridaceae**
 2. Leaves alternate or opposite, perianth of calyx and corolla, flowers with 4 stamens
 3. Leaves alternate, flowers mostly in a capitulum, rarely in a spike; shrubs, subshrubs or perennial herbs with woody base, corolla zygomorphic, fruit a nut. 2/25, western Eurasia, Macaronesia, North Africa, Somalia and Sokotra **Globulariaceae**
 3. Leaves opposite, flowers in a raceme; perennial herbs, corolla zygomorphic, fruit a nut. 1/1, temperate eastern North America and eastern Asia **Phrymaceae**
1. Ovary with at least two ovules, sometimes only one developing into seed
 4. Mangrove trees or shrubs with erect pneumatophores, cosmopolitan **Avicenniaceae** (included in Acanthaceae; not treated in this volume)
 4. Not as above
 5. Plants carnivorous with various types of leaf traps; leaves alternate, fruits capsular
 6. Corolla more or less actinomorphic, nectary spur absent; placentation axile; evergreen shrubs or annual herbs. 1/6, Australia and New Guinea **Byblidaceae**
 6. Corolla zygomorphic, nectary spur present; placentation free central; plants herbaceous. 3/320, cosmopolitan **Lentibulariaceae**
 5. Plants not carnivorous
 7. Habit ericoid, leaves densely crowded, verticillate; shrubs or shrublets with actinomorphic or zygomorphic corolla and capsular fruits. 6/28, South Africa **Stilbaceae**
 7. Habit not ericoid
 8. Flowers unisexual, male flowers with a single stamen, or flowers functionally unisexual (anthers sterile in functional females, ovary without style and stigma in functional males), style of functionally female flowers with 4 branches
 9. Flowers unisexual, male flowers with 1 stamen; aquatic to terrestrial herbs with decussate leaves and schizocarpic fruits. 1/40–50, cosmopolitan **Callitrichaceae**
 9. Flowers functionally unisexual, functionally male flowers with 5 (or 6) stamens, style of functionally female flowers with 4 slender branches; terrestrial shrubs with actinomorphic corolla and capsular fruits. 1/1, northern Central America **Plocospermataceae**
 8. Flowers usually bisexual, when unisexual male flowers with 2 or more stamens or female flowers not with style of 4 branches
 10. Calyx reduced to rim or absent, flowers enclosed by 2 large bracteoles; subshrubs to shrubs with sub-opposite to opposite leaves, zygomorphic corolla and capsular or schizocarpic fruits. 2/4, Horn of Africa to Arabia **Cyclocheilaceae**
 10. Calyx present and not reduced to rim
 11. Corolla scarious; herbaceous or rarely woody plants with parallel-veined and usually alternate leaves and actinomorphic corolla, fruit a capsule or nut. 1/270, widespread in temperate regions and tropical mountains **Plantaginaceae**
 11. Corolla not scarious
 12. Flowers minute ($\ll 1$ cm), actinomorphic, tetramerous, style gynobasic; small perennial herbs with opposite leaves, fruit a capsule or schizocarp. 2/3, America and New Zealand **Tetrachondraceae**
 12. Flowers usually larger, actinomorphic or zygomorphic, tetra- or mostly pentamerous; if style gynobasic, flowers not actinomorphic
 13. Stamens 2, no staminodes present, ovary inferior; terrestrial perennial herbs or shrubs with opposite leaves, corolla 4- or 5-merous, weakly zygomorphic to subregular, fruit a dry or fleshy capsule. 2/5, tropical Asia **Carlemanniaceae**
 13. Not as above
 14. Plants with conspicuous mucilaginous trichomes on all aerial parts, pedicels usually with 2 to several extrafloral nectaries; woody to herbaceous plants with usually zygomorphic corolla, fruit dehiscent or not, usually with emergences such as spines, horns and wings. 13/70, arid parts of the Old World **Pedaliaceae**
 14. Not as above
 15. Corolla tetramerous, actinomorphic, plants usually woody
 16. Stamens 2, ovules usually 2 per locule; trees, shrubs or climbers with mostly opposite leaves, fruit a drupe, capsule, berry or samara. 25/600, cosmopolitan **Oleaceae**
 16. Stamens 4, ovules usually more than 2 per locule; trees, shrubs, climbers or suffrutescent herbs with mostly opposite leaves, fruit usually a capsule. 5/100, widely distributed in subtropical to tropical regions **Buddlejaceae**
 15. Corolla usually pentamerous, zygomorphic, plants woody or herbaceous; if flowers tetramerous and actinomorphic, plants with 4 stamens and two ovules per locule

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