TAXONOMY

Myriolepis, a new genus segregated from Limonium (Plumbaginaceae)

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Taxonomic features of *Limonium* subg. *Myriolepis* are reviewed and compared with those of other taxa in Plumbaginaceae. The new genus *Myriolepis* is proposed on the basis of morphological, karyological and phytochemical characters to include two western Mediterranean species of *Limonium* sect. *Myriolepis*: *L. ferulaceum* and *L. diffusum*. Remaining taxa belonging to *L.* subg. *Myriolepis* (those in *L.* sects. *Siphonantha* and *Polyarthrion*) are recognised as sections in *L.* subg. *Limonium*. Affinities to other taxa of *Limonium*, sometimes suggested as related to *Myriolepis*, are also discussed.

KEYWORDS: Limonium, Myriolepis, Plumbaginaceae, nomenclature, taxonomy.

Limonium Mill. (the sea lavenders) is the largest genus of Plumbaginaceae. Kubitzki (1993) estimated about 350 species of *Limonium*, but the actual number is probably higher as new species continue to be described (Lobin & al., 1995; Brullo & al., 1996; Roselló & al., 1997; Crespo & Lledó, 1998; Sáez & al., 1998; Rizzotto, 1999; Sáez & Rosselló, 1999; Artelari & Kamari, 2000; Erben, 2001; among others). The centre of diversity of the genus is the Mediterranean region, where *Limonium* species have an important role in coastal ecosystems, from salt marshes to maritime cliffs. Species of *Limonium* can also be found in other parts of the world mostly with Mediterranean-type climates.

In a wide sense, *Limonium* includes dwarf shrubs and a few herbs with rosulate leaves and scapose inflorescences. Flowers are crowded in 3-bracteate terminal spikelets. The calyx varies in shape, commonly has a ribbed tube with a membranous terminal limb, and is often coloured. Petals are usually free, or more rarely connate only at the base. Styles are free and stigmas are filiform. Fruits are 1-seeded, utriculate (with basal or irregular dehiscence) or sometimes pixidiate (circumscissile).

The taxonomic arrangement of *Limonium* is extremely complex at both infra- and supraspecific levels. The isolated and fragmented nature of habitats where *Limonium* species grow, together with the frequent occurrence of apomixis within the genus, greatly favour the existence of many geographical variants which are often defined on the basis of little morphological discontinuity (Erben, 1978; Pignatti, 1982: 302; Cowan & al., 1998). Moreover, the circumscriptions of subgenera and sections are not yet satisfactorily defined and many sections appear to be heterogeneous. Currently accepted genera (e.g., Afrolimon Lincz., Ikonnikovia Lincz.) established on the basis of former sections of the genus when it was known as Statice (nom. rej. vs. Armeria; cf. Greuter & al., 2000: 268), are perhaps no more distinct than some groups still included within Limonium. The aim of the present work is to discuss the taxonomic status of one such group, Limonium sect. Myriolepis. A nomenclatural complication in discussing the taxonomy of Limonium should be noted at this point. Until around 1930, the present genus Limonium was known as Statice (a name now correctly treated as homotypic with Armeria), and some sections recognised within Statice have never been formally transferred to Limonium. For this reason, we also refer to the groups by their former names within Statice.

Historical background: the genus *Limonium* **Mill.** — Only a few comprehensive reviews of the whole genus *Limonium* have been published, among which the synopsis of Plumbaginaceae by Boissier (1848) is probably one of the most complete. In his work, Boissier split off genera such as *Acantholimon* (= *Statice* subgen. *Armeriastrum* Jaub. & Spach) or *Goniolimon* (= *Statice* sect. *Tropidice* Griseb.) from the former *Statice*, and also accepted *Armeria* Willd., *Aegialitis* R. Br. and *Limoniastrum* Heist. ex Fabr. On the basis of floral characteristics he divided the former *Statice* into 12 sections, belonging to two main groups: "*Corolla polypetala*" (with eight sections) and "*Corolla gamopetala*" (including four sections). Later, Boissier (1859) completed his compendium when describing the new *Statice* sect. *Schizopetalum* for plants from the Middle East. Boissier's taxonomic arrangement was followed by several authors with few modifications. In order to fully understand the relationships among taxa included in Boissier's "*Corolla gamopetala*" group, to which *S*. sect. *Myriolepis* belongs, further details of the taxonomic changes that this group has undergone are explained.

The "Corolla gamopetala" group. — The four sections in "Corolla gamopetala" as defined by Boissier (1848) are characterised as follows: S. sect. Polyarthrion Boiss. for plants with many sterile branches in the lower regions of the stems and pink corollas (S. caesia Girard); S. sect. Myriolepis Boiss. for plants with leaves vestigial or absent, articulate branches densely covered with whitish scales and a convolute inner floral bract (S. ferulacea L. and S. diffusa Pourr.); S. sect. Siphonantha Boiss. for plants with scorpioid spikes in the inflorescence and calyx lobes shortly bifid, hyaline-bicuspidate, with an awn arising from the notch (S. tubiflora Delile); and S. sect. Psylliostachys Jaub. & Spach. for annual plants with long cylindrical-spicate inflorescences, lobed leaves and bibracteate spikelets (S. spicata Willd., and related taxa). The last-named group was later raised to generic rank as Psylliostachys (Jaub. & Spach) Nevski.

Hooker (1876) rearranged the "Corolla gamopetala" group as S. sect. Siphonantha (including Boissier's S. sects. Myriolepis, Siphonantha and Polyarthrion). He also accepted S. sect. Psylliostachys and described the new S. sect. Pterolimon for two unusual plants: S. plumosa Phil. from the Atacama Desert (Chile) and S. peruviana Kuntze nomen illeg. from territories formerly included in Peru, but nowadays part of Chile. A similar classification was adopted by Pax (1891), who raised S. sect. Siphonantha to subgeneric rank and included three sections in it: S. sect. Psylliostachys, S. sect. Eusiphonantha (in the same sense as Hooker's S. sect. Siphonantha), and S. sect. Pterolimon. Statice sect. Pterolimon was later elevated to generic rank by Linczevski (1968) as Bakerolimon Lincz. The last taxon to be described that is related to the "Corolla gamopetala" group was the monotypic S. sect. Arthrolimon (Mueller, 1878) for a plant growing in desert areas of Western Australia. Mueller called this species Statice salicorniacea F. Muell., since it is similar in habit to some taxa of Salicornia. Linczevski (1982) established the monotypic genus Muellerolimon on the basis of Statice sect.

Arthrolimon F. Muell.

Sections commonly included in Boissier's "Corolla gamopetala" group and more recently described related taxa form a highly heterogeneous group, only sharing long, apparently connate petals. Statice sect. Psylliostachys is now widely accepted as the separate genus, Psylliostachys (Jaub. & Spach) Nevski. Most modern floras follow this treatment (e.g., Rechinger & Shaiman-Czeika, 1974; Kubitzki, 1993) and phylogenetic analyses based on plastid DNA sequences have shown that Psylliostachys is more closely related to Armeria than to Limonium (Lledó & al., 1998, 2000). Other taxa sometimes related to Boissier's gamopetalous group, such as Bakerolimon or Muellerolimon, are to be excluded since they have petals only connate at the base and have morphological peculiarities warranting recognition as separate genera (Kubitzki, 1993).

The other three sections included in Boissier's "Corolla gamopetala" (S. sects. Myriolepis, Siphonantha and Polyarthrion) currently form Limonium subg. Myriolepis following Pignatti's system (1971, 1982), and are the focus of our discussion. Despite the descriptions provided by Boissier (1848) and followed by later authors, the petals are free and imbricate in his S. sects. Polyarthrion and Siphonantha, only when dry giving the wrong impression that the corolla forms a tube. The only representative of the "Corolla gamopetala" group truly matching the name is the former Statice sect. Myriolepis [= L. sect. Myriolepis (Boiss.) Sauv. & Vindt], in whichthe petals are truly coherent and stick together forming a tube longer than the calyx (Fig. 1C, E). The misplacement of his S. sects. Siphonantha and Polyarthrion [= L.sect. Siphonantha (Boiss.) Sauv. & Vindt and L. sect. Polyarthrion (Boiss.) Sauv. & Vindt] in the "Corolla gamopetala" group by Boissier (1848) and later authors was probably due to studies based only on dried material, but the character can be easily recognised in fresh specimens. In addition to the tubular corolla, other characters also differentiate the members of L. sect. Myriolepis from those of L. sects. Siphonantha and Polyarthrion. In L. sect. Myriolepis the inner bract is convolute and completely conceals the calyx, as well as in other genera of Plumbaginaceae not related to Limonium such as Muellerolimon and Limoniastrum. Moreover, the calyx is hyaline and ecostate, the stems are articulate and the leaves are vestigial and present only in springtime (L. diffusum) or completely absent (L. ferulaceum). Stems and branches are completely covered with long acuminate, subimbricate white scales giving rise to the epithet "myriolepis" (Figs. 1 and 2). The fruit is circumscissile, a characteristic only present in a few deviant sections of Limonium such as L. sects. Pteroclados, Ctenostachys and Jovibarba. These particular morphological features of L. ferulaceum and L. dif-

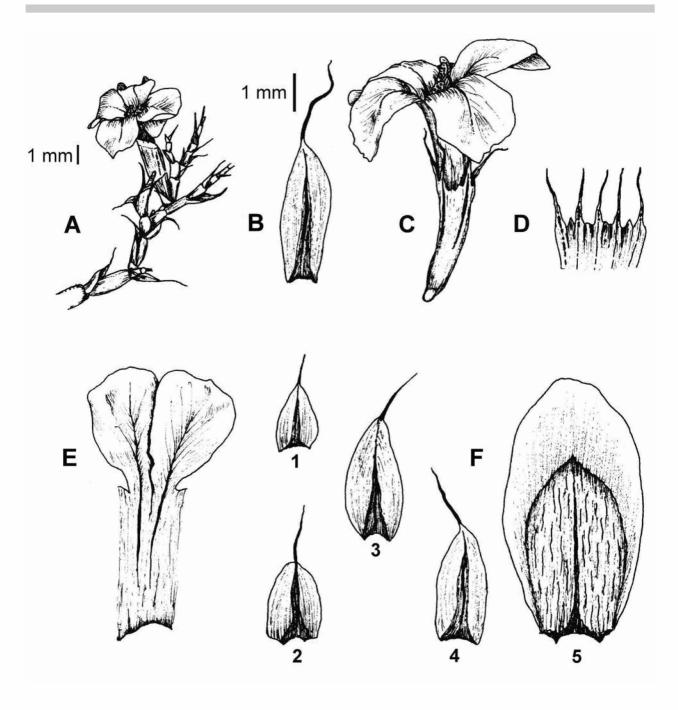


Fig. 1. *Myriolepis ferulacea*. A, flowering branchlet; B, hyaline scale of the stem; C, single flower; D, apex of the calyx; E, part of the corolla tube; E, bracts and scales surrounding the spikelet (1, outer scale of the branchlet, 2, inner scale; 3, outer bract of the spikelet, 4, middle, 5, inner). B–F, same scale.

fusum are present in neither *L*. sect. *Polyarthrion* nor *L*. sect. *Siphonantha*. Stem articulation and branching pattern and spikelet structure are unique in *L*. sect. *Myriolepis* (Fig. 2). Spikelets are situated at the top of short branches surrounded and hidden by two hyaline caulinar bracts, and the single flower thus appears to be protected by five and not three bracts (Fig. 2) as erro-

neously reported by Pount (1979) and then clarified by Erben (1981). The outer and the middle bracts of the spikelets are long-aristate or mucronate and almost completely hyaline, and the inner bract is convolute and conceals the calyx (Pount, 1979; Erben, 1981, 1993).

Morphological relationships among those peculiar taxa are also supported by chemical features (Hanson &

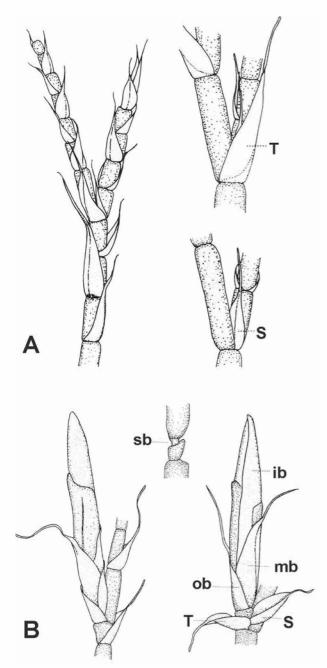


Fig. 2. A, branching pattern of stems (A) and spikelets (B) in *Myriolepis.* T, outer scale from which the branchlet arises; S, first inner scale of the branchlet itself (outer scale removed in A); sb, short internode at the top of which the spikelet is inserted; ob, outer bract of the spikelet; mb, middle bract; ib, inner bract. Modified from Erben (1981).

al., 1994). Both species in *L*. sect. *Myriolepis* show a unique pattern of osmoprotective compounds. They lack β -alanine betaine, a compound widely present in Plumbaginaceae (including *L*. sects. *Siphonantha* and *Polyarthrion*) that is absent as well in *Aegialitis*,

Gladiolimon Mobayen and genera of subfamily Plumbaginoideae not related to Limonium. Moreover, proline betaine, an unusual compound in Plumbaginaceae, is only present in L. ferulaceum and L. diffusum as well as Limoniastrum and Muellerolimon. The distribution of osmoprotective compounds in L. sects. Siphonantha and Polyarthrion is the same as for the rest of the sections of Limonium, supporting the lack of affinity among members of the former "Corolla gamopetala" group, as suggested by morphology. Harborne (1967) also reported the unique occurrence in L. ferulaceum of the flavonoid azeleatin, common otherwise in members of subfamily Plumbaginoideae, but not Staticoideae to which Limonium belongs. The phenolic compounds of L. caesium were similar to the rest of the sections of Limonium studied. However, members of L. sect. Siphonantha were not included in that study.

Cytological studies of several species of Limonium (Erben, 1978, 1979) have stressed the peculiarities of karyotypes of L. sect. Myriolepis. Both L. ferulaceum and *L. diffusum* are diploids with 2n = 16 chromosomes. However, they always lack the large metacentric chromosome, otherwise typical of diploid taxa of L. subg. *Limonium* with x = 8 [e.g., *L. cymuliferum* (Boiss.) Sauvage & Vindt]. The presence of large metacentric chromosomes in members of the subgenus with x = 8 has been interpreted as a reduction from x = 9 after fusion of one pair (Erben, 1978, 1979), but this explanation cannot be applied to L. sect. Myriolepis, in which two different patterns are present. In the case of L. ferulaceum, the chromosomes are more or less metacentric and all equal in length (Fig. 3A), but in L. diffusum they are unequal in length (Fig. 3B). The same chromosome number 2n = 16is also present in some species of the Limonium sinuatum (L.) Mill. group (L. subg. Pteroclados), but in this case,

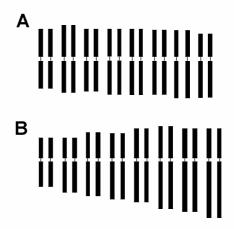


Fig. 3. Karyotypes of *Myriolepis ferulacea* (A) and *Myriolepis diffusa* (B). Original chromosome numbers previously published in Erben (1978), where cytological techniques are fully explained.

all chromosomes are acrocentric and equal in length. Certainly, the base chromosome number x = 8 has arisen several times in the family, and it cannot be taken as an homologous character. Members of *L*. sects. *Siphonantha* and *Polyarthrion* have a chromosome number of 2n = 18. This points to the diploid taxa of *L*. sect. *Myriolepis* as isolated lineages not closely connected to diploids in other sections of *Limonium* with similar base chromosome numbers or to other taxa from *L*. subgen. *Myriolepis*.

Breeding systems have been well studied in Plumbaginaceae (Baker, 1953) but do not provide any more additional characters to differentiate sections within the "*Corolla gamopetala*" group. Both *L. ferulaceum* and *L. diffusum* show the typical pollen-stigma dimorphism widely present in subfamily Staticoideae. Wild populations are sexual and self-incompatible, showing the same ratio of combinations A and B (terminology according to Erben, 1979), to species in *L.* sects. *Siphonantha* and *Polyarthrion*. Some populations of *L. ferulaceum* and of species of *L.* sect. *Siphonantha* may show only the self-compatible combination C (Erben, 1978, 1979).

Conclusions: taxonomic proposals. — On the basis of the evidence reviewed here, we believe that L. ferulaceum and L. diffusum (comprising Limonium sect. Myriolepis) are morphologically distinct from other taxa in Limonium (including other taxa currently subordinated to L. subg. Myriolepis) and should be regarded as a different genus formally recognised below because it appears to be more closely related to taxa outside Limonium than to the members of this genus. Both Limonium sects. Siphonantha and Polyarthrion should be treated at least for the moment as sections within L. subg. Limonium, to which they show the greatest morphological, karyological and phytochemical affinities. The genus Limonium as a whole needs further taxonomic study that may result in the re-arrangement of several taxa. Nevertheless, without a more comprehensive study, we believe that attempts to reclassify the genus Limonium are, at this moment, premature.

- Myriolepis (Boiss.) Lledó, Erben & M. B. Crespo, stat.
 nov. Basionym: Statice sect. Myriolepis Boiss. in DC., Prodr. 12: 667. 1848. = Limonium sect. Myriolepis (Boiss.) Sauvage & Vindt, Fl. Maroc 1: 47, 74 (1952).
- Limonium subgen. Myriolepis (Boiss.) Pignatti in Bot. J. Linn. Soc. 64(4): 361. 1971 [excl. Statice sect. Polyarthrion Boiss., loc. cit., atque S. sect. Siphonantha Boiss., op. cit.: 668. 1848]. – Statice subgen. Siphonantha (Boiss.) Pax sect. Eusiphonantha Pax in Engl. & Prantl, Nat. Pflanzenfam. 4(1): 125. 1891, pro min. parte, typo

excluso. Lectotypus (hic designatus): *Statice ferulacea* L., Sp. Pl. ed. 2: 396. $1762 \equiv Limonium feru$ *laceum*(L.) Chaz., Dict. Jard., Suppl. 2: 35. 1790 =*Myriolepis ferulacea*(L.) Lledó, Erben & M. B.Crespo.

Dwarf shrubs, glabrous. Basal leaves absent or present only at springtime, small, subulate, one-nerved. Stems numerous, usually prostrate or ascendent, densely covered with subimbricate, spirally arranged and long acuminate or mucronate whitish-hyaline scales. Flowering stems with many sterile branches. Spikelets one-flowered, at the top of very short branches that are hidden by two whitish-hyaline scales; inner bract convolute and completely concealing the calyx; middle and outer bracts almost completely membranous, whitishhyaline, long aristate or mucronate. Calyx slender without prominent ribs, weakly 5-nerved, with nerves ending in a short mucro or a long arista, without limb. Petals fused in the lower half to two-thirds, forming a tube much longer than the calyx. Fruit a circumscissile capsule. Chromosome number 2n = 16, all more or less metacentric.

Ecology and distribution: The only two known species grow on periodically submerged soils in salt marshes and saline steppes of coastal areas. They are discontinuously distributed along the central and western coast of the Mediterranean region.

Myriolepis ferulacea (L.) Lledó, Erben & M. B. Crespo, comb. nov. Basionym: Statice ferulacea L., Sp. Pl. ed. 2: 396. 1762. – Lectotypus (designated by Erben, 1979: 398): LINN 395.20. = Limonium ferulaceum (L.) Chaz., Dict. Jard., Suppl. 2: 35. 1790. Ind. loc.: "Habitat in Barbaria, Lusitania, Hispania". Icon: Reichb., Icon. Fl. Germ. Helv. 17, pl. 1147, I 1–2. 1855.

Diagnostic characters: Leaves absent; spikelets 5–7 mm, densely crowed at the apex of the flowering branches; outer bract with a long arista 1–2.5 mm; inner bract 5.5–6.5 mm, truncate and hyaline-membranous in the apical third; calyx 4.5–5 mm, glabrous, with long aristate teeth; corolla 5-6.5 mm in diameter; petals 9–10 mm long, the lower 2/3 fused to form a tube.

Distribution: Western Mediterranean Region. Coastal areas of Sicily, the Balearic Islands, southern France, southwestern and northeastern Iberian Peninsula, northern Morocco and Tunisia.

Myriolepis diffusa (Pourr.) Lledó, Erben & M. B. Crespo, *comb. nov.* Basionym: *Statice diffusa* Pourr.,

Mém. Acad. Sci. Toulouse 3: 330. 1788. – Lectotypus (hic designatus vide etiam Aymonin, 1963): "(France) Le long de la mer", "*Statice diffusa* Pour." (LY – Herb. Pourret). \equiv *Limonium diffusum* (Pourr.) Kuntze, Revis. Gen. 2: 395. 1891. Ind. loc.: "A la mer, à Gruissan, Ste. Lucie, la Nouvelle, & c." Icon: Reichb., Icon. Fl. Germ. Helv. 17, pl. 1147, II 3–4. 1855.

Diagnostic characters: Leaves present only in the springtime, vestigial, small, subulate, one-nerved, $4-14 \times 0.3-1.0$ mm, withered at the anthesis; spikelets 3-3.5 mm, loosely disposed along flowering branches; outer bract 2.5–3.0 mm with a short mucro up to 0.5 mm; inner bract 3.4–4.0 mm, oblique truncate and hyaline-membranous only at the apex; calyx 2.5–3.5 mm, shortly and laxely pubescent, with short mucronate teeth, corolla 3–4 mm in diameter; petals 6–7 mm, fused in the lower half.

Distribution: Western Mediterranean Region. Coastal territories of southeastern France, the Atlantic coast of southwestern Iberian Peninsula and northern Morocco.

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