What is done and what has to be done in Lamiaceae, a review of phylogenetics.

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Abstract

The most recent classification proposed by Harley et al. in 2004 recognized seven subfamilies within the family Lamiaceae (Symphorematoideae, Viticoideae, Ajugoideae, Prostantheroideae, Scutellarioideae, Lamioideae and Nepetoideae). Symphorematoideae (formerly as part of Verbenaceae) is recognized as a subfamily of Lamiaceae for the first. Recognition of Viticoideae is one of the major modifications introduced in Harley’s treatment but yet it is the least satisfactory circumscribed subfamily which appeared to be clearly non-monophyletic. Subsequent studies based on molecular analysis also reported the non-monophyly of Viticoideae. New combinations are proposed in later studies at the generic level in subfamily Ajugoideae and Prostantheroideae. Suprageneric relationships among the Lamioideae remained poorly understood providing no tribal ranks in the Harley’s classification. Therefore, new tribes have been erected in the recent investigations to reflect improved phylogenetic understanding of the Lamioideae. Subtribal delimitation of Mentheae (Nepetoideae) according to recent studies is not congruent with the Harley’s and new subtribes are recommended to establish the monophyly of Mentheae. Although the clade structure is relatively well established in the Lamiaceae, but tribal compositions remain unclear and needs to be further investigated to transform their taxonomy into a more ‘natural’ classification.

Additional Keywords: Labiatae, Symphorematoideae, Viticoideae, Ajugoideae, Prostantheroideae, Scutellarioideae, Lamioideae, Nepetoideae.
Introduction & Background

The plant family Lamiaceae Martinov (= Labiatae Adans., the mint family) with an almost cosmopolitan distribution contains about 7173 species across approximately 236 genera but not inhabiting the coldest regions of high altitude or high latitude. It is the sixth largest family of flowering plants and one of the most economically important (Drew and Sytsma, 2012). Hedge (1992) recognized six regions of high Lamiaceae diversity viz (1) Mediterranean and SW Central Asia; (2) Africa south of the Sahel and Madagascar; (3) China; (4) Australia; (5) South America; (6) Northern America and Mexico. Another region was added by Harley et al. (2004) known as Indomalesian region (SE Asia).

The oldest complete taxonomic classification of Lamiaceae was proposed by Bentham (1832-1836) which was modified in 1876. Briquet (1895–1897) made improvements to Bentham’s system. Another modification of this system was proposed by Melchior in 1964. An alternative classification of the Lamiaceae based on the palynological characters was proposed by Erdtman (1945). According to this system of classification Lamiaceae was split into two subfamilies: Lamioideae having tricolpate pollen shed in a two-celled stage and Nepetoideae having hexacolpate pollen shed in a three-celled stage. This split was congruent with other studies based on a variety of embryological and phytochemical characters (Wunderlich, 1967; Zoz & Litvinenko, 1979; Cantino & Sanders, 1986). Wunderlich (1967) put forth a new system of classification which was built on Briquet’s system with many important modifications.

A close relationship between Lamiaceae and Verbenaceae has long been recognized by Cronquist (1981) due to sharing many common characters. The common characters between these two families are presence of opposite leaves, zygomorphic flowers and a bicarpellate gynoecium that by false partitions develop into 4 uniovulate locules. The distinguishing character is presence of deeply 4 lobed ovary with a gynobasic style in Lamiaceae whereas an unlobed ovary with terminal style is found in Verbenaceae. However Cronquist (1988) proposed that boundaries between the two families are somewhat arbitrary and taxa with intermediate morphology are found in both families. It was supported by studies of Cantino (1992a, 1992b) that Lamiaceae was polyphyletic, with several clades arising independently from within Verbenaceae. He proposed the transfer of cymose genera of subfamilies Caryopteridoideae, Chloanthoideae, Viticoideae and tribe Monochileae from Verbenaceae to Lamiaceae. The
reconstituted Verbenaceae will be left only with subfamily Verbenoideae having its
distinguishing racemose inflorescences and tricolporate pollen also proposed earlier by Junell
(1934). Cantino et al. (1992) published the list of accepted genera with their subfamilies, tribes
and subtribes belonging to family Lamiaceae which was largely adopted by Thorne (1992). The
phylogeny of Lamiaceae and Verbenaceae constructed from rbcL showed the similar findings
(Wagstaff and Olmstead, 1997). The transfer of Clerodendrum L., Vitex L. and Tectona L. f.
from Verbenaceae to Lamiaceae is also suggested by other studies (Judd et al. 2002; APG II,
2003; Sivadas and Sreeleekha, 2011). Cronquist (1981) also included Boraginaceae and
Lennoaceae within his small order Lamiales. Cantino (1982) reported the closer affinity of
Lamiaceae with Scrophulariaceae instead of Lamiaceae with Boraginaceae. The closest relatives
of Verbenaceae s. st. are Martyniaceae and Bignoniaceae rather than Lamiaceae, is reported by
Olmstead et al. (2001) with weak bootstrap support.

The most recent full taxonomic treatment of Lamiaceae defined by Harley et al. (2004) was
heavily influenced by morphological (Cantino and Sanders, 1986; Cantino et al. 1992) and more
recent molecular findings (Wagstaff et al. 1995; Wagstaff and Olmstead, 1997; Wagstaff et al.
1998). Harley et al. (2004) classified the Lamiaceae in seven subfamilies: (1)
Symphorematoideae Briq. (2) Viticoideae Briq. (3) Ajugoideae Kostel. (4) Prostantheroideae
Luerss. (5) Scutellarioideae (Dumort.) Caruel (6) Lamioideae Harley (7) Nepetoideae (Dumort.)
Luerss. Synapomorphies for the family include opposite leaves, a quadrangular stem,
indumentums and hypogynous flowers, although there are rare irregularities in the first three
traits (Harley et al. 2004). During the past fifteen years the Lamiaceae has undergone numerous
molecular phylogenetic studies (Wagstaff et al. 1995; Wagstaff and Olmstead, 1997; Wagstaff et
al. 1998; Prather et al. 2002; Paton et al. 2004; Trusty et al. 2004; Walker et al. 2004; Bräuchler
et al. 2005; Edwards et al. 2006; Walker and Sytsma, 2007; Bramley et al. 2009; Bräuchler et al.
2010; Scheen et al. 2010; Yuan et al. 2010a). These studies have impelled taxonomic revisions at
several levels (Cantino and Wagstaff, 1998; Harley et al. 2004; Walker et al. 2004; Bräuchler et
al. 2005; Yuan et al. 2010b), However, despite this recent progress the relationships between
many genera remain unclear, especially within the subfamily Nepetoideae (Cantino et al. 1992;
Wagstaff et al. 1995; Paton et al. 2004; Walker et al. 2004; Bräuchler et al. 2010). The present
review corresponds to Harley’s et al. pattern wherein discussing the modifications in the
Lamiaceae classification, comparison among the major classifications (Table S1) and the relationships within Lamiaceae trying to highlight the taxa yet to be resolved.

**Subfamily Symphorematoideae**

It is characterized by inflorescence 3–7 flowered capitate cymes with an involucre of bracts, ovary imperfectly 2-locular, ovules apical pendulous and fruit dry or subdrupaceous. The subfamily Symphorematoideae consists of only three genera viz. *Sphenodesme* Jack, *Symphorema* Roxb. and *Congea* Roxb. distributed in India, Sri Lanka, South East Asia, Malaysia (Harley et al. 2004). Recognition of Symphorematoideae by Harley et al. (2004) within Lamiaceae is one of the major changes to the traditional classification (earlier considered as a distinct family: Symphoremataceae Wight). Bentham (1876) and Briquet (1895-1897) ranked it as tribe Symphoremeae and subfamily Symphoremeoideae under the family Verbenaceae respectively. Junell (1934) recognized that the gynoecial structure of *Congea* (Symphoremataceae) was distinct from other Labiatae and Verbenaceae, but suggested its viticoid ancestry. Throne (1992) and Cantino et al. (1992) placed it as a separate family Symphoremataceae under suborder Lamiineae. Wagstaff et al. (1998) carried out a study where they showed *Congea tomentosa* nested within Labiatae s. l. and as sister group to subfamily Nepetoideae based on ndhF and combined analysis but concluded that the addition of more members from Symphoremataceae is required to further establish the relationship. Bendiksby et al. (2011) showed *Congea* as sister to a clade of Viticoid genera.

**Subfamily Vитicoideae**

Recognition of Vитicoideae by Harley et al. (2004) within Lamiaceae is another of the major modifications to the traditional treatment where it has been part of Verbenaceae. Bentham (1876) treated it as tribe Vитiceae of Verbenaceae. Briquet (1895-1897) placed it as subfamily Vитicoideae belonging to Verbenaceae and divided the group into four tribes (Callicarpeae, Tectoneae, Vитiceae, Clerodendreae) having the characteristic features of presence of cymes; hemianatropous ovules; whole fruit or divided into 4-10 locules and seeds without endosperm. Briquet’s Vитicoideae included *Vitex*, *Gmelina* L., *Premna* L., *Callicarpa* L., *Cornutia* L., *Petitia* Jacq., *Tectona*, *Clerodendrum* and other allied genera. Pieper (1928) stated that it was not yet possible to establish the exact generic boundaries between *Vitex* and *Premna*. Junell (1934) made
some modifications to Briquet's four tribes within the Viticoideae. He remarked the affinity of
Viticipremna J. Lam, Tsoongia Merr. and Pseudocarpidium Millsp. to Vitex which was reported
by Pieper (1928). In addition, Junell moved Peronema Jack, Hymenopyramis Wall. ex Griff. and
Petraeovitex Oliv. from the subfamily Caryopteridoideae into the Viticeae based on the
characteristic feature of Caryopteridoideae where fruits split easily into four. These genera have
fruit which does not split, therefore transferred to Viticeae. Teijsmanniodendron was placed into
its own tribe Teijsmanniodendreae, based on it having fruit which is a one-celled, one-seeded
indehiscent capsule (Koorders, 1904).

Throne (1992) and Cantino et al. (1992) recognized the subfamily Viticoideae as part of Labiatae
for the first time which was later followed by Harley et al. (2004). Of the seven subfamilies
proposed by Harley et al. 2004, the Viticoideae has been considered as the least satisfactory
circumscribed, which is clearly paraphyletic or possibly polyphyletic as shown by
morphological, phytochemical and molecular evidences. It became the part of Labiatae with the
removal of several genera. Clerodendrum and Rottheca Raf. were transferred to form part of the
Ajugoideae, while Tectona, Peronema, Hymenopyramis, Petraeovitex and Callicarpa became
listed as incertae sedis. This Viticoideae composed of the following genera: Vitex, Premna,
Teijsmanniodendron, Gmelina, Paravitex H.R. Fletcher, Tsoongia, Viticipremna, Petitia,
Cornutia L. and Pseudocarpidium. Viticipremna, Tsoongia and Teijsmanniodendron are
suggested to be closely related to Vitex in Cantino's (1992b) cladistic analysis based on
morphological characters. Wagstaff et al. (1998) suggested through a molecular study that
Gmelina, Premna form a clade while Vitex, Petitia form another, therefore, monophyly of
Viticoideae was not supported. Recent molecular findings (Olmstead, unpubl. data) indicate that
Hymenopyramis is sister to Petraeovitex and that the two are not close to other genera of
Viticoideae. According to the same study, both Callicarpa and Tectona come out in relatively
basal positions, Callicarpa being weakly supported as sister group to Prostantheroideae, while
Tectona is weakly supported as sister group to most of the family. The removal of these four
genera to incertae sedis would leave Viticoideae more homogeneous.

In a recent study, Bramley et al. (2009) on the basis of phylogenetic analyses of ITS and ndhF
sequence data provided evidence that the Viticoideae is not monophyletic. According to this
study the most well supported clade, the Vitex group, contains Vitex, Paravitex, Tsoongia,
Viticipremna, Petitia and Teijsmanniodendron. The inclusion of Paravitex, Viticipremna and Tsoongia in a larger Vitex is supported by molecular and morphological evidences, therefore new combinations are being proposed. The generic status of Teijsmanniodendron and Petitia is not resolved and upheld yet in this investigation. Currently, different studies are giving conflicting results and it is clear that the whole group needs combination of approaches for much more detailed studies. Bendisby et al. (2011) also demonstrated Viticoideae as non-monophyletic.

**Subfamily Ajugoideae**

Subfamily Ajugoideae (Teucrioideae) as proposed by Harley et al. (2004) has ca. 1000 species divided into 24 genera, cosmopolitan, but many temperate, and especially South East Asia to Australia. In earlier classifications it was known as tribe Ajugeae sensu Bentham and Briquet and subfamily Ajugoideae sensu Wunderlich and reported as polyphyletic by Cantino (1992b). The traditional family boundary between Lamiaceae and Verbenaceae was transcended into Teucrioideae recognized by Cantino et al. (1992). Wagstaff and Olmstead (1997); Wagstaff et al. (1998) reported Teucrioideae to be paraphyletic with Ajuga L. in Ajugoideae sensu Cantino et al. (1992) nested within it, on the basis of rbcL and ndhF sequence data. On the basis of these results, the inclusion of Ajuga and related genera in Teucrioideae was recommended. In later study, together they appeared to be monophyletic in Lamiaceae s. I. (Cantino et al. 1999). The name Ajugoideae has priority over Teucrioideae under the International Code of Botanical Nomenclature, therefore, corrected by Judd et al. (1999). The genera included in Ajugoideae are Rotheca, Clerodendrum, Aegiphila Jacq., Teucridium Hook. f., Teucrium L., Ajuga, Pseudocaryopteris P.D. Cantino, Schnabelia Hand.-Mazz., Trichostema L., Caryopteris Bunge, Faradaya F. Muell. and relatives.

Throughout the taxonomic history of Clerodendrum s. l., it has been grouped between as many as a dozen different genera which are sometime divided among different families (De Necker, 1790; Westman, 1744). Clerodendrum L. which is a diverse genus having about 580 species widely distributed in Asia, Australia, Africa and America has high degree of morphological and cytological variation among the species which suggests its paraphyletic or polyphyletic origin (El Mokni et al. 2013). With the advent of molecular systematic approaches, the delimitation of Clerodendrum still continues to be modified. Based on the cpDNA restriction site analysis
performed by Steane et al. (1997) and ITS sequence data of Steane et al. (1999) resulted in the transfer of a large group of species from Clerodendrum s. l. to genus Rotheca (Steane and Mabberley, 1998). ndhF gene provided preliminary evidence that Clerodendrum is polyphyletic (Steane et al. 1997). Based on morphological characters like length of the corolla tube, size of leaves, and type of inflorescence some authors have divided the genus into two major sub-genera, Clerodendrum and Cyclonema (Hochst.) Guirke (Steane et al. 1999). Steane et al. (2004) reported the morphological similarity of Aegiphila, Amasonia L. f., Huxleya Ewart and Rees, and Kalaharia Baillon to Clerodendrum. On the basis of molecular data presented in this study Huxleya was sunk into Clerodendrum to make a new combination, Clerodendrum linifolium, already supported by De Kok et al. (2000) who reported morphological and chemical affinities between Huxleya and Clerodendrum. Yuan et al. (2010b) segregated the genus Volkameria L. from a formerly polyphyletic Clerodendrum based on molecular analysis. Recently Barrabe et al. (2015) reassessed the relationships of Oxera and reported that Clerodendrum is sister to Oxera. They have placed polyphyletic Faradaya in synonymy with Oxera because Faradaya was found partly nested within Oxera.

Another interesting group belonging to the subfamily Ajugoideae s. l. is Caryopteris-Trichostema complex. The complex also includes monotypic or very small genera i.e Amethystea L., Discretitheca P. D. Cantino, Pseudocaryopteris, Tripora P. D. Cantino, Rubiteucris Kudo and Schnabelia Hand.-Mazz. Chen and Gilbert (1994); Li and Hedge (1994); Moldenke (1983) placed the Caryopteris and Schnabelia in Verbenaceae. All the genera belonging to this complex are Asiatic except Trichostema which is North American. Most of the Caryopteris is endemic to China (Pei and Chen, 1982; Abu- Asab et al. 1993; Chen and Gilbert, 1994). The genus is treated either in Verbenaceae (Clarke, 1885; Briquet, 1895; Moldenke, 1980; Jafri and Ghafoor, 1974; Long, 1999; Press et al. 2000; Rajendran and Daniel, 2002) or in Lamiaceae (Junell, 1934; Cantino et al. 1992; Thorne, 1992; Harley et al. 2004). Cantino (1992b) and Rimpler et al. (1992) suggested that the genus Caryopteris is para or polyphyletic. Cantino et al. (1999) based on non molecular data as well as rbcL and ndhF sequences found the similar corroborating results. Amethystea is a monotypic genus while Rubiteucris and Schnabelia include two and five species respectively after their expansion by Cantino et al. (1999) who transferred species from Caryopteris. Similarly Discretitheca, Pseudocaryopteris and Tripora were disintegrated from Caryopteris s. l. in the same study to delimit the Caryopteris as monophyletic. The genera
comprising *Caryopteris-Trichostema* complex are closely related based on shared characters like pollen morphology, androecial structure, corolla and fruit morphology (Abu- Asab and Cantino 1989; Cantino, 1992a; Abu- Asab *et al.* 1993). The close affinity of *Caryopteris* to *Trichostema* was reported by Rimpler *et al.* (1992) based on phytochemical and morphological characters. Molecular phylogenetic studies further proved the sister relationship between these two genera (Steane *et al.* 1997; Wagstaff and Olmstead, 1997; Wagstaff *et al.* 1998). The close ties of genera constituting the complex based on combined morphological and molecular analysis were supported by low bootstrap (Cantino *et al.* 1999), therefore, intriguing the further investigations. *Caryopteris s. str.*, *Pseudocaryopteris*, Schnabelia and *Trichostema* appeared to be monophyletic while *Caryopteris s. l.* as polyphyletic in a molecular study of ndhF conducted by Huang (2008). Same study based on ndhF data proved that the sister group of *Trichostema* is *Caryopteris*, with *Amethystea* the next most closely related taxon but on the other hand the combined ITS and ndhF data with morphological data showed that the sister group of *Trichostema* is *Amethystea*. Therefore, suggesting the need of further probe into this *Caryopteris-Trichostema* complex.

In a recent investigation by Shi *et al.* (2003) based on matK and ITS sequence data, Schnabelia is found to be close to some species of *Caryopteris*. This sister group relationship between Schnabelia oligophylla and *Caryopteris terniflora* is strongly supported by the bootstrap values. Ajugoideae also showed the high bootstrap values to prove its monophyly but *Caryopteris* complex is not monophyletic according to this study, hence corroborating with the previous findings of Cantino (1992b), Cantino *et al.* (1999) and Huang *et al.* (2000).

**Subfamily Prostantheroideae**

Harley *et al.* (2004) divided the Australian subfamily Prostantheroideae into two tribes viz. tribe Chloantheae Benth. & Hook. f. comprising of 10 genera and tribe Westringiieae Bartl. including 6 genera. Bentham (1876) classified it as tribe Prostanthereae but in the later classifications of Briquet (1895-1897) and Wunderlich (1967) it was ranked as subfamily Prostantheroideae. The Australian tribe Prostanthereae showed close relationships with Verbenaceae subfamily Chloanthoideae based on gynoecial similarities proposed by Junell (1934). Cantino *et al.* (1992) included the Verbenaceous subfamily Chloanthoideae to Labiatae s. l. which was adopted by Thorne (1992). Chloanthoideae, a primarily Australian group circumscribed by Cantino *et al.*
(1992) included members of Prostanthereae (traditionally in Labiatae s. str.) and Chloantheae, plus Tectona (traditionally in Verbenaceae s. l.). Olmstead et al. (1998) also proposed the monophyly of Prostantheroideae. Recently Bendiksby et al. (2011); Li et al. (2012) showed the monophyly of Prostantheroideae, however, the analysis includes members of tribe Westringeae only. The most recent synopsis of Chloantheae was presented by Conn et al. (2011) based on morphological and molecular study. They presented a key to distinguish the genera of tribe Chloantheae.

Wrixonia F. Muell. is one of the six genera within the Australian endemic tribe Westringeae which includes only two species (Conn, 2004; Harley et al. 2004). This genus has clear morphological resemblance with the genus Prostanthera Labill. which is the largest genus of the tribe Westringieae. Phylogenetic analyses based on morphological characters showed that Wrixonia and Prostanthera (including Eichlerago) are sister taxa (Cantino, 1992b; Conn, 1992; Abu-Asab and Cantino, 1993). Cantino (1992b) also demonstrated that Wrixonia has closer affinity to Prostanthera section Prostanthera than to section Klanderia by one synapomorphy: the closed fruiting calyx. Wilson (2010) using nuclear (ETS) and plastid (trnT-F) DNA reported that Prostanthera is paraphyletic with respect to Wrixonia. Based on these findings, Wrixonia is reduced to the synonymy of Prostanthera in order to maintain a monophyletic Prostanthera (Wilson et al. 2012).

There are other two genera Hemigenia R. Br. and Microcorys R. Br. of tribe Westringieae reported to be polyphyletic by means of morphological and molecular analysis (Guerin, 2008). However further use of molecular markers and additional taxa are recommended to evaluate the complete implications on the taxonomy of these genera (Guerin, 2008).

Subfamily Scutellarioideae

Inclusion of Holmskioldia Retz. within subfamily Scutellarioideae is one of the notable modifications done by Harley et al. (2004) in the traditional classification. The other four genera are Wenchengia C. Y. Wu & S. Chow, Renschia Vatke, Tinnea Kotschy ex Hook. f. and Scutellaria L. (Harley et al. 2004). Bentham placed Brazoria Engelm. ex A. Gray, Prunella L. and Cleonia L. in his subtribe Scutellariinae which were excluded by Briquet in his subfamily Scutellarioideae but he also excluded Perilomia which was correctly placed by Bentham.
Therefore, Briquet’s Scutellarioideae was paraphyletic. Wunderlich’s Scutellarioideae was monophyletic as she included the Perilomia. Cantino (1992a) supported the monophyly of Scutellarioideae based on two synapomorphies, bilabiate calyx with entire rounded lips and fruits having a distinctive tuberculate surface. Wagstaff et al. (1998) reported Scutellarioideae as the sister group to subfamily Lamioideae and Pogostemonoideae based on a molecular phylogenetic analysis.

The phylogenetic position of Wenchengia has long been controversial, though it is a monotypic genus. The characteristic features of Wenchengia are alternate leaves, racemose inflorescences, vascular funicles and slender stalks. Wu and Chow (1965) established a separate subfamily Wenchengioideae based on morphological uniqueness of Wenchengia and adopted by Wu and Li (1977); Li and Hedge (1994); Takhtajan (2009). Abu Asab and Cantino (1993) recommended the genus as incertae sedis based on their morphological cladistic analysis which showed Wenchengia belonging to or near to Ajugoideae but its position in Scutellarioideae appeared to be only one step less parsimonious. Ryding (1996) suggested to keep considering the Wenchengia incertae sedis based on his morphological observations. However, Wenchengia is placed in subfamily Scutellarioideae by Cantino in Harley et al. (2004). Li et al. (2012) conducted a recent study on phylogenetic position of Wenchengia within mint family and revealed that Wenchengia emerged as a sister to the Holmskioldia-Tinnea-Scutellaria clade based on ndhF and rbcL analysis. The placement of Wenchengia in subfamily Scutellarioideae is recommended by this study with further support of morphological, anatomical and cytological features.

**Subfamily Lamioideae**

Subfamily Lamioideae (including Pogostemonoideae) is the second largest subfamily among the seven subfamilies proposed by Harley et al. (2004) classification. It contains 63 genera and about 1260 species. Briquet (1895-1897) recognized the huge subfamily Lamioideae (Stachyoideae) by subsuming the Bentham’s tribe Nepeteae, Salvieae (Monardeae), Mentheae (Satureineae) and most of his Lamieae (Stachydeae). Erdtman (1945) reported that Labiatae could be divided into two groups – Lamioideae, which usually have tricolpate pollen shed at the two-celled stage, a character which they share with many of Verbenaceae and the other is Nepetoideae, having hexacolpate pollen shed at the three-celled stage. This division was further correlated with other
characters including myxospermy, presence or absence of endosperm, embryo shape, as well as a number of phytochemical characters (Wunderlich, 1967; Cantino and Sanders, 1986). Cantino and Sanders (1986) could not find an evidence for monophyly of Lamioideae. Wunderlich (1967) recognized Lamioideae (Stachyoideae) comprising Bentham’s Prasieae, most of Bentham’s Lamieae and five other genera.

Cantino et al. (1992) could not draw clear distinction between Pogostemonoideae and Lamioideae, although they proposed Pogostemonoideae as a separate subfamily from Lamioideae. The characteristic feature of Pogostemonoideae is stamens of equal length, and Lamiod’s are marked by presence of laballenic acid and an unusual embryo sac. On the other hand, pericarp structure (Ryding, 1995) and pollen morphology (Abu-Asab and Cantino, 1994) provide no distinction between the two groups. The cpDNA molecular phylogeny provides a poor support for segregation of Pogostemonoideae and Lamioideae, whereas the monophyletic group consisting of both subfamilies is strongly supported (Wagstaff et al. 1998). In later classification of the Lamiaceae, pogostemonoid taxa have been subsumed into Lamioideae, but the suprageneric relationships among the Lamioideae remained poorly understood providing no tribal ranks (sensu Harley et al. 2004). Wink and Kuaßmann (1996); Wagstaff & Olmstead (1997); Wagstaff et al. (1998) reported Scutellarioideae as the closest relatives of the Pogostemonoideae–Lamioideae clade based on molecular analysis.

Scheen et al. (2010) presented another phylogenetic investigation based on three plastid markers (trnL, trnL-trnF, rps16) analyzing 159 species belonging to 50 genera. They found strong support for monophyly of Lamioideae s. l. (i.e., including Pogostemonoideae) with Cymaria Benth. as its sister group. Lamioideae is divided into nine tribes. Three new tribes are established: Gomphostemmateae Scheen & Lindqvist, Phlomideae Mathiesen, and Leucadeae Scheen & Ryding. The other six tribes are: Pogostemoneae Briq., Synandreae Raf., Stachydeae Dumort., Leonureae Dumort., Lamieae Coss. & Germ., and Marrubieae Vis. The genus Betonica L. is reestablished and confirmed by Dundar et al. (2012) . The results also strongly suggest that the genera Stachys L., Sideritis L., Ballota L., and Leucas R. Br. are polyphyletic or paraphyletic. Yet 16 genera remained unclassified at the tribal level due to formation of monogeneric groups (Betonica, Colquhounia Wall., Eriophyton Benth., Galeopsis L., Paraphlomis (Prain) Prain, Roylea Wall. ex Benth.) or unavailability of molecular evidence (Ajugoides Makino, Alajja
Despite the reasonable progress in the Lamioideae phylogenetics which has been recently made, yet it is considered as one of the most poorly resolved subfamily of Lamiaceae. Only limited groups have undergone phylogenetic analysis e.g tribe Lamieae (Ryding, 2003), tribe Leucadeae (Ryding, 1998; Scheen and Albert, 2009), tribe Phlomoideae (Ryding, 2008; Pan et al. 2009), tribe Synandrea (Scheen et al. 2008), Sideritis (Barbar et al. 2000, 2002, 2007) and the indigenous Hawaiin Labiates (Lindqvist and Albert, 2002; Lindqvist et al. 2003).

Bendiksby et al. (2011) proposed a taxonomic update of subfamily Lamioideae based on four plastid markers whose main purpose was to focus the genera which were omitted in the phylogenetic investigation by Scheen et al. (2010). They made 13 new combinations at rank of species and one at subgenus, established a new tribe Paraphlomideae Bendiksby which includes Ajugoides, Matsumurella and Paraphlomis. Only three genera (Metastachydium, Paralamium, Pseudomarrubium) remain unrepresented in this study, remaining 61 presently recognized genera of Lamioideae are investigated. The incertae sedis genera, Cymaria Benth. and Acrymia Prain forms a clade with Lamioideae which has a strong support for subfamily Scutellarioideae as its sister clade. Another incertae sedis genus, Garrettia H. R. Fletcher appears as the sister of this larger clade constituting these four groups. Cymaria, Acrymia and Garrettia have shown a close morphological relationship previously (Cantino, 1992a; Harley et al. 2004). However, due to obvious morphological differences, none of these genera fit into Lamioideae (Bendiksby et al. 2011).

Bendiksby et al. (2013) amalgamated the Stachyopsis and Eriophyton and also transferred Stachys tibetica to this expanded Eriophyton now containing 11 species. The group is supported as monophyletic by molecular phylogenetic tree. The morphological characters featuring this expanded Eriophyton are presence of usually hairy anthers, prominent and apically rounded to slightly emarginate lateral lobes of the lower lip of the corolla and apically truncate or subtruncate nutlets. Molecular phylogenetics of tribe Stachydeae has been recently investigated to confirm the monophyly and to better resolve the poorly understood relationships within the tribe (Salmaki et
Tribe Stachydeae, or some of its component genera, have previously been the subject of molecular phylogenetic investigations (e.g. Lindqvist and Albert, 2002; Lindqvist et al. 2003; Barber et al. 2002, 2007; Scheen et al. 2010; Bendiksby et al. 2011; Roy et al. 2013). The complexity of Stachydeae includes paraphyletic genera, considerable morphological plasticity, a range of ploidy levels, and presumably frequent natural hybridization. Salmaki et al. (2013) carried out the analysis of nuclear and plastid DNA sequence data to identify major evolutionary lineages and to test taxonomic hypotheses within this largest of all lamioid tribes. Both nuclear and plastid data corroborate monophyly of the tribe, with *Melittis* L. as sister to all remaining Stachydeae. Still this study could not transform the taxonomy of Stachydeae into a more ‘natural’ classification.

Tribe Gomphostemmateae comprises 46 species divided into three genera—*Bostrychanthera* Benth., *Gomphostemma* Wall. ex Benth. and *Chelonopsis* Miq., and have strong support for its monophyly (Scheen et al. 2010; Bendiksby et al. 2011; Xiang et al. 2013). Members of this clade tend to have relatively large, four-lobed corollas that are strongly dilated distally (Harley et al. 2004). Possible synapomorphies include similarities in fruit pericarp structure (Ryding, 1994a, b) and the apparent branching of the columellae in the pollen exine (Pozhidaev, 1989; Abu-Asab & Cantino, 1994), but the sample size in these studies was too limited to be conclusive. Xiang et al. (2013) recently proposed the transfer of *Bostrychanthera* to *Chelonopsis* based on molecular, morphological and cytological data.

The first ever study of Lamioideae based on low-copy nuclear marker has been recently conducted by Roy and Lindqvist (2015) by using *PPR* locus. They found the results consistent with previously studied cpDNA data of Scheen et al. (2010) and Bendiksby et al. (2011), however, observed some important discordance among the cpDNA and *PPR* data, suggesting increased taxon sampling and use of multiple independent nuclear loci for further studies. Yao et al. (2016) proposed a new infrageneric classification of *Pogostemon* consisting of two subgenera.

**Subfamily Nepetoideae**

The subfamily Nepetoideae is made up of about 105 genera (Harley et al. 2004) and is the largest subfamily in the Lamiaceae (Wagstaff et al. 1995; Wagstaff et al. 1998; Paton et al. 2004).
Hexacolpate pollen, gynobasic style, an investing embryo, presence of rosmarinic acid and exalbuminous seeds are the noteworthy synapomorphies through which it appeared to be monophyletic (Cantino and Sanders 1986; Harley et al. 2004). Other studies also reported it as monophyletic (Wagstaff et al. 1995; Wagstaff and Olmstead, 1997).

The tribal segregation of Nepetoideae varied fundamentally from treatment to treatment (Bentham, 1876; Briquet, 1895–1897; Wunderlich, 1967). Nepetoideae sensu Wunderlich corresponds closely to Erdtman’s Nepetoideae, the only difference between these two circumscriptions is the Wunderlich’s segregation of Catoferia Benth. to Subfamily Catoferioideae. Cantino (1992) provided a detailed overview of these treatments. Cantino et al. (1992) proposed a new classification for Nepetoideae based on morphological and molecular analysis. The authors recognized four tribes Elsholtzieae, Ocimeae, Lavanduleae and Mentheae, with the last undergoing the most significant modifications as compared to earlier taxonomic classifications. Harley et al. (2004) adopted these findings with slight modifications and recognized three tribes i.e. Elsholtzieae, Mentheae, and Ocimeae with the Mentheae the largest, containing about 65 genera. Tribe Mentheae is further divided into three subtribes: Salviinae, Menthinae and Nepetinae. They repositioned the Lavandula L. which was the only member of Lavandulinae, within tribe Ocimeae, together with four other subtribes: Hanceolinae, Hyptidinae, Ociminae and Plectranthinae. Subtribe Hanceolinae has been recently recognized and includes the large, primarily Asiatic genus Isodon (Benth.) Schrader ex Spach, which often had been placed in Plectranthus L’Her. A number of molecular studies have been conducted within the Nepetoideae (Wagstaff et al. 1995; Prather et al. 2002; Paton et al. 2004; Trusty et al. 2004; Walker et al. 2004; Bräuchler et al. 2005; Edwards et al. 2006; Walker and Sytsma 2007; Bräuchler et al. 2010).

Tribe Mentheae is not only the largest tribe of Lamiaceae in terms of species and genera but also exhibits diversity in distribution, habit, breeding system and floral form (Drew and Sytsma, 2012). Mentheae has undergone a number of molecular phylogenetic investigations (Wagstaff et al. 1995; Prather et al. 2002; Trusty et al. 2004; Paton et al. 2004; Walker et al. 2004; Bräuchler et al. 2005, 2010; Edwards et al. 2006; Walker and Sytsma, 2007; Drew and Sytsma, 2011), where Mentheae appeared to be monophyletic. Since the treatment proposed by Harley et al. (2004), several molecular (Trusty et al. 2004; Walker et al. 2004; Bräuchler et al. 2005, 2010; Edwards et al. 2006; Walker and Sytsma, 2007; Drew and Sytsma, 2011) and morphological
studies have focused on Mentheae and groups within it. These studies showed the non-monophyly of the three subtribes of Mentheae proposed by Harley et al. (2004) and reported that a number of genera remain unplaced/misplaced (Ryding, 2010a; Drew and Sytsma, 2011).

Generic boundaries in subtribe Menthininae have been under debate especially those taxa associated with the former Satureja s. l. complex (Satureja L., Micromeria Benth., Clinopodium L., Acinos). Many authors favored Briquet’s (1895–1897) broad concept of Satureja (e.g. Thonner, 1915; Brenan, 1954; Hedberg, 1957; Killick, 1961; Epling and Jativa, 1964, 1966; Greuter et al. 1986) while others (Chater and Guinea, 1972; Ball and Getliffe, 1972; Davis, 1982; Morales, 1993) were in favour of the narrow delimitation classified by Bentham (1848, 1876).

Recently there have been an increasing number of molecular studies in Nepetoideae with focus on the tribes Ocimeae (Paton et al. 2004) and especially Mentheae. All of the latter were restricted to selected genera, e.g. Bystropogon L’Her. (Trusty et al. 2004, 2005), Conradina A. Gray (Edwards et al. 2006, 2008a, b), Mentha L. (Bunsawat et al. 2004), Micromeria (Bräuchler et al. 2005), Minnthostachys (Schmidt-Lebuhn, 2007, 2008), Monarda L. (Prather et al. 2002) and Salvia L. (Walker et al. 2004; Walker and Sytsma, 2007) with some preliminary investigations at the tribal level only.

Drew and Sytsma (2012) in their recent study based on cpDNA and nrDNA phylogenetics showed conflicts with the subtribal delimitation of Mentheae proposed by Harley et al. (2004). They showed the monophyly of Mentheae and proposed two new subtribes, Prunellinae and Lycopinae in addition to Harley’s.

Harley et al. (2004) treated ten genera as incertae sedis (Acrymia Prain, Callicarpa L., Cymaria Benth., Garrettia H.R.Fletcher, Holochilea (Kudô) S.Chow, Hymenopyramis Wall. ex Griff., Ombrocharis Hand.-Mazz., Peronema Jack, Petraeovitex Oliv., and Tectona L.f.). These were not placed into any of the seven subfamilies.

Recently Chen et al. (2016) placed incertae sedis Ombrocharis in Nepetoideae, a placement that is also supported by its hexacolpate pollen grains. They demonstrated that Ombrocharis and another monotypic genus of Nepetoideae, Perillula, form a clade that is sister to the remaining genera of tribe Elsholtzieae. The monophyly of Elsholtzieae (including Ombrocharis) is well
supported, there is weak support for Elsholtzieae as sister to the rest of Nepetoideae and Elsholtzia may be polyphyletic.

Conclusion

Since Harlay et al. (2004), estimates of tribal and generic composition of many groups have been revised, particularly in Lamioideae and Nepetoideae. Tribe Stachydeae still needs to be transformed into a more natural classification. The recent studies showed the non-monophyly of the three subtribes of Mentheae proposed by Harley et al. (2004) and reported that a number of genera remain unplaced/misplaced. Therefore, Drew and Sytsma (2012) proposed additional two new subtribes, Prunellinae and Lycopinae to make the Mentheae monophyletic. Relationships of Symphoremeoideae and Viticoideae require further investigations. Viticoideae is yet non-monophyletic. The incertae sedis genera Callicarpa, Hymenopyramis, Petraeovitex, Cymaria, Acrymia, Garrettia, Peronema, Holocheila, Tectona, and Ombrocharis remain unplaced. The major challenges now lie in recognizing characters that can articulate these genera in a formal classification.
References


