

## OVERVIEW OF PHRYMACEAE — FAMILY AND GENERA

The Phrymaceae currently includes 199 species, divided among 12 genera, in the sense of Barker et al. (2012). Barker et al. provided an account of all the species, except for a few others formally described since that time (see Recent Taxonomic Literature). The largest genera are *Diplacus* (46 species) and the primarily western North American *Erythranthe* (123 species).

*Diplacus* (46 species)

*Erythranthe* (123 species)

*Mimetanthe* (1 species)

*Phryma* (1 species)

primarily North American; *Erythranthe* has secondary radiations in Andean South America and in Himalayan Asia; *Phryma* is divided between e North America and sw Asia

*Hemichaena* (5 species)

*Leucocarpus* (1 species)

Mexico to northern South America

*Elacholoma* (2 species)

*Glossostigma* (5 species)

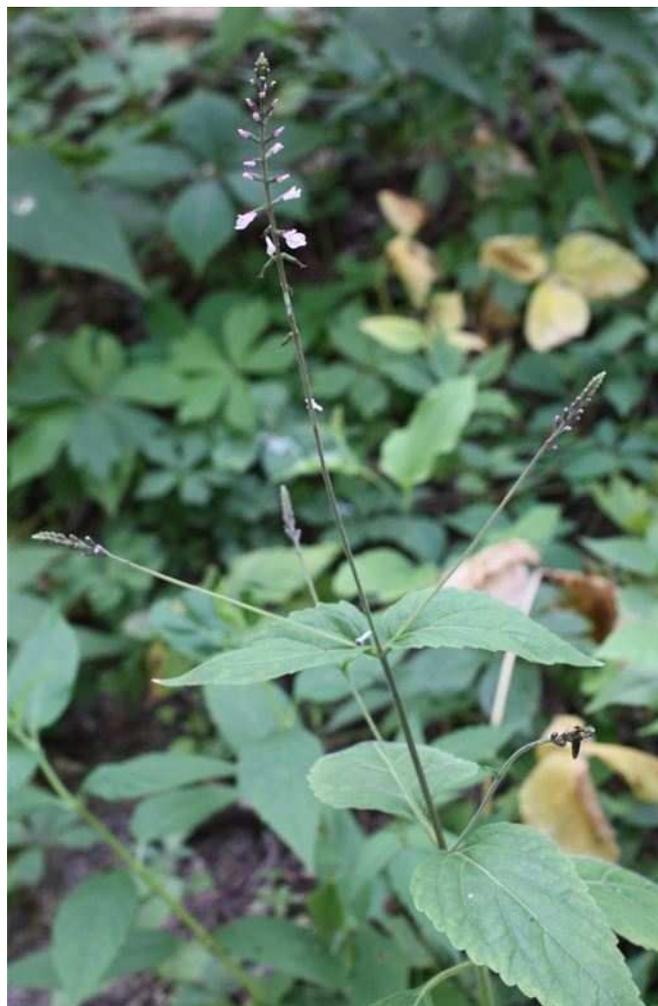
*Microcarpaea* (2 species)

*Mimulus* (7 species)

*Peplidium* (4 species)

*Uvedalia* (2 species)

primarily Australian; *Mimulus* in the strict sense has 2 species native to eastern North America



*Phryma leptostachya*.

Left: Photo by R.W. Smith, Univ. of Michigan Herbarium.

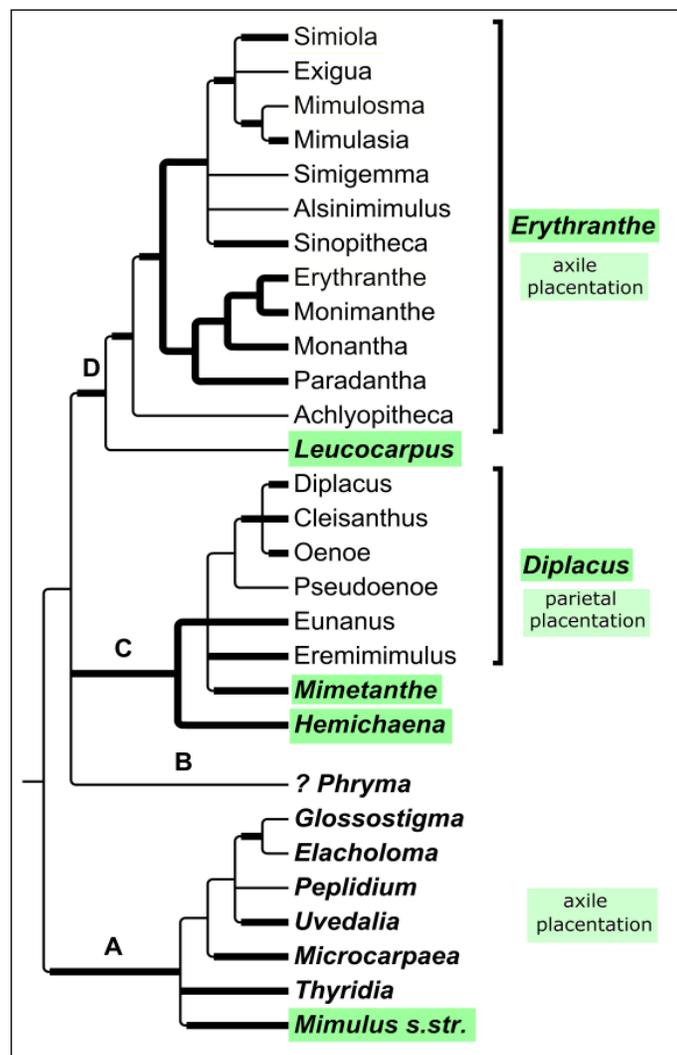
Right: Photo by B.S. Walters, Univ. of Michigan Herbarium. Sharply deflexed calyces enclose the maturing fruits. The calyces deflex after the corollas are shed. The pink extensions are elongate apices of upper calyx lobes.

The name of the family is based on the least representative species of the whole group, *Phryma leptostachya*, long regarded as a peculiar and morphologically isolated species. The name Phrymaceae was published in 1847 and would have priority over any other family name proposed after that (although no other name has ever been ventured for the monkeyflowers as a family). Molecular data place *Phryma* among the monkeyflower species, but its phylogenetic position there is surprising — Verbenaceae and Lamiaceae had been more commonly supposed to be closer relatives. The gynoecium of *Phryma*, at maturity, is a 1-locular ovary with only a single, near-basally positioned ovule, but Whipple (1972) observed that the *Phryma* pistil is 2-carpellate, the ovary becoming 1-locular and 1-ovular through suppression of the dorsal carpel. There are five sepals and petals but only four stamens, without even developmental indication of the presence of a fifth stamen. The morphological and anatomical details are phylogenetically ambiguous.

Molecular data provide two alternative relationships of *Phryma* to the primarily American (Northern Hemisphere) and Australian (Southern Hemisphere) clades. A maximum likelihood tree inferred using combined data (Beardsley & Olmstead 2002) places it as sister to the "American-Asian lineage," as shown in the diagram here. Alternatively, the ML tree resulting from the analysis of nrDNA ITS and ETS sequence data positions *Phryma* as sister to the remaining genera (including Australian) of Phrymaceae. In view of its morphological disparity, the latter position is not unlikely for *Phryma*, which could ultimately return to its status as a monotypic family.

If the evolutionary position of *Phryma* among the monkeyflowers were confirmed, the seemingly saltational modification of its gynoecium may be developmentally related (and homologous) to the origin of parietal placentation in *Diplacus*, *Mimetanthe*, and *Hemichaena*.

Adele Grant (1924) observed that the western North American monkeyflower species could be divided into two main groups — those with axile placentation and with long pedicels (*Erythranthe*) vs. those with parietal placentation and short pedicels (*Diplacus*). Molecular data confirm that each of these groups is placed in a different lineage and that the two are not each other's closest relative. Closest to *Diplacus* are *Mimetanthe*



Summary/hypothesis of phylogenetic relationships of Phrymaceae, primarily from data from Beardsley et al. (2004) and Beardsley and Barker (2005). This is Figure 1 of Barker et al. (2012) with a few modifications. Green highlights are genera with species in North America. Bolded branches indicate greater than 80% bootstrap support. The position of *Phryma* is ambiguous — in an ITS/ETS analysis, it is placed as sister to all the rest of the Phrymaceae.

and the Mexican-Central American *Hemichaena*, which also are characterized by the specialized condition of parietal placentation. Closest to *Erythranthe* is the monotypic *Leucocarpus* of Central America-northern South America, which has axile placentation (as do the species of *Mimulus* and its closest relatives).

Molecular data show that the eastern North American *Mimulus alatus* and *M. ringens*, as well as the five Southern Hemisphere species of the genus, are within a clade sister to the essentially Northern Hemisphere groups. The closest relatives of *Mimulus* are mostly Australian, including *Mimulus* in the strict sense as well as other species divided among a small group of morphologically and cytologically diverse genera.

Current knowledge of phylogenetic structure within the Phrymaceae relies on molecular analyses led by Paul Beardsley and Bill Barker (see Recent Taxonomic Literature).

The monkeyflowers, without *Phryma*, had long been regarded as members of the Scrophulariaceae, but molecular-phylogenetic studies (e.g., Olmstead et al. 2001; Oxelman et al. 2005) have shown that the classical Scrophulariaceae was polyphyletic, and its component genera have been distributed among various other families, especially Plantaginaceae and Orobanchaceae, leaving a much smaller nucleus of the family.

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