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 undersanding 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 boundries 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 *rbc*L 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 Sreelekha, 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 ancestory. 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 Viticoideae

Recognition of Viticoideae by Harley *et al.* (2004) within Lamiaceae is another of the major modifications to the traditional treatment where it has been part of Verbanaceae. Bentham (1876) treated it as tribe Viticeae of Verbenaceae. Briquet (1895-1897) placed it as subfamily Viticoideae belonging to Verbenaceae and divided the group into four tribes (Callicarpeae, Tectoneae, Viticeae, 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 Viticoideae 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 boundries 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 *Rotheca* 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. Bendiksby *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 boundry 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 Westringieae 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 Chloanthoideae, 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 n 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 Lamioid'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 Kuafmann (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*

Ikonn., *Hypogomphia* Bunge, *Loxocalyx* Hemsl., *Matsumurella* Makino, *Metastachydium* Airy Shaw ex C. Y. Wu & H. W. Li, *Paralamium* Dunn, *Pseudomarrubium* Popov, *Stachyopsis* Popov & Vved.)

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*

al. 2013). 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

(Moon *et al*. 2008, 2009, 2010; Ryding, 2010a , b) 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 Menthinae have been under debate especially those taxa associated with the former *Satureja s. l.* complex (*Satureja* L., *Micromeria* Benth., *Calamintha*, *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), *Minthostachys* (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, *Holocheila* (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 *incertea 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, Peronem*a, *Holocheila, Tectona,* and *Ombrocharis* remain unplaced. The major challenges now lie in recognizing characters that can articulate these genera in a formal classification.

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