

Taxonomy, phylogeny and biogeography of *Limonium* sect. *Pteroclados* (Plumbaginaceae), based on morphological data

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Limonium Mill. sect. *Pteroclados* (Boiss.) Bokhari (Plumbaginaceae Juss.) was surveyed in this study. Morphology was used for investigating taxonomy as well as for making a cladistic analysis containing 18 ingroup taxa. The two previously recognized subsections *Nobiles* and *Odontolepidae* were found to constitute two sister groups. *Limonium mouretii* (Pit.) Maire shares synapomorphies with both subsections and is positioned as sister group of *Limonium sinuatum* (L.) Mill. *s.l.* plus *L. lobatum* (L. f.) Kuntze but with weak support. Based on the results of the cladistic analyses, a single introduction of a common ancestor to *Limonium* sect. *Pteroclados* subsect. *Nobiles* into the Canary Islands is postulated. Comparisons with cladistic and biogeographical studies of other Macaronesian flowering plant groups were made. An identification key to the taxa, descriptions and discussions on the taxonomy is provided. Morphological differences were found to be minor between *Limonium sinuatum*, *L. bonduellei* (T. Lestib.) Kuntze, and *L. beaumierianum* (Maire) Maire and they are hence suggested to be recognized as subspecies under *L. sinuatum*. © 2004 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2004, 144, 461–482.

ADDITIONAL KEYWORDS: Canary Islands – identification key – *Limonium sinuatum* – *Nobiles* – *Odontolepidae*.

INTRODUCTION

The Caryophyllid family Plumbaginaceae has been subject to a handful of studies since it was established as sister group of Polygonaceae Juss. in the large *rbcL*-based angiosperm phylogeny by Chase *et al.* (1993). Lledó *et al.* (1998) used 40 ingroup terminals, of which 18 were from Plumbaginaceae, when analysing intrafamilial relations of the Caryophyllids. One result obtained by Lledó *et al.* (1998) was that long recognized Plumbaginaceae subfamilies, namely the Plumbaginoideae Burnett and Statioideae Kostel., came out as strongly supported sister groups. Subsequently, Lledó *et al.* (2001) showed that *Limoniastrum* Heist. ex Fabr. *s.l.* is paraphyletic when using sequences from the plastid regions *rbcL* and *trnL-F*. More recently, Lledó *et al.* (2001) scrutinized subfamilial and tribal limits of Plumbaginaceae with an emphasis on systematic position of the Asian mangrove plant *Aegialitis* R. Br. The latter study was based on both molecular

and morphological data using three representatives of Polygonaceae as outgroup. Again, both subfamilies were well-supported clades, and *Aegialitis* constitutes the sister group of the rest of Statioideae. Despite the efforts of Lledó *et al.* (1998, 2000, 2001) many uncertainties concerning generic taxonomy of the Statioideae remain. Most of these problems are linked to delimitation and circumscription of the large genera *Acantholimon* Boiss. and *Limonium*, from which many small genera have been segregated (Linczevski, 1968, 1971, 1979, 1985).

In connection with the study of generic boundaries within the Statioideae (Lledó *et al.*, 2001) it became clear that taxonomy is also insufficiently studied within some putative clades. One example is *Limonium* sect. *Pteroclados*, currently with 18 recognized species. Boissier (1848) enumerated characteristics such as winged or un-winged stems, calyx with straight insertion and an expanded, plicate limb, pale yellow corolla, and circumscissile fruits for this distinctive taxon. For a further 80 years, *Limonium* sect. *Pteroclados* was treated under *Statice* L., a generic

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name subsequently vanishing into synonymy in favour of the conserved names *Limonium* and *Armeria* (Lledó, Erben & Crespo, 2003). Boissier (1848) divided *Statice* sect. *Pteroclados*, at that point containing 11 species, into two somewhat poetically named subsections (Bokhari, 1972), namely *Limonium* sect. *Pteroclados* subsect. *Odontolepidae* occurring in the Mediterranean and north Africa, and *Limonium* sect. *Pteroclados* subsect. *Nobiles* confined to the Canary Islands. This division was based on cuspidate inner bracts and conspicuous erect, leaf-like stem wing extensions in *Limonium* sect. *Pteroclados* subsect. *Odontolepidae*, and truncate inner bracts and more inconspicuous wing extensions in *Limonium* sect. *Pteroclados* subsect. *Nobiles*. Lledó *et al.* (1998) gained strong support for a clade consisting of three *Limonium* sect. *Pteroclados* species in their cladistic analysis of Plumbaginaceae using molecular data. Included therein was one species each of *Limonium* sect. *Pteroclados* subsect. *Nobiles* and *Limonium* sect. *Pteroclados* subsect. *Odontolepidae*, as well as *Limonium mouretii*, the latter being the only species that shares characters with both the other taxa. This rather limited sampling covers the morphological variation within *Limonium* sect. *Pteroclados* well enough for arguing that the group is monophyletic. Although *Limonium* sect. *Pteroclados* also are readily recognized morphologically, they do not display a single unique character, but are rather diagnosed by homoplastic putative synapomorphies that occur in other taxa of Staticoideae as well as synapomorphies not found in all of the species. One such feature is the winged stem, which is also found in *Goniolimon* Boiss., *Psylliostachys* (Jaub. & Spach) Nevski, and *Limonium* sect. *Ctenostachys*. Since Lledó *et al.* (2001) obtained a phylogeny in which the three stem-winged terminals *Limonium sinuatum*, *Psylliostachys* and *Goniolimon* were placed at positions making it most parsimonious to explain the stem wings as three parallel gains, the winged stems might be interpreted as a synapomorphy for *Limonium* sect. *Pteroclados* after all. By contrast, the vividly blue calyx is absent in *Limonium mouretii*, *L. bonduellei* and *L. lobatum*. Furthermore, Bokhari (1972) mentioned the pinnate venation of the rosette leaves as distinguishing *Limonium* sect. *Pteroclados*, but he was aware of similar venation in *Limonium* sect. *Limonium*. It might be noted that the monophyly of such a notable flowering plant clade as the Ericales is rarely questioned, but they share the same fate in terms of morphological synapomorphies as do *Limonium* sect. *Pteroclados* (Anderberg, Rydin & Källersjö, 2002).

Various sources mention problems with species delimitation in *Limonium* sect. *Pteroclados*, such as between *Limonium bourgaei* (Webb ex Boiss.) Kuntze and *L. puberulum* (Webb) Kuntze (Bramwell & Bram-

well, 1994; Schönfelder & Schönfelder, 1997). These species were also considered to be indistinguishable by Bokhari (1972). Bramwell & Bramwell (1994) treated *L. brassicifolium* (Webb & Berthel.) Kuntze and *L. macropterum* Webb & Berthel. as separate species, whereas Schönfelder & Schönfelder (1997) followed the interpretation by Kunkel (1980) acknowledging two subspecies under *L. brassicifolium*. The first authors argued that there were morphological differences between the taxa. Bokhari (1972) noted differences in petiolar anatomy between *Limonium brassicifolium* and *L. macropterum*, and argued that the anatomical differences were large enough to imply specific status for the two taxa. Bokhari might have been misled to some extent, because he mentioned the two taxa as being sympatric although they are confined to different islands. Another pair of species has been claimed to be problematic, or rather, conspecific, namely *Limonium preauxii* (Webb & Berthel.) Kuntze and *L. perezii* (Stapf) C. E. Hubb. (Bramwell & Bramwell, 1974). The sometimes weedy *Limonium sinuatum* was expanded by Sauvage & Vindt (1952) to include *L. bonduellei* and *L. beaumierianum*, but several other infraspecific taxa have also been described (Sauvage & Vindt, 1952; Täckholm & Boulos, 1972).

It has been claimed that insular taxa might be morphologically very different compared with their mainland counterparts, and that morphologically based studies therefore might suffer from severe difficulties (Francisco-Ortega *et al.*, 2001). One example given by Francisco-Ortega *et al.* (2001) comes from the Asteraceae–Madiinae (Baldwin *et al.*, 1991), but nonetheless Baldwin (1996) discussed morphological characters (synapomorphies) in support for the Pacific silversword alliance and their close relation to American west coast taxa, although these plants admittedly are very dissimilar in external morphology.

The distribution of *Limonium* sect. *Pteroclados* is Macaronesian–Mediterranean–Iranoturanian. This is particularly interesting because the old view that Macaronesian woodiness is ancestral in various groups and that Macaronesian taxa may constitute Tertiary relicts (Bramwell, 1972; Sunding, 1979; Mai, 1989) is either sustained (Ray, 1995; Bremer, 1996), but also contradicted by various investigations (Barber *et al.*, 2000; Helfgott *et al.*, 2000; Mort *et al.*, 2002). Moreover, recent cladistic studies on Mediterranean–Macaronesian flowering plant groups have accumulated evidence pointing towards single origins for Canarian clades (Böhle, Hilger & Martin, 1996; Francisco-Ortega, Jansen & Santos-Guerra, 1996; Panero *et al.*, 1999; Barber *et al.*, 2000; Mort *et al.*, 2002). A single introduction of a clade was also postulated for two sister species within *Saxifraga* L. (Vargas, Morton & Jury, 1999b), although involving the Madeiran islands. By contrast, some clades display other biogeo-

graphical patterns, in which more than one introduction to the Canaries (Bohs & Olmstead, 2001; Goertzen *et al.*, 2002) or dispersal from these islands are hypothesized (Mort *et al.*, 2002). Even more complicated biogeographical patterns have also been discerned, for example, in the cosmopolitan *Ilex* L. (Aquifoliaceae; Cuenoud *et al.*, 2000), in which the two Macaronesian species do not form a clade, and show disparate sister group relationships. The same might be the case for *Hedera* L. (Vargas *et al.*, 1999a) but a biogeographical scenario including the Canarian *H. canariensis* Willd. could not be sufficiently elucidated. Yet another distribution pattern is shown by the laurel forest endemic *Ixanthus viscosus* (Aiton) Griseb. (Gentianaceae; Thiv, Struwe & Kadereit, 1999), in which a sole, woody, Canarian species is the sister group of the Mediterranean annuals of the genus *Blackstonia* Huds.

All recent studies rest on molecular evidence but a morphologically based cladistic analysis of the rather small group *Limonium* sect. *Pteroclados* will also contribute to the understanding of Canary Islands biogeography.

The principal aim of this study was to discuss the taxonomy, to provide a working key and to present a phylogeny of *Limonium* sect. *Pteroclados*. Another aim was to see if the phylogeny corresponds to a single origin of the Canarian species, and if the taxa on the African mainland and in the Mediterranean show a distinctive distribution pattern.

MATERIAL AND METHODS

This study is based mainly on examination of herbarium sheets borrowed from BM, K and S (one sheet is to be filed in UPS). Types for most taxa have not been investigated and the nomenclature is hence not scrutinized in detail. Living material of *Limonium sinuatum* and *L. arborescens* (Brouss.) Kuntze located in the Bergius Botanic Garden, Stockholm, was also studied. In addition, naturalized populations of *Limonium sinuatum*, as well as some ornamentally grown *Limonium fruticans* (Webb) Kuntze were studied during a field trip to the Western Cape in South Africa in October 2001. Most species have been here in the same way as in Lledó *et al.* (2001), but in cases where there was very limited material, no anatomical preparations were made. Leaves were transversely sectioned at three different positions, at the middle of the petiole, and middle part of the lamina across both the midvein and the margin. Branches were transversely sectioned a few centimetres below the inflorescence as well as within the inflorescence. The sections were stained with safranin dissolved in ethanol and/or methylene blue and subsequently mounted on microscope slides in glycer-

ine. When describing the ultimate inflorescence parts, the spicules, the terminology and interpretations of Schoute (1935) are adopted. The terminology for calyx characters is the same as in Lledó *et al.* (2001).

In the species descriptions, rosette leaves are usually described. If a taxon is stated to be generally pubescent, it implies that most described parts are hairy, i.e. stems, rosette and cauline leaves, wings, prophylls and calyx.

The characters used in the cladistic analyses are in general based on my own observations of the material, but limited information from Bokhari (1972) was also used.

The characters are presented and discussed below, and the assembled data matrix is displayed in Table 1.

The terminals. Species of *Limonium* sect. *Pteroclados* subsect. *Nobiles* are confined to parts of one or sometimes two islands of the Canary Islands. Consequently, all these species are listed as 'endangered' or 'vulnerable' by the IUCN (Walter & Gillett, 1998) and it is strongly recommended that they should not be collected. This is also the main reason for the present study despite only a single specimen having been examined for a few species. All species currently recognized in *Limonium* sect. *Pteroclados* subsection *Nobiles* (Bramwell & Bramwell, 1994) were included as terminals (see also notes under respective species). Santos & Fernández (1983) convincingly argued that *Limonium rumicifolium* (Svent.) G. Kunkel & Sunding merely represents a taxonomic synonym of *L. preuxii* (Webb & Berthel.) Kuntze, and these taxa were merged into a single terminal. By contrast, both *L. bourgaei* and *L. puberulum* (Webb) Kuntze were included as terminals because they differ in leaf morphology, although they were claimed to differ only in height by Bramwell & Bramwell (1994) and Schönfelder & Schönfelder (1997).

It should be pointed out that *Pteroclados* is recognized both as *Limonium* subgenus *Pteroclados* (Boiss.) Pignatti (Pignatti, 1971, for subsequent application in Flora Europaea; Erben, 1993), and *Limonium* section *Pteroclados* (Boiss.) Bokhari (Labbe, 1962; Harborne, 1967; Bokhari, 1972; Rechinger & Schiman-Czeika, 1974; Ingrouille, 1984). The latter approach is always used when it is found necessary to divide *Limonium* sect. *Pteroclados* further into the two groups *Limonium* sect. *Pteroclados* subsect. *Nobiles* and *Limonium* sect. *Pteroclados* subsect. *Odontolepidae* when one discusses the Canarian species (Kunkel & Sunding, 1967; Bokhari, 1972). The choice between different infrageneric levels like subgenus and section must be considered arbitrary. A formal treatment of *Nobiles* and *Odontolepidae* as taxa under *Limonium* subgenus *Pteroclados* has never been carried out. Hence *Ptero-*

Table 1. Data matrix for *Limonium* sect. *Pteroclados*. Missing or unknown states are scored as ?, inapplicable states are scored as -. Polymorphisms are coded as follows: A = 0 & 1, B = 0 & 1 & 2, C = 0 & 3, D = 0 & 2, E = 1 & 2, F = 3 & 4, and G = 4 & 5

	00000	00001	11111	11112	22222	22223	3
	12345	67890	12345	67890	12345	67890	1
<i>arborescens</i>	00011	1A000	A0121	00101	00110	11101	2
<i>beaumierianum</i>	10232	04101	?0232	11011	00001	20100	1
<i>bonduelei</i>	10E32	0G101	?0232	11011	00001	201A0	1
<i>bourgaei</i>	00021	?1020	10111	001?0	11000	10111	2
<i>brassicifolium</i>	02021	1E0B0	11121	00100	11010	10101	2
<i>fruticans</i>	00021	0A000	01121	00101	00110	11101	2
<i>imbricatum</i>	02121	05000	12121	00100	11010	1A101	2
<i>lobatum</i>	11E22	04101	0123E	10000	00001	21110	1
<i>macrophyllum</i>	01021	0C000	01131	00100	11110	10101	2
<i>macropterum</i>	02021	1E0B0	12131	00100	11010	1A10A	2
<i>mouretii</i>	00020	AF101	00201	00011	01110	01010	0
<i>perezii</i>	000D2	?00B0	00122	0011A	A0110	101A1	2
<i>preauxii</i>	00021	?0000	1?111	0010A	A0110	10100	2
<i>puberulum</i>	00021	00020	10111	00100	11010	10111	2
<i>redivivum</i>	01021	-00E0	1?111	00100	11110	1110-	2
<i>sinuatum</i>	0A232	?G101	?0232	11011	00001	20100	B
<i>spectabile</i>	00021	0G000	-2E11	00100	11110	11101	2
<i>sventenii</i>	00121	?0000	11121	00101	00110	11101	2
OUT, <i>vulgare</i>	00000	00000	00--0	00000	00000	00000	0

clados is treated as *Limonium* sect. *Pteroclados* in this paper.

In order to simplify discussion of characters, the Canarian endemics are collectively called 'Nobiles' and the rest of the species 'Odontolepidae'.

The outgroup. When selecting an appropriate outgroup it is important that it unequivocally belongs outside the ingroup. Preferably it should be the sister group, which is morphologically comparable with the ingroup terminals. These criteria were fulfilled by *Limonium vulgare* Mill., as evidenced by the analyses made by Lledó *et al.* (1998, 2001), and consequently this species was used as outgroup.

The analyses. The cladistic analyses were undertaken using the two programs PAUP 4.0 (Swofford, 2000) and NONA (Goloboff, 1996, spawned in Winclada, Nixon, 1999). The settings in PAUP were as follows. All characters were unordered and equally weighted, multistate character polymorphisms were interpreted as uncertainties, and collapsing of zero minimum length branches (amb-) was used. This minimizes the number of equally parsimonious, but often redundant, trees, and the calculation of uninformative multistate character steps on terminal branches, respectively. The data set was analysed with the

branch and bound procedure. The settings in NONA were chosen as to be as compatible as possible with those in PAUP, i.e. all characters were unordered and equally weighted, multistate character polymorphisms were interpreted as uncertainties, and collapsing of zero minimum length branches (amb-) was used. The NONA analysis used the following commands: hold 10 000, hold/500 and mult*500. This corresponds to a heuristic search followed by TBR branch swapping. Further analysis of a small data set like this with additional TBR branch swapping (MSWAP) is not likely to produce further equally parsimonious trees, and this was the case here. Bremer support (Källersjö *et al.*, 1992) was calculated in PAUP simply by saving trees of one additional step in length. A parsimony jackknife analysis (XAC, Farris, 1997) was also used to estimate support for the achieved clades, and here the following settings were used: 1000 replicates, each with branch-swapping and ten random addition sequences.

Terminology for climatic regions and ecological zones follows Francisco-Ortega *et al.* (1996).

MORPHOLOGY

The following characters were used in the cladistic analyses.

Life form

It was impossible to distinguish shrubs or shrublets from perennial herbs and hence only annuals are distinguished from the rest.

Char. 1. Perennial herbs–shrublets–shrubs (0); annuals (1).

Stems. As mentioned above, the name *Pteroclados* (Boissier, 1848) refers to the winged stems, or literally, branches. As can be seen in the descriptions, all the species have stem wings, but they are inconspicuous in many cases, or even absent from some internodes on some exemplars. In keys to the Canarian species many of these are interpreted as wing-less (Bramwell & Bramwell, 1974, 1994). The last order inflorescence parts, the spicules (Schoute, 1935), are aggregated into diaspores (disseminules), and the branch below the spicule is therefore called the ‘diaspore branch’. The diaspores are efficiently detached from the main stem by means of a conspicuous abscission zone (Lledó *et al.*, 2001), a feature characteristic for many genera of the Staticoideae, but not in other sections of *Limonium*. Occasionally there is an abscission zone at the joint between the main stem and a larger branch, i.e. branches other than those leading directly to spicule aggregates. The inflorescences are variously branched, but it is common that the branches to each diaspore are gradually shorter towards the tip of the main stem.

Char. 2. Main stem wings absent or up to 1 mm broad (0); wings 2–4 mm broad (1); wings 12–20 mm broad (2).

Limonium sinuatum, *L. beaumierianum* (Maire) Maire in Jahand. & Maire, *L. bonduellei* and *L. lobatum* in general have conspicuous linear to subulate extensions of the wings at the nodes. Although these might be inconspicuous or absent in especially small specimens of the annual species, they have been coded as present in all the four terminals mentioned above.

Char. 3. Wing extensions at main stem nodes absent (0); wing extensions at main stem nodes inconspicuous, sometimes up to 7 mm (1); wing extensions at main stem nodes linear–subulate, mostly 15–60 mm (2).

Both the main stems and diaspore branches have wings generally placed in one, two, three or four lines in an abaxial, adaxial and lateral position relatively to the cauline leaves. As the position of the wings differs between the main stem and diaspore branch, it is treated as two separate characters.

Char. 4. Wings at main stem nodes absent (0); wings abaxial from leaf (1); wings abaxial and adaxial from leaf (2); wings abaxial, adaxial and bilateral from leaf (3).

In all species except *L. mouretii* there are wings (albeit inconspicuous in some species) along the

diaspore branch situated adaxially to the bract of the first spicule in each of the two rows of spicules. In the ‘*Odontolepidae*’ species (except *L. mouretii*) there is also a conspicuous wing at a lateral position to both bracts of the first spicules at each side of the spicule-bearing axis. This wing is much larger than the other two and is also more conspicuously extended.

Char. 5. Wings along diaspore branches absent (0); wings mainly adaxial to bract of first spicule (1); wings adaxial and lateral to bract of first spicule (2) (Fig. 1A).

The only useful character after studying cross-sections of stems was the number of layers of parenchyma cells between the fibre ring and the chlorophyllous cells towards the periphery of the stem. This proved to be not coupled to the diameter of the stems.

Char. 6. Number of layers of parenchyma cells between fibre ring and chlorophyllous cells in cross-section of main stem, 0–3 (0); 6–8 (1).

Leaves. Bokhari (1972) claimed a few leaf characters as discrete between ‘*Odontolepidae*’ and ‘*Nobiles*’, but only the morphology of the leaf blade midvein agreed with Bokhari’s reported observations. Note that some species are polymorphic for leaf blade shape (Char. 7).

Char. 7. Leaf blade entire with entire margins (0); entire, but shallowly sinous-lobed towards the base, lyrate (1); deeply lobed towards the base (2); sinuate (3); deeply lobed (4); pinnatisect (5).

In ‘*Odontolepidae*’ most specimens have large, often flattened hairs, and they are especially abundant along the margin of the leaves (rosette leaves, cauline leaves, bracts and prophylls). In *L. sinuatum* there are often smaller hairs present as well.

Char. 8. Leaves, bracts and prophylls without large, flattened hairs, though often with smaller hairs (0); leaves, bracts and prophylls with often-flattened hairs (as well as with or without smaller hairs), up to 2 mm long (1).

Boissier (1848) mentioned stellate hairs under *Limonium bourgaei* and *L. puberulum*. Bokhari (1972) also established this, but he showed that these hairs are tufted uniseriate hairs and not branched, stellate hairs. After examining all taxa it became clear that Bokhari was right, but also that the leaf hairs either are simple, in pairs or 3–5 together. Furthermore, these hairs are also present in *L. perezii*, *L. redivivum* (Svent.) G. Kunkel & Sunding and *L. brassicifolium*, and especially along the leaf margins in the first two species. All these terminals are coded as polymorphic.

Char. 9. Leaf hairs only single (0); some hairs double (1); some hairs in threes–fives (2).

Both the ingroup and the outgroup have pinnately veined rosette leaves. Bokhari (1972) reported a special case of pinnate venation from ‘*Odontolepidae*’, namely that the midvein consists of three larger bun-

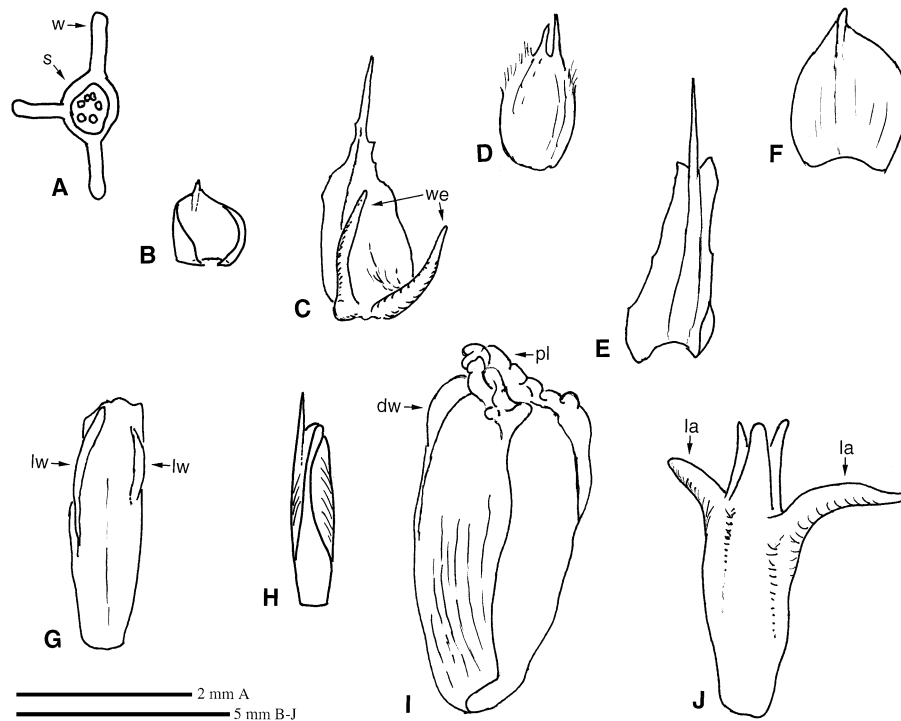


Figure 1. Morphology of certain parts of *Limonium* sect. *Pteroclados*. A. Cross-section of diaspore branch, w = diaspore wing, s = stem with stele indicated. B. Spicule bract. C. Spicule bract, we = wing extension. D. Two-tipped bract of first spicule in a diaspore. E. Aristate, emarginate α 1-prophyll. F. Mucronate, rounded α 1-prophyll. G. α 2-prophyll with unequal, dorsal lateral wings = lw. H. Aristate α 2-prophyll. I. β -prophyll, pl = plicate apical margin, dw = dorsal wing. J. β -prophyll, la = lateral appendages. A: *Limonium sinuatum* ssp. *beaumierianum*, Maire 3072 (S); B: *Limonium arborescens*, Sventenius 155 (S); C, E, H: *Limonium sinuatum* ssp. *sinuatum*, Samuelsson 1191 (S); D: *Limonium sinuatum* ssp. *bonduellei*, Chevallier s. n. (S); F, G: *Limonium brassicifolium* ssp. *brassicifolium*, Santesson 26768 (S); I: *Limonium macrophyllum*, Asplund 1316 (S); J: *Limonium lobatum*, Anderberg 413 (S).

dles and that the two laterals give rise to the secondaries. This was verified in the present study, although it was not so evident in every single specimen.

Char. 10. Secondary veins in leaf blades of rosettes arise directly from the midvein (0); secondary veins arise mainly from two laterals (1).

When studying many species from the *Statioideae* (Lledó *et al.*, 2001) it became obvious that it is most common with an evident whitish rosette leaf margin. This proved to vary among the species of *Pteroclados*, but also within some of the species.

Char. 11. Rosette leaves marginally with a row of *c.* 10 hyaline cells (0); with a row of *c.* 4 hyaline cells (1).

Transverse sections of the rosette leaf midrib revealed collateral bundles apart from the main, larger ones in the central part of the midrib. These smaller bundles were absent or few in some species, but many in a ring-like pattern, or merely scattered, in others.

Char. 12. Rosette leaf midrib with few or no collateral bundles (0); several in 1–2 rings (1); several scattered (2).

Inflorescences. The last order inflorescence parts, the spicules, are distichous in lax to dense aggregates which detach from the plant and obviously act as diaspores. Each spicule arises in the axil of a bract and if the spicules are densely packed the bracts are more or less asymmetric and overlap each other. In each spicule, there is a bract-like leaf, considered as a prophyll to the first flower in the spicule (α 1-prophyll of Schoute, 1935). Both these leaves resemble reduced cauline leaves in all aspects. The first flower in each spicule has a second very conspicuous prophyll, a β -prophyll (Schoute, 1935). The β -prophyll envelopes the rest of the spicule, but the perianth and especially the corolla protrude well above the apex of the β -prophyll. The spicules in all ingroup species are three- or four-flowered and the second, third and fourth flowers have just one prophyll each, considered as α 2-, α 3- and α 4-prophylls, respectively, by Schoute (1935). Apart from the β 1-prophyll no further β -prophylls (to the second, third and fourth flowers) develop. Whereas the α 1-prophyll is similar to the spicule bracts and the cauline leaves,

the inner ones (α 2-, α 3-, etc., prophylls) are narrowly oblong and approach the conspicuous β -prophyll in length, but not at all in shape and size. In *Limonium redivivum* the inner α -prophylls have a narrow showy margin, similar to that of the β -prophylls. This is also found in *L. perezii* but is much less conspicuous and is absent in the rest of the species. *Limonium sventenii* A. Santos & M. L. Fernández has two conspicuous lateral wings on the α 2- and α 3-prophylls. These laterals are present to varying extent in all species, being merely bulge-like in some. These prophylls are 3-lobed apically, and the lobes do not necessarily correspond to the fold lines occurring in younger stages. In most 'Odontolepidae' species these protrusions continue into long aristae. Some of the characters below are inapplicable in *L. vulgare* because it does not have its spicules arranged into distinct diaspores.

Char. 13. 1–4 spicules per diaspore (1); ≥ 6 spicules per diaspore (2).

Char. 14. Diaspore branch length 4–7 mm (1); (10–)12–13(–15) mm (2); 25–60 mm (3).

Char. 15. Spicule bract apically rounded, entire (0); mucronate (Fig. 1B) (1); conspicuously aristate (Fig. 1C) (2).

Char. 16. Bract to the first spicule with single tip, entire (0); bracts to the first spicule often two-lobed and also often two-tipped (Fig. 1D) (1).

In *Limonium beaumerianum*, *L. bonduellei* and *L. sinuatum* the spicule bracts bear two lateral, subulate, thorn-like, hard, pointed and curved wing extensions. These structures are possibly homologous with the wing extensions on the stems and should easily adhere to dispersal agents but also pack the spicules tightly within the diaspore.

Char. 17. Lateral wing extensions on spicule bracts absent (0); conspicuous, thorn-like (Fig. 1C) (1).

Char. 18. α 1-prophylls emarginate (Fig. 1E) (0); entire (rounded-subtruncate, Fig. 1F) (1).

Char. 19. α 2-prophylls more or less truncate (0); α 2-prophylls mucronate to aristate (Fig. 1H) (1).

Char. 20. β -prophylls with an apical scarious margin (0); β -prophylls without an apical scarious margin (1).

Char. 21. β -prophylls not showy (0); β -prophylls apically showy, coloured like the calyx (1).

Char. 22. β -prophylls apically smooth (0); β -prophylls apically plicate (Fig. 1I) (1).

Most 'Nobiles' species have a conspicuous dorsal wing on the β -prophylls, but it is also present in *L. mouretii*.

Char. 23. β -prophylls without a dorsal wing (0); β -prophylls with an apical, dorsal often fin-like wing (Fig. 1I) (1).

Char. 24. β -prophylls with inconspicuous veins abaxially (0); β -prophylls with conspicuous, coarse, often whitish parallel veins (1).

In all 'Odontolepidae' species except *L. mouretii* the β -prophylls have two lateral, hard and often subulate to anvil-shaped appendages. Although they are parts of a leaf they might be homologous to the wing extension on the stems. Together with the marked wing extensions on the spicule bracts they obviously act as adherents for efficient dispersal.

Char. 25. β -prophylls without lateral appendages (0); β -prophylls with two lateral subulate to anvil-shaped appendages (Fig. 1J) (1).

Char. 26. β -prophylls bifid, emarginate (0); β -prophylls apically entire (1); β -prophylls apically 3-lobed (Fig. 1J) (2).

Morphology of the calyx is very constant among all ingroup species, but *L. mouretii* differs markedly with its inconspicuous, not showy calyx, whereas *L. lobatum* has markedly five-lobed calyx with primary ribs extended very far above the limb, and the lobes arise between the primary ribs. The calyx is slightly zygomorphic at the base with five larger primary ribs and five slightly smaller secondary ribs (Fig. 2). Two or three vascular strands are present in the primary ribs and the secondary ribs have one or two strands. A continuous layer of fibres is situated between the epidermis and the vascular strands. The same pattern is present in other Staticoideae taxa with a similar calyx, such as *Acantholimon* (my pers. observ.).

Char. 27. Calyx hairy (0); calyx glabrous (1).

Char. 28. Calyx not showy (0); calyx showy (1).

Char. 29. Primary ribs in calyx not extended above the limb (0); primary ribs in calyx extended well above the limb (1).

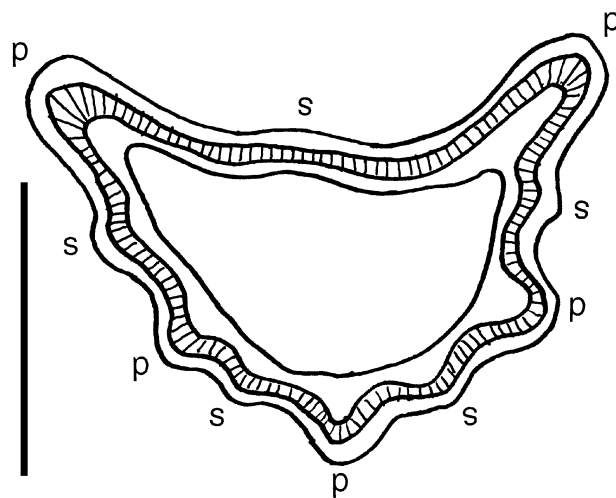


Figure 2. Cross-section of lower part of calyx of *Limonium brassicifolium* ssp. *macropterum*. p = primary rib, s = secondary rib, hatched area = continuous fibre layer. Scale bar = 0.5 mm. Asplund 1316 (S).

Char. 30. Secondary ribs not extending into the limb, above the tube–limb junction (0); secondary ribs extending well into the limb (1).

Limonium sinuatum is stated in various floras to have yellow or pinkish corolla, but most of the naturalized populations in the Western Cape have a white corolla (my pers. observ.), and this species possesses all three states.

Char 31. Corolla pink (0); yellow (1); white (2).

RESULTS

The analyses using both programs produced two equally parsimonious cladograms, with a length of 77 steps, a consistency index (CI) of 0.57 and a retention index (RI) of 0.76. The strict consensus tree is rather collapsed (Fig. 3), but Boissier's subsections 'Nobiles' and 'Odontolepidae' (without *L. mouretii*) are monophyletic, the first with a reasonable support (73%) and the latter with high support (90%). Five nonhomoplastic characters unite the 'Odontolepidae' species (excl. *L. mouretii*), namely the conspicuous wing extensions at the stem nodes (char. 3), the often two-pointed bract to the first spicule (char. 16), the β -prophylls with lateral appendages (char. 25), a 3-cleft apex (char. 26) and the yellow corolla (char. 31). It should be emphasized that *Limonium sinuatum* has all three corolla colours used in character 31. The following characters diagnose the 'Nobiles' species: diaspores with 1–4 spicules (char. 13), apically entire α 1-prophylls (char. 18) and β -prophylls (char. 26), as well as the white corolla (char. 31). *Limonium mouretii* is united with the 'Odontolepidae' species by four non-homoplastic characters but the node in question has low support.

The remaining clades are rather poorly supported, even those recognized in the strict consensus tree (Fig. 3). In the strict consensus tree *L. bourgaei* +

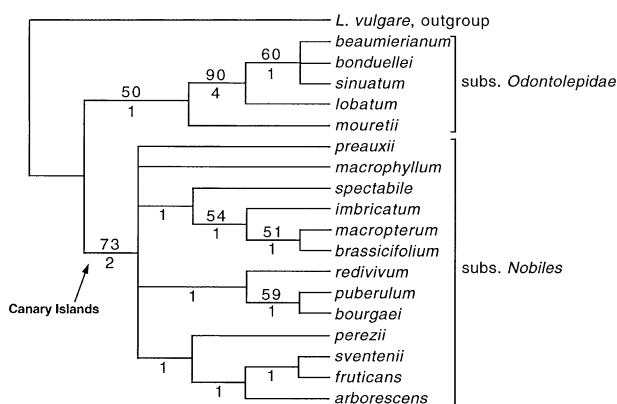


Figure 3. Strict consensus tree resulting from the cladistic analyses. Figures above internodes denote jackknife support values, the figures below internodes denote Bremer support.

L. puberulum + *L. redivivum* are united by their seemingly stellate hairs (char. 4), but such hairs also occur in *L. brassicifolium* and *L. macropterum*. In the analysis, however, the latter two have not been assigned this character, because they are coded as polymorphic. *Limonium sinuatum*, *L. beaumierianum* and *L. bonduellei* share two non-homoplastic characters, namely the often four wings along the stems (char. 4), and spicule bracts with conspicuous lateral wing extensions (char. 17). The analyses do not resolve the relations between these three species but this is due to lack of phylogenetic information, rather than being caused by character conflict.

DISCUSSION

As was argued by Karis (1995) a few of the (multi-state) character states might be interpreted as partitions of one another, meaning that a multistate character should be treated as ordered in the analyses. Examples of such characters are 16, 17 and 23. However, the resulting topologies are identical when scoring all characters as unordered.

Limonium mouretii shares synapomorphies with both 'Nobiles' and 'Odontolepidae' and it takes just an extra step to make it sister group of 'Nobiles'. Characters shared with this clade are features of the β -prophylls, such as the dorsal fin-like wing, and the venation. It should be noted that a few plesiomorphic features are found only in *L. mouretii* of the ingroup, and examples are the apically bifid β -prophylls and the inconspicuous non-showy calyx. The last feature together with the very inconspicuous stem wings were obvious reasons for Sauvage & Vindt (1952) to place *L. mouretii* in *Limonium* section *Ctenostachys*. By contrast, the mode of branching with inflorescence-bearing shoots from most axils, as well as the very short diaspore branches must be interpreted as autapomorphies for *L. mouretii*. The low support for the 'Odontolepidae' plus *L. mouretii* despite the four non-homoplastic characters on this node might be explained by the many parallelisms on the *L. mouretii* and *L. lobatum* terminal branches. In other words, the non-homoplastic characters are contradicted by other characters.

Several *Limonium* sect. *Pterocladus* species have been described since Boissier's (1848) treatment, but only *Limonium mouretii* has been placed outside it. *Limonium bonduellei* is rather easily assigned to 'Odontolepidae', and the rest of the 'post-Boissier' species all come from the Canary Islands, and are readily placed in 'Nobiles'. It should be noted that Kunkel & Sunding (1967) enumerated *Limonium spectabile* (Svent.) G. Kunkel & Sunding under 'Nobiles', and not under 'Odontolepidae', where it was originally placed by Sventenius (1949).

Even though *Limonium bourgaei* and *L. puberulum* are very similar they differ, for example, in leaf shape, and for the time being they are kept as separate species. It is interesting to note, however, that the difference in height between these taxa, and which was used in keys (Bramwell & Bramwell, 1974, 1994), is not at all clear cut, because some specimens of *L. puberulum* attain 35 cm in length.

Limonium brassicifolium and *L. macropterum* differ by rosette leaf midrib anatomy (char. 12), diaspore branch length (char. 14), but *L. macropterum* is polymorphic for yet two other characters, namely calyx hairiness (char. 27) and secondary ribs extending well into the calyx limb (char. 30). Considering their distribution, close resemblance to one another, but at the same time their clear morphological differences from all other species, it is best to unite them under a single species, but keeping the two taxa as subspecies. Kunkel (1980) also proposed this. In addition, the presence of the seemingly stellate hairs might be interpreted as a synapomorphy (though homoplastic) for the two taxa, even though these hairs do not occur on all individuals.

In the two equally parsimonious cladograms the three terminals *sinuatum*–*bonduellei*–*beaumierianum* came out as a moderately supported clade (60%) but without resolution between them. Although *L. bonduellei* is readily distinguished from *L. sinuatum* and *L. beaumierianum* by its yellow calyx, this is not sufficient grounds for recognizing *L. bonduellei* as a species, especially given that the other two taxa are devoid of diagnostic characters. *Limonium beaumierianum* is not clearly delimited from *L. sinuatum* and might merely represent annual populations growing under harsh conditions in the Atlas Mountains. Consequently, the three taxa are recognized as subspecies under *Limonium sinuatum* in the taxonomic treatment.

BIOGEOGRAPHY

There are a few nodes sufficiently supported to allow a sound biogeographical hypothesis covering the entire clade. As the Canarian 'Nobiles' are monophyletic, regardless of whether *L. mouretii* is the sister group to them or to 'Odontolepidae', it is plausible to postulate a single introduction of a common 'Nobiles' ancestor into the Canaries. This is in line with other results (Helfgott *et al.*, 2000; Francisco-Ortega *et al.*, 1996, 1999, 2001), although other taxa occur in more or even all of the Macaronesian island groups. For example, Barber *et al.* (2000) also yielded a scenario with a large Canarian clade but with a single Madeiran species embedded deeply within the clade, and this could be explained a posteriori by dispersal. Another Macaronesian endemic, *Argyranthemum* Webb, was shown

to be monophyletic in a study by Francisco-Ortega *et al.* (1995), but with moderate support. In this case, the sister group of the Macaronesian clade (*Argyranthemum*) is complex, constituting a branch with three genera. Under these circumstances (Francisco-Ortega *et al.*, 2001) it might be appropriate to argue that a morphological study of an island clade having its closest relatives on a mainland might prove to be difficult. Even though 'Nobiles' are morphologically divergent if compared with 'Odontolepidae', problems in character state distinction were not insurmountable. The supposed double or even more introductions into the Canaries of *Olea europaea* L. subspecies might be explained by efficient bird dispersal of the fruits (Hess, Kadereit & Vargas, 2000).

The poor resolution and low support for clades within 'Nobiles' weaken attempts to decipher Canary Island biogeography, but some points can be made. It is often stated that the two eastern Canary Islands Fuerteventura and Lanzarote have a different climate from the western islands, because of the shorter distance to the African mainland (Bramwell, 1972), and that geology also differs between the island groups. Neither Fuerteventura nor Lanzarote reach much above 800 m in altitude, whereas the small western islands El Hierro and La Gomera have peaks around 1500 m, and the remaining western islands reach far above the latter altitude. The proximity to the African mainland together with the much narrower range of altitude may well be the cause for fewer taxa in different clades inhabiting Fuerteventura and Lanzarote, if compared with the number of taxa in the other islands. The opportunities for speciation are simply much less, when niches are fewer as a result of less variable habitat factors. This might explain why only one clade, namely *Limonium bourgaei* and *L. puberulum*, is found on the eastern islands. On the other hand, this reasoning does not explain why only one or two 'Nobiles' species are found on La Gomera, La Palma and El Hierro, notwithstanding the fact that the latter two islands are much younger, and that there simply has been insufficient time for either radiation or dispersal. It is notable that the species on La Gomera, *Limonium redivivum* and *L. brassicifolium*, are not found in the direct vicinity of one another in the strict consensus tree (Fig. 3). *Limonium brassicifolium* ssp. *brassicifolium* is instead more closely related to *L. brassicifolium* ssp. *macropterum* and *L. imbricatum*, on El Hierro, and La Palma and Tenerife, respectively. In turn this indicates that La Gomera has been subject to two events of colonization or vicariance. The same is obviously the case with *Limonium preauxii* and *L. sventenii* on Gran Canaria, but the premises for discussing these species are obscured by the lack of support in the corresponding

part of the phylogeny. *Limonium sinuatum* and *L. lobatum* have the conspicuous wing extensions on the β -prophylls and on the spicule bracts (not in *L. lobatum*), i.e. morphological features that probably enable dispersal of the diaspores via fur-bearing animals. Although the calyx is elaborate and possibly acted as a parachute in a common ancestor, the rather elaborate diaspores with many spicules are comparatively heavy, making wind dispersal inefficient. There is nothing in the morphology that could facilitate animal dispersal in the 'Nobiles' species, and although the diaspores contain fewer spicules, they are heavy enough to prevent efficient wind dispersal.

If assuming that *Limonium lobatum* occurs in natural populations on Tenerife and Fuerteventura, one must of course postulate a dispersal of this species from the African mainland, possibly first to Fuerteventura and subsequently also to Tenerife. A somewhat similar distribution was demonstrated for *Nanorrhinum elegans* (G. Forst.) Ghebr. (Scrophulariaceae; Ghebrehiwet, 1999), but this species does not extend into the Irano-Turanian region, as does *Limonium lobatum*. Little can be hypothesized for the 'Odontolepidae' other than that the pattern with a large Canarian clade ('Nobiles') with close relatives also in the Atlas mountains (*L. mouretii* and *L. sinuatum* ssp. *beaumierianum*) and/or the Mediterranean area (*L. sinuatum*, all ssp., and *L. lobatum*) is shared with other groups, such as *Argyranthemum* (Asteraceae–Anthemideae; Francisco-Ortega *et al.*, 1996), *Bencomia* Webb & Berthel. (Rosaceae–Rosoideae; Helfgott *et al.*, 2000), Asteraceae–Inuleae (Francisco-Ortega *et al.*, 1999) and *Crambe* L. (Brassicaceae–Brassicaceae; Francisco-Ortega *et al.*, 1999). A distribution pattern involving the Atlas Mountains and Canary Islands is also shown by another putative *Limonium* clade, namely *Limonium* sect. *Ctenostachys*, but here the widespread *Limonium pectinatum* Kuntze is the sole species found throughout the islands, whereas some of its closest relatives, *L. fallax* (Coss.) Maire and *L. mucronatum* Kuntze occur on the African mainland, and two other species are endemic to the Cape Verde Islands (Lobin *et al.*, 1995; Brochmann *et al.*, 1997). The high and middle Atlas Mountain region was identified by Médail & Quétzel (1997) as a hot spot with particularly high biodiversity and with an assumed 20% endemism. Both *Limonium mouretii* and *L. sinuatum* ssp. *beaumierianum* are examples of taxa endemic to this region. Furthermore, Morrone, Katinas & Crisci (1996) also argued that it should not be taken for granted that areas with high biodiversity are restricted to tropical regions. *Limonium mouretii* lacks both the supposedly adhesive thorn-like extensions on the spicule bracts as well as the parachute-like calyx. This might explain the restricted distribu-

tion but at the same time this is contradicted by the similarly distributed *Limonium sinuatum* ssp. *beaumierianum*, which possesses both these properties. The disparate biogeographical pattern in *Ilex* might be explained by the supposedly great age of the genus (Cuenoud *et al.*, 2000), but because *Ilex* has not radiated in Macaronesia, the two separate introductions are supposedly rather recent.

ECOLOGICAL ZONES

It has been claimed that the combination of dramatic topography and broad range of climatic conditions have made it possible for a number of vegetation types to develop on the Canary Islands (Bramwell, 1972). They were classified in more or less distinct ecological zones (Francisco-Ortega *et al.*, 1996), some of which are under the influence of the prevailing north-east trade winds. For *Argyranthemum* it proved useful to use the ecological zonation when discussing adaptive radiation and evolution (Francisco-Ortega *et al.*, 1996) within the clade. When scrutinizing each 'Nobiles' species it seems that a few taxa either have a very wide ecological amplitude or that their habitats are more homogeneous than is the impression given after simply listing all taxa in a table, following the ecological zonation by Francisco-Ortega *et al.* (1996). For example, *Limonium macrophyllum* (Brouss. ex Spreng.) Kuntze must be placed in the three zones Coastal Desert, Humid Lowland Scrub and Laurel Forest, given that the altitudes provided for the collections are accurate. This is also the case with *Limonium sventenii* on Gran Canaria, although the distribution of this species is less narrow than that of *L. macrophyllum*. Five taxa occur entirely outside the otherwise prevailing Coastal Desert zone, namely *Limonium brassicifolium* ssp. *macropterum*, *L. perezii*, *L. preauxii*, *L. redivivum* and *L. spectabile*. If optimizing the ecological zones in the form of a multistate character for the *Limonium brassicifolium* clade, the Coastal Desert becomes autapomorphic for *L. imbricatum*, whereas Humid Lowland Scrub is plesiomorphic for this clade. This supports the suggestion of Francisco-Ortega *et al.* (1996) and the results obtained by Panero *et al.* (1999) that infra-island dispersal takes place between similar ecological zones. The distribution of the *Limonium brassicifolium* clade on the four westernmost Canary islands agrees with the results by Barber *et al.* (2000), for their 'clade 1' in *Sideritis* L.

Francisco-Ortega *et al.* (2001) concluded that the several molecular phylogenies indicate unique evolutionary patterns for the Macaronesian clades, and this might also be the case for the biogeography in the area as well, especially in the light of the results put forward in this paper.

TAXONOMIC TREATMENT

Limonium Mill. sect. *Pteroclados* (Boiss.) Bokhari, Notes Roy. Bot. Gard. Edinburgh 32: 59 (1972). – *Statice* sect. *Pteroclados* Boiss., Prodrum 7: 635 (1848). – *Limonium* subg. *Pteroclados* (Boiss.) Pignatti, Bot. J. Linn. Soc. 64: 361 (1971). Type: *Limonium sinuatum* (L.) Mill.

Variably hairy to glabrous shrubs, shrublets, perennial or rarely annual herbs with larger rosette leaves and reduced, scale-like cauline leaves. Hairs simple, sometimes gathered and seemingly stellate. Wings on stems and branches beneath those leading to a spicule aggregate 0.3–23 mm wide, sometimes absent, \pm adaxial–abaxial, sometimes also lateral to cauline leaves, extensions at the nodes generally absent or inconspicuous, rarely one–three 5–60 mm long (*L. sinuatum*, *L. lobatum*). Rosette leaves often ovate to oblanceolate, sometimes elliptic, rarely broadly ovate or lanceolate, generally entire and then often attenuate or sometimes sinuate or rarely cordate, truncate or lobed towards the base, sometimes deeply lobed to pinnatisect, rarely shallowly but wide-lobed, tips shortly to conspicuously aristate, often petiolate or sometimes epetiolate. Cauline leaves reduced, scale-like, with or without a ciliate margin, mucronate to aristate. Inflorescence corymboid, often rather lax or rarely dense or very dense, often much-branched, with conspicuous abscission zones in axils of terminal branches, these generally with adaxial, abaxial and sometimes also lateral wings up to 4(–12) mm wide and which sometimes are extended up to 20 mm above the node to bract of the first spicule. Spicules distichous, loosely or densely packed and detached in aggregates (diaspores) comprising 1–4(–5) or 6–8(–14) spicules. Spicule bracts cauline leaf-like, the one to the first spicule rarely two-pointed, in *L. sinuatum* with two lateral subulate appendages; α 1-prophyll cauline leaf-like, apically often entire or sometimes emarginate, mucronate sometimes aristate; β -prophyll larger, hard, enveloping flowers and their bracts, generally with coarse, raised often whitish veins, sometimes with a scarious and/or showy and/or plicate apical margin, sometimes with an apical fin-like wing abaxially or two lateral thorn-like, often subulate sometimes anvil-shaped or 3-lobed and flattened appendages, apically entire, sometimes 3-lobed, rarely bifid; α 2-, α 3- and α 4-prophylls narrowly oblong, apically rounded to truncate or sometimes irregularly 3-lobed, generally with two dorsal unequal rarely subequal wings ('*Nobiles*'). Calyx infundibuliform or rarely narrowly campanulate (*L. mouretii*), tube 10-ribbed, zygomorphic at the base, primary ribs epilobal or rarely interlobal (*L. lobatum*) reaching well above limb or not, the expanding limb generally of various shades of blue, or lilac, rarely

yellow (*L. sinuatum* ssp. *bonduellei*) or white (*L. sinuatum* ssp. *sinuatum*), secondary ribs extended into the limb or not. Corolla often white, sometimes pinkish or yellow, lobes faintly emarginate. Fruit with circumscissile dehiscence.

THE SPECIES OF *LIMONIUM* SECT.
PTEROCLADOS (ORDER AS IN THE STRICT
CONSENSUS TREE)

1. *Limonium sinuatum* (L.) Mill., The Gardeners Dictionary ed. 8 n. 6 (1768). – *Statice sinuata* L., Sp. Pl. 276 (1753). Type: LINN 395.33, designated by Bokhari in Nasir & Ali, Fl. W. Pakistan 28: 9 (1972).

Hispid to subglabrous perennial, rarely annual, up to 0.7 m, generally with terminal inflorescences, sometimes with inflorescence-bearing branches also at lower nodes, wings conspicuous, up to 3 mm wide, \pm adaxial–abaxial and bilateral to cauline leaves, and often with two–three 5–50 mm long, often longitudinally lobed extensions at the nodes, wings sometimes inconspicuous or absent (especially on smaller exemplars). Hairs large, flattened up to 2 mm long, often mixed with smaller hairs. Leaves 20–160 \times 5–40 mm, narrowly obovate to oblanceolate, deeply lobed to pinnatisect, sometimes sinuate in small exemplars, aristae conspicuous. Cauline leaves with ciliate margins. Inflorescences in simple or compound corymbs, dense, diaspore branches up to 50 mm long, with three conspicuous wings up to 5 mm wide, middle wing extended into a \leq 12-mm-long, acute, and generally longitudinally 3-lobed projection, lateral wings smaller. Diaspores with 6–8(–14) spicules, bract conspicuously aristate, with two lateral, subulate, thorn-like wing extensions, the first bract in each row often two-pointed, α 1-prophyll emarginate, conspicuously aristate, β -prophyll with two subulate to anvil-shaped, sometimes 3-lobed and flattened, thorn-like, often curved and decurrent projections, 3-lobed, without a scarious margin, α 2-prophyll apically irregularly rounded and 2–3-lobed, aristate. Calyx infundibuliform, conspicuous, primary ribs epilobal, not reaching lobe tips, or reaching lobe tips or slightly longer, mauve, often hairy along ribs, bluish or yellow, rarely whitish. Corolla yellow, sometimes pink or white.

Taxonomic note: With the broad concept adopted here and which follows the interpretation of Sauvage & Vindt (1952), *L. sinuatum* is distinguished by its often four stem wings, the thorn-like projections of the spicule bracts, and the inversely T-shaped, large adaxial diaspore branch wing (Fig. 1A). The last feature occurs also in *L. brassicifolium* and *L. perezii*, but less conspicuously. Even though the subspecies concept of Sauvage & Vindt (1952) seems sound, their approach

KEY TO THE SPECIES

1. Leaves shallowly sinuate or often deeply lobed; α 1-prophylls emarginate; at least 6 spicules per diaspore 2.
1. Leaves entire, sometimes shallowly or deeply lobed towards the base, or pinnatisect or occasionally coarsely lobed; α 1-prophylls entire; 1–4 spicules per diaspore 4.
2. Inflorescences on branches arising from nodes towards the base of the main stem; diaspore branches absent or inconspicuous, wing-less; β -prophylls apically plicate (Fig. 1I), emarginate, with a dorsal fin-like wing (Fig. 1I), without lateral appendages; calyx rather inconspicuous, funnel-shaped, without an expanded limb 3. *L. mouretii*
2. Inflorescence \pm terminal; diaspore branches mostly 15–60 mm long, with three conspicuous wings; β -prophylls apically smooth, 3-lobed (Fig. 1J), without a dorsal wing, with two lateral, subulate to anvil-shaped (sometimes 3-lobed) appendages; calyx showy, with an expanded limb 3.
3. Spicule bracts without wing extensions; calyx pale blue, deeply lobed, with primary ribs arising between the lobes 2. *L. lobatum*
3. Spicule bracts with two lateral, subulate, thorn-like wing extensions (Fig. 1C); calyx vividly blue to mauve or yellow, with primary ribs protruding from lobe tips (or not protruding at all) 1. *L. sinuatum*
4. β -prophylls apically not plicate, often scarious 5.
4. β -prophylls apically plicate (Fig. 1I), often showy and coloured like the calyx 9.
5. Marginal leaf hairs often 2–5 together; leaf aristae often ≥ 4 mm; diaspore branch wings adaxial and lateral to bract of first spicule; mucro to bract of first spicule and α 1-prophyll at least half as long as respective lamina 12. *L. perezii*
5. Marginal leaf hairs single or leaves glabrous; leaf aristae often < 3 mm; diaspore branch wings mainly adaxial to bract of first spicule; mucro to bract of first spicule and α 1-prophyll much shorter than respective lamina 6.
6. Shrub up to 1.8 m; stem wings abaxial from leaf 15. *L. arborescens*
6. Shrublets up to 0.75 m; stem wings abaxial and adaxial from leaf 7.
7. Leaf bases often cordate, lamina 1–2 \times as long as petiole; diaspore branches up to 5 mm long; calyx sparsely pubescent along ribs; secondary ribs not extending into the calyx limb 4. *L. preauxii*
7. Leaf bases often attenuate along petiole, lamina up to as long as petiole; at least some diaspore branches 10–15 mm long; calyx glabrous; secondary ribs extending well into the calyx limb 8.
8. Wing extensions at first node of diaspore branch absent or inconspicuous; lateral wings on α 2-prophylls equal-subequal 13. *L. sventenii*
8. Wing extensions at first node of diaspore branch conspicuous, rounded to acute; lateral wings on α 2-prophylls unequal (Fig. 1G) 14. *L. fruticans*
9. Stem wings 12–20 mm broad 10.
9. Stem wings up to 5 mm broad 11.
10. Plant pilose; leaves deeply lobed to pinnatisect 7. *L. imbricatum*
10. Plant not pilose; leaves entire but lobed at the narrowing base 8. *L. brassicifolium*
11. Leaves epetiolate; diaspore branches up to 30 mm long 5. *L. macrophyllum*
11. Leaves petiolate; diaspore branches less than 10 mm long 12.
12. Leaves deeply lobed to pinnatisect, with single hairs 6. *L. spectabile*
12. Leaves entire though sometimes shallowly lobed towards the base of the blade, at least some hairs in groups of 2–5 13.
13. Stem wings conspicuous, up to 5 mm broad; α 2-prophylls apically showy 9. *L. redivivum*
13. Stem wings inconspicuous, up to 5 mm broad; α 2-prophylls apically scarious 14.
14. Plants up to 15(–35) cm; leaves entire 10. *L. puberulum*
14. Plants up to 50 cm; leaves shallowly lobed towards the base of blade 11. *L. bourgaei*

KEY TO THE SUBSPECIES OF *LIMONIUM SINUATUM*

1. Calyx yellow *L. sinuatum* ssp. *bonduellei*
1. Calyx blue to mauve, sometimes whitish 2.
2. Annuals *L. sinuatum* ssp. *beaumierianum*
2. Perennials *L. sinuatum* ssp. *sinuatum*

to include many other infraspecific taxa founded on minor morphological variation is not sensible. For comparison with *Limonium lobatum* see Taxonomic note under that species.

1A. *Limonium sinuatum* (L.) Mill. ssp. *sinuatum*. – *Limonium sinuatum* (L.) Mill. ssp. *romanum* Täckh. & Boulos, Publ. Cairo University Herb. 5: 90 (1972).

Perennial or rarely annual. Calyx mauve to bluish or rarely whitish, sometimes yellow in flower shop specimens.

Nomenclatural note: Täckholm & Boulos (1972) described *Limonium sinuatum* ssp. *romanum* based on the annual habit, the glabrous appearance, and the lack of wing extensions on the stems. These characteristics fall well within the concept of *Limonium sinuatum* ssp. *sinuatum* as recognized here.

Distribution: *L. sinuatum* ssp. *sinuatum* is a fairly common garden plant in many parts of the world, and it also occurs as an escape. It is also globally common in shops as freshly cut and everlasting flowers. The native range of the taxon is the Mediterranean region and the habitat is dry sandy or rocky places mainly at the coast. As an alien, such as in South Africa, *Limonium sinuatum* occurs along roadsides and on disturbed or open ground.

1B. *Limonium sinuatum* (L.) Mill. ssp. *bonduellei* (T. Lestib.) Sauvage & Vindt. – *Statice bonduellei* T. Lestib., Ann. Sc. Nat. Ser. 3, 16: 81 (1851). – *Limonium bonduellei* (T. Lestib.) Kuntze, Rev. Gen. Pl. 2: 395 (1891).

Taxonomic note: An annual with a conspicuous yellow calyx, and often appearing rigid with harder diaspore wings and extensions than in *Limonium sinuatum* ssp. *sinuatum*. As in small specimens of *Limonium sinuatum* ssp. *sinuatum* and *Limonium sinuatum* ssp. *baumierianum*, the stems usually lack wing extensions.

Distribution: Native to North Africa.

1C. *Limonium sinuatum* (L.) Mill. ssp. *baumierianum* (Maire) Maire, Cat. Pl. Maroc, 3: 568 (1934). – *Statice baumierana* Maire, Bull. Soc. Hist. Nat. Afr. Nord. 16: 93 (1925). Type: Mardochée s. n. in herb. Cosson, P, lectotype, here selected.

Taxonomic note: Annual with mauve, bluish or whitish calyx, and with truly thorn-like pungent wing extensions on the diaspores, often more rigid than ssp. *sinuatum*. Apart from the colour of the calyx ssp.

baumierianum is hence habitually more similar to ssp. *bonduellei*.

Nomenclatural note: This plant was collected by, and named after, the French consul in Mogador, but his specimens are not cited in the protologue (Maire, 1925).

Distribution: Confined to the southern part of Anti-Atlas in Morocco.

2. *Limonium lobatum* (L. f.) Kuntze, Rev. Gen. Pl. 2: 395 (1891). – *Statice lobata* L. f., Suppl. Pl. 187 (1781). – *Limonium thouinii* (Viv.) Kuntze, Rev. Gen. Pl. 2: 395 (1891).

Glabrous annual up to 0.5 m, generally with terminal inflorescences, sometimes with inflorescence-bearing branches also at lower nodes, wings conspicuous, up to 5 mm wide, \pm adaxial–abaxial to cauline leaves, and often with one (sometimes 2) 5–35 mm long, \pm flat extension at the nodes on larger exemplars, wings on smaller exemplars inconspicuous or absent. Leaves (10–)15–140 \times 5–75 mm long, narrowly obovate sometimes obovate, deeply lobed, sparsely hairy marginally and along midvein, aristae conspicuous. Cauline leaves glabrous. Inflorescences in simple or compound corymbs, dense, diaspore branches up to 60 mm long, with three conspicuous wings up to 12 mm wide, middle wing extended into a \leq 20-mm-long, acute, and generally flat projection, lateral wings smaller. Diaspores with 6–7 spicules, bract mucronate, without lateral wing extensions, α 1-prophylls slightly and irregularly emarginate, mucronate, β -prophyll smooth, with two subulate, thorn-like, often curved and decurrent projections, 3-lobed, lobes apically scarious, α 2-prophyll apically irregularly rounded. Calyx infundibuliform, conspicuous, primary ribs interlobal, reaching lobe tips or slightly longer, pale blue to whitish. Corolla yellow.

Taxonomic note: *Limonium lobatum* is immediately recognized by its conspicuous pale blue to whitish calyx with the very long primary ribs arising between the lobes. It resembles *L. sinuatum* but differs by the mostly two stem wings often with one extension at each node, the large and acute middle wing extension of the diaspore branches, the absence of thorn-like projections on the bracts to the first spicule, as well as by the calyx features. The calyx characters are unique in the family.

Distribution: *Limonium lobatum* occurs in North Africa, southern Spain, southern Greece, in the eastern Mediterranean and eastwards into Iraq and southern Iran (Rechinger & Schiman-Czeika, 1974). More interestingly, it grows also on Tenerife and

Furteventura apparently in natural populations (Kunkel & Sunding, 1967; Schönfelder & Schönfelder, 1997; but see also above under Discussion). Bramwell & Bramwell (1994) did not include *L. lobatum* in their flora, thus probably indicating the introduced nature of the species.

3. *Limonium mouretii* (Pit.) Maire, Cat. Pl. Maroc, 3: 569 (1934). – *Statice mouretii* Pit., Contrib. Etude Fl. Maroc: 33 (1918).

Glabrous perennial herb up to 0.4 m with inflorescence-bearing branches arising from most axils of main stem, wings inconspicuous, less than 0.5 mm wide. Leaves 20–70 × 10–25 mm, narrowly obovate, sinuate to deeply lobed, sparsely hairy marginally, greyish green. Inflorescences scorpioid, very dense, diaspores sessile or subsessile, wing-less. Diaspores with about 6 spicules, bract mucronate, without lateral projections, α 1-prophyll emarginate, mucronate, β -prophyll emarginate, apically with a dorsal wing, often plicate and with a narrow scarious margin, conspicuously veined beneath, α 2-prophyll mucronate. Calyx narrowly campanulate, inconspicuous, primary ribs extended well above lobes, pink. Corolla pink.

Taxonomic note: An easily distinguished species recognized by the several branches bearing inflorescences emerging from most axils, the very dense inflorescences with almost sessile diaspores and by the pink, inconspicuous calyx. All these features contrast with the rest of the species of *Limonium* sect. *Pteroclados*.

Distribution: Endemic to Moyen Atlas of Morocco at elevations between 1300 and 2000 m.

4. *Limonium preauxii* (Webb & Berthel.) Kuntze, Rev. Gen. Pl. 2: 396 (1892) – *Statice preauxii* Webb & Berthel., Phyt. Canar. 3: 181 (1846). Holotype in FI (La Serna, León & Wildpret, 1982). – *Limonium rumicifolium* (Svent.) G. Kunkel & Sunding, Cuad. Bot. 2: 13. – *Statice rumicifolia* Svent., Bol. Institute Nac. Invest. Agron. Madrid 14: 38 (1954).

Shrublet up to 0.5 m with mostly terminal inflorescences, sometimes with inflorescence-bearing branches arising from axils up to 20–25 cm from the tip, wings inconspicuous, less than 0.5 mm wide, \pm adaxial–abaxial to cauline leaves. Leaf blades 30–100 × 30–100 mm, ovate, entire, generally cordate at base, glabrous, tips aristate, petiole 40–110 mm. Inflorescences much-branched, rather lax, diaspore branches up to 5 mm long, wings inconspicuous and up to 1.2 mm wide, mostly \pm adaxial–abaxial to bract of first spicule. Diaspores with 2–4 spicules, bract

mucronate, glabrous or puberulous, α 1-prophyll \pm truncate, β -prophyll apically with a dorsal rounded to acute wing, flat and without scarious margin, inconspicuously veined beneath, glabrous or puberulous, α 2-prophyll rounded, mucronate, lateral wings 1 or 2, unequal. Calyx infundibuliform, conspicuous, primary ribs epilobal, reaching lobe tips or slightly below, glabrous or puberulous, mauve. Corolla white.

Taxonomic note: *Limonium preauxii* is distinguished by being medium-sized and having comparatively long-petiolate leaves generally with a cordate base. It differs from the similar *L. sventenii*, *L. arborescens* and *L. fruticans* by all these features. Bramwell & Bramwell (1974) suggested that *L. preauxii* might be conspecific with *L. perezii*, but the latter differs by its very long-aristate cauline leaves and bracts.

Distribution: Endemic to the southern part of Gran Canaria between 400 and 800 m.

Ecological zone: Pine forest. Status in IUCN red data list: V (vulnerable).

5. *Limonium macrophyllum* (Brouss. ex Spreng.) Kuntze, Rev. Gen. Pl. 2: 395 (1891). – *Statice macrophylla* Brouss. ex Spreng., Syst. Veg. 1: 959 (1825).

Shrublet up to 0.8 m with inflorescence-bearing branches arising from axils at least 40 cm from the top, wings conspicuous, up to 4 mm wide, \pm adaxial–abaxial to cauline leaves. Leaves 90–350 × 40–90 mm, oblanceolate to narrowly obovate, entire or sometimes shallowly sinuate, sessile, glabrous or margins with few single hairs, mucronate or sometimes aristate. Inflorescences much-branched, rather lax, often elongate, diaspore branches up to 30 mm long, \pm adaxial–abaxial wings up to 4 mm wide, middle (lateral) up to 1.5 mm wide, extensions inconspicuous or sometimes up to 1.5 mm long. Diaspores with 2–4 spicules, bract mucronate, pubescent, α 1-prophyll entire, mucronate, pubescent, β -prophyll with a dorsal wing, apically with a plicate and showy margin, coarsely veined beneath, densely pubescent, α 2-prophyll rounded to truncate, lateral wings 1 or 2, unequal. Calyx infundibuliform, conspicuous, primary ribs epilobal, reaching lobe tips or slightly below, hairy along ribs, bluish. Corolla white.

Taxonomic note: *Limonium macrophyllum* is easily recognized with its sessile, large, entire leaves being broadest towards the tip. This together with the more elongate inflorescences and the more conspicuous stem wings makes it different from other entire-leaved species. The other species with even more apparent stem wings all have at least lobed leaves.

Distribution: *Limonium macrophyllum* is a quite narrow endemic found at the north-east tip of Tenerife at Anaga. Kunkel & Sunding (1967) enumerates both Tenerife and Gran Canaria under *L. macrophyllum*, but this view has no support either from the specimen labels or any of the floras. The altitudes given on two sheets, namely 600 m and 650 m, results in placement in no less than three different ecological zones as outlined by Francisco-Ortega *et al.* (1996), whereas the range of altitude reported by Gómez-Campo (1996) is 50–200 m.

Ecological zone: Coastal desert, laurel forest, humid lowland scrub. Status in IUCN red data list: E (endangered).

6. *Limonium spectabile* (Svent.) G. Kunkel & Sunding, Cuad. Bot. 2: 10 (1967). – *Statice spectabilis* Svent., Bol. Inst. Nac. Invest. Agron. Madrid 9: 204 (1949).

Shrublet up to 0.8 m with inflorescence-bearing branches arising from axils up to 30 cm from the tip, wings absent or inconspicuous and <0.5 mm wide, generally \pm adaxial–abaxial to cauline leaves. Leaf blade 80–300 \times 25–70 mm, lanceolate to oblanceolate, deeply lobed to pinnatisect, lobes linear to oblong and obtuse, slightly longer at about the middle of blade, ultimate lobe much larger and broadly ovate to ovate, seemingly glabrous but with few single hairs, tips aristate, petiole 40–80 mm. Inflorescences much-branched, rather lax, diaspore branches up to 6 mm long, \pm adaxial–abaxial and lateral wings up to 0.5 mm wide, extensions absent or inconspicuous. Diaspores with 2–6 spicules, bract mucronate to shortly aristate, α 1-prophyll entire, mucronate to shortly aristate, β -prophyll apically with a plicate and showy margin, inconspicuously veined beneath, α 2-prophyll rounded to truncate, lateral wings 1 or 2, unequal. Calyx infundibuliform, conspicuous, primary ribs epilobal, reaching lobe tips or slightly below, glabrous, mauve. Corolla white.

Taxonomic note: This is an easily recognized species with its inconspicuous stem wings, dissected leaves and diaspores with 2–6 spicules. *Limonium imbricatum* has similar foliage but differs by the conspicuous stem wings and the distinctly thin-hairy leaves and wings. It also gives an overall coarser impression.

Distribution: *Limonium spectabile* is confined to the north-west corner of Tenerife near the Valle de Masca.

Ecological zone: Humid lowland scrub. Status in IUCN red data list: E (endangered).

7. *Limonium imbricatum* (Webb ex Girard) C. E. Hubb. (1916). – *Statice imbricata* Webb ex Girard, Ann. Sc. Nat. Ser. 3 (2): 330 (1844).

Pilose–villous shrublet up to 0.5 m with inflorescence-bearing branches arising from axils up to 25 cm from the tip, wings conspicuous, up to 23 mm wide, \pm adaxial–abaxial to cauline leaves, blunt at nodes or sometimes with up to 6-mm-long extensions. Leaves 50–320 \times 25–75 mm, oblanceolate to narrowly obovate, pinnatisect, lobes reniform to oblong to obovate, and obtuse, decreasing in size towards the base, ultimate lobe much larger and cordate to broadly ovate or lunate, aristate. Inflorescences much-branched, rather lax, diaspore branches up to 12 mm long, \pm adaxial–abaxial wings up to 4 mm wide, extensions conspicuous, flat, up to 6 mm long. Diaspores with 1–2 spicules, bract mucronate to shortly aristate, α 1-prophyll entire, mucronate to shortly aristate, β -prophyll apically with a plicate and showy margin, coarsely veined beneath, α 2-prophyll rounded to truncate, lateral wings 1 or 2, unequal. Calyx infundibuliform, conspicuous, primary ribs epilobal, reaching lobe tips or slightly below, mauve. Corolla white.

Taxonomic note: *Limonium imbricatum* is immediately distinguished by its short to long and thin hairs that occur on all parts, by the deeply dissected leaves, and by the conspicuous stem wings. Most other species with very apparent stem wings have entire leaves and should not be confused with *L. imbricatum*. *Limonium brassicifolium* has prominent stem wings and lobed, but not pinnatisect, leaves. It also lacks the thin hairs typical of *L. imbricatum*. *Limonium spectabile* has a similar foliage but differs by the very inconspicuous stem wings.

Distribution: *Limonium imbricatum* occurs on the north coast of both Tenerife and La Palma.

Ecological zone: Coastal desert. Status in IUCN red data list: E (endangered).

8. *Limonium brassicifolium* (Webb & Berthel.) Kuntze, Rev. Gen. Pl. 2: 395 (1891). – *Statice brassicaefolia* Webb & Berthel., Phyt. Canar. 3: 181 (1846). Holotype in FI (La Serna *et al.*, 1982).

Puberulous to subglabrous shrublet up to 0.6 m with inflorescence-bearing branches arising from axils up to 25 cm from the tip, wings conspicuous, broadened towards the upper node of an internode, up to 20 mm wide, \pm adaxial–abaxial to cauline leaves, blunt at nodes or sometimes slightly extended. Leaf blade 80–350 \times 35–120 mm, narrowly obovate to obovate, entire but lobed to deeply lobed towards the attenuate base,

KEY TO THE SUBSPECIES OF *LIMONIUM BRASSICIFOLIUM*

1. Diaspore branches up to 12 mm long. *L. brassicifolium* ssp. *brassicifolium*
 1. Diaspore branches up to 25 mm long. *L. brassicifolium* ssp. *macropterum*

tips aristate, petiole itself 40–60 mm. Inflorescences much-branched, rather dense, diaspore branches up to 25 mm long, \pm adaxial–abaxial wings up to 8 mm wide, extensions mostly conspicuous, flat, to 6 mm long. Diaspores with 2–4 spicules, bract mucronate, α 1-prophyll entire, mucronate, β -prophyll apically with a plicate and showy margin, coarsely veined beneath, α 2-prophyll rounded to truncate, lateral wings 1 or 2, unequal. Calyx infundibuliform, conspicuous, primary ribs epilobal, not reaching lobe tips, puberulous along ribs, mauve. Corolla white.

Taxonomic note: *Limonium brassicifolium* and *L. macropterum* differ only in one external morphological feature, namely the length of the diaspore branches, and the two taxa are very similar. Bramwell & Bramwell's (1994) contention that the taxa contrast by stem wing width and calyx colour was not verified in this study.

8A. *Limonium brassicifolium* (Webb & Berthel.) Kuntze ssp. *brassicifolium*

Taxonomic note: See above in the key.

Distribution: This taxon is confined to the northern coast of La Gomera.

Ecological zone: Coastal desert, humid lowland scrub. Status in IUCN red data list: E (endangered).

8B. *Limonium brassicifolium* (Webb & Berthel.) Kuntze ssp. *macropterum* (Webb & Berthel.) G. Kunkel. – *Statice macroptera* Webb & Berthel., Phyt. Canar. 3: 182 (1846). Holotype in FI (La Serna *et al.*, 1982), isotype in K.

Taxonomic note: See above in the key.

Distribution: This subspecies occurs only on the western part of El Hierro.

Ecological zone: Humid lowland scrub, laurel forest. Status in IUCN red data list: E (endangered).

9. *Limonium redivivum* (Svent.) G. Kunkel & Sunding, Cuad. Bot. 2: 12 (1967). – *Statice rediviva* Svent., Bol. Inst. Nac. Invest. Agron. Madrid 30: 31 (1954). – *Limonium redivivum* (Svent.) G. Kunkel & Sunding

var. *pilosum* (Svent.) G. Kunkel & Sunding, Cuad. Bot. 2: 12 (1967). – *Statice rediviva* Svent. var. *pilosa* Svent., Bol. Inst. Nac. Invest. Agron. Madrid 30: 31 (1954).

Shrublet up to 0.4 m with inflorescence-bearing branches arising from axils up to 15 cm from the tip, wings conspicuous, up to 6 mm wide, \pm adaxial–abaxial to cauline leaves. Leaf blades 30–100 \times 20–40 mm, ovate to rhomboid, entire, base attenuate, surface sparsely pubescent with single, double and triple seemingly stellate hairs, tips aristate, petiole 40–70 mm. Inflorescences much-branched, rather lax, diaspore branches up to 7 mm long, wings up to 1.2 mm wide, mostly \pm adaxial–abaxial to bract of first spicule. Diaspores with 1–4 spicules, bract mucronate, α 1-prophyll entire, mucronate, β -prophyll apically with a dorsal rounded wing, apically with a plicate and showy margin, inconspicuously veined beneath, α 2-prophyll rounded, mucronate, lateral wings 1 or 2 unequal, apically with a showy margin. Calyx infundibuliform, conspicuous, primary ribs epilobal, reaching lobe tips or slightly below, glabrous, bluish. Corolla white.

Taxonomic note: *Limonium redivivum* resembles *L. arborescens*, *L. fruticans* and *L. sventenii* in its foliage, but differs by its wider stem wings, and the apically showy α 2-prophylls. It is distinguished from the other wide-winged species by its entire and distinctly petiolate leaves, as well as the apically showy α 2-prophylls.

Distribution: *Limonium redivivum* is endemic on La Gomera at altitudes between 600 and 1100 m.

Ecological zone: Laurel forest, pine forest. Status in IUCN red data list: E (endangered).

10. *Limonium puberulum* (Webb) Kuntze, Rev. Gen. Pl. 2: 395 (1891). – *Statice puberula* Webb, Bot. Reg. 17, t. 1450 (1831).

Pubescent dwarf shrub with scattered and seemingly stellate hairs generally in fours–fives, up to *c.* 0.15–0.35 m with inflorescence-bearing branches arising from axils up to 7(–29) 30 cm from the tip, wings absent or very inconspicuous, <0.5 mm wide, generally \pm adaxial–abaxial to cauline leaves. Leaf blade

10–45(–80) × 5–20(–45) mm, elliptic to ovate, entire, base attenuate, tips aristate, petiole 15–30(–45) mm. Inflorescences much-branched, rather lax, diaspore branches up to 4 mm long, wings very inconspicuous <0.5 mm wide, mostly ± adaxial–abaxial to bract of first spicule. Diaspores with 1–4 spicules, bract mucronate, pubescent, α1-prophyll entire, mucronate to aristate, pubescent, β-prophyll with a dorsal ridge, apically often with a plicate and showy margin, ± coarsely veined beneath, pubescent, α2-prophyll rounded to truncate, lateral wings 1 or 2, unequal. Calyx infundibuliform, conspicuous, primary ribs epilobal, reaching lobe tips or slightly longer, pubescent, bluish. Corolla white.

Taxonomic note: *Limonium puberulum* is often the smallest of all *Pteroclados* species, and it is also readily recognized by entire often small leaves, the pubescence and by the bluish calyx. For comparison with *L. bourgaei*, see below.

Distribution: Like *Limonium bourgaei*, *L. puberulum* is present on both Lanzarote and Fuerteventura.

Ecological zone: Coastal desert. Status in IUCN red data list: V (vulnerable).

11. *Limonium bourgaei* (Webb ex Boiss.) Kuntze, Rev. Gen. Pl. 2: 395 (1891). – *Statice bourgaei* Webb ex Boiss., Prodr. 12: 638 (1848). Lectotype in FI (La Serna *et al.*, 1982), isotype in K.

Pubescent shrublet with scattered and seemingly stellate hairs generally in fours–fives, up to 0.6 m with inflorescence-bearing branches arising from axils up to 30 cm from the tip, wings inconspicuous, <1 mm wide, generally ± adaxial–abaxial to cauline leaves. Leaf blade 50–180 × 30–95 mm, elliptic to obovate, entire but lobed at the attenuate base, tips aristate, petiole 60–100 mm. Inflorescences much-branched, rather lax, diaspore branches up to 5 mm long, wings very inconspicuous <0.5 mm wide, mostly ± adaxial–abaxial to bract of first spicule. Diaspores with 1–4 spicules, bract mucronate, pubescent, α1-prophyll entire, mucronate to aristate, pubescent, β-prophyll with a dorsal ridge, apically often with a plicate and showy margin, ± coarsely veined beneath, pubescent, α2-prophyll rounded to truncate, lateral wings 1 or 2, unequal. Calyx infundibuliform, conspicuous, primary ribs epilobal, reaching lobe tips or slightly longer, pubescent, pinkish. Corolla white.

Taxonomic note: *Limonium bourgaei* is recognized by the inflorescence-bearing branches at nodes well below the tip of the stem, by the leaves with shallow

lobes towards the base and by the pinkish calyx. The close resemblance to *Limonium puberulum* has been noted in all floras, with which *L. bourgaei* shares the seemingly stellate-haired pubescence. The main differences between the two are the generally taller appearance, the leaf shape and the pinkish calyx in *L. bourgaei*, as opposed to the often shorter *L. puberulum* with entire leaves, and more bluish calyx. Another species with similar foliage is *L. brassicifolium* but it has conspicuous stem wings, as well as simple hairs.

Distribution: *Limonium bourgaei* is reported from the northern tip of Lanzarote at Famara, and the southern tip of Fuerteventura at Pico de la Zarza (Gómez-Campo, 1996). These localities are situated in the opposite ends of the respective islands. A record from the small island, La Graciosa, north-west of the tip of Lanzarote, needs to be confirmed (Gómez-Campo, 1996).

Ecological zone: Coastal desert. Status in IUCN red data list: V (vulnerable).

12. *Limonium perezii* (Stapf) C. E. Hubb., Rhodora 18: 158 (1916). – *Statice perezii* Stapf, Ann. Bot. 22: 116 (1908). Type: G. V. Perez s. n., Tenerife, Masca, August, 1907 (holotype and isotypes in K).

Shrublet up to 0.5 m with terminal inflorescences, or with inflorescence-bearing branches arising from axils up to 25 cm from the tip, wings inconspicuous, less than 0.5 mm wide, ± adaxial–abaxial to cauline leaves. Leaf blades 40–120 × 30–100 mm, ovate to broadly ovate, entire, bases truncate to attenuate, margins sparsely pubescent with single, double and triple hairs, tips conspicuously aristate, petiole 40–150 mm. Inflorescences much-branched, rather lax, diaspore branches up to 10 mm long, wings up to 1 mm wide, ± adaxial–abaxial and lateral to bract of first spicule and extended into linear, flat sometimes inversely T-shaped projections up to 8 mm long, lateral extensions smaller. Diaspores with 2–3 spicules, bract conspicuously aristate, α1-prophyll entire, conspicuously aristate, β-prophyll apically with a dorsal rounded to acute wing, flat and sometimes with scarious or showy margin, inconspicuously veined beneath, α2-prophyll rounded, mucronate, with an edge-like rib, sometimes with a trace of pink apically. Calyx infundibuliform, conspicuous, primary ribs epilobal, reaching lobe tips or slightly below, slightly hairy along ribs, mauve. Corolla white.

Taxonomic note: *Limonium perezii* resembles *L. preauxii*, *L. fruticans* and *L. sventenii* but differs by its conspicuously aristate cauline leaves and spicule

bracts, as well as by the marked wing extensions on the diaspore branches. In this respect it attains the 'Odontolepidae' more than any of the other 'Nobiles' species. *Limonium bourgaei* and *L. puberulum* are also similar in habit but differ by being more tomentose, by the marked scarious-showy-plicate β -prophylls, and the mucronate rather than aristate cauline leaves and spicule bracts.

Distribution: *Limonium perezii* has a very limited distribution and is confined to the western part of Tenerife at Masca.

Ecological zone: Laurel forest. Status in IUCN red data list: V (vulnerable).

13. *Limonium sventenii* A. Santos & M. L. Fernández, An. Jard. Bot. Madrid 40: 90 (1983). Holotype in ORT.

Shrublet often not exceeding 0.70 m with inflorescence-bearing branches arising from axils up to 25 cm from the tip, wings rather inconspicuous, up to 1.5 mm wide, generally \pm adaxial-abaxial to cauline leaves. Leaf blade 70–140 \times 30–80 mm, elliptic to obovate, entire, base attenuate, seemingly glabrous but marginally with few single hairs, tips aristate, petiole 60–90 mm. Inflorescences much-branched, rather lax, diaspore branches up to 15 mm long, wings rather conspicuous and up to 2 mm wide, mostly \pm adaxial-abaxial to bract of first spicule. Diaspores with 1–4(–5) spicules, bract mucronate, sparsely pubescent or glabrous, sometimes with a ciliate margin, α 1-prophyll entire, mucronate, puberulous or glabrous, β -prophyll with a dorsal ridge and a fin-like wing apically, apically flat, coarsely veined beneath, puberulous or glabrous but with a ciliate margin, α 2-prophyll rounded to truncate, lateral wings 2, conspicuous, equal. Calyx infundibuliform, conspicuous, primary ribs epilobal, not reaching lobe tips, glabrous, bluish. Corolla white.

Taxonomic note: *Limonium sventenii* resembles the often larger *L. arborescens*, but differs by the slightly more marked adaxial-abaxial stem wings, by the diaspore branches without wing extensions and by the α 2-prophylls with their marked equal, lateral wings. Material previously identified as the rather similar *L. preauxii* by Sventenius, a species also endemic to Gran Canaria, constitutes the holotype. It is exactly the same as the specimen in BM, grown from seeds collected by Kunkel at Galdar. For comparison with *L. preauxii*, see taxonomic note under that species.

Distribution: Endemic in the north-west part of Gran Canaria.

Ecological zone: Coastal desert, humid lowland scrub, arid lowland scrub. Status in IUCN red data list: R (rare).

14. *Limonium fruticans* (Webb) Kuntze, Rev. Gen. Pl. 2: 395 (1891). – *Statice fruticans* Webb, Pl. Can. Exs. 565 (1847).

Shrublet up to 0.75 m with inflorescence-bearing branches arising from axils up to 20 cm from the tip, wings inconspicuous, up to 1 mm wide, generally \pm adaxial-abaxial to cauline leaves. Leaf blade 25–160 \times 20–80 mm, ovate to elliptic to obovate, entire, base attenuate or sometimes shallowly sinuate, seemingly glabrous but marginally with few single hairs, tips aristate, petiole 20–80 mm. Inflorescences much-branched, rather lax, diaspore branches up to 13 mm long, \pm adaxial-abaxial wings up to 4 mm wide, middle (lateral) up to 1.5 mm wide, extensions up to 6 mm long and 3.5 mm wide, subulate to flat. Diaspores with 1–4(–5) spicules, bract mucronate, sparsely pubescent or glabrous, but with a ciliate margin, α 1-prophyll entire, mucronate, pubescent or glabrous, with ciliate margin, β -prophyll with a dorsal ridge and a fin-like wing apically, apically flat, coarsely veined beneath, pubescent or glabrous but with a ciliate margin, α 2-prophyll rounded to truncate, lateral wings 1 or 2, unequal. Calyx infundibuliform, conspicuous, primary ribs epilobal, not reaching lobe tips, glabrous, bluish. Corolla white.

Taxonomic note: For comparison with *L. arborescens*, see taxonomic note under that species. *Limonium sventenii* is similar, but differs by more inconspicuous wing extensions on the spicules, and by the α 2-prophylls with two equal rather than unequal, lateral wings.

Distribution: *Limonium fruticans* is endemic at the north-east tip of Tenerife in the vicinity of Teno.

Ecological zone: Coastal desert. Status in IUCN red data list: E (endangered).

15. *Limonium arborescens* (Brouss.) Kuntze, Rev. Gen. Pl. 2: 395 (1891). – *Statice arborescens* Brouss., Cat. Hort. Monsp. 85 (1804). – *Statice arborea* Brouss. ex Willd., Enum. Hort. Berol. 1: 337 (1809), fide Kunkel & Sunding (1967). *Type:* probably in MPU (not seen).

Shrublet or shrub up to 1.8 m with inflorescence-bearing branches arising from axils up to 30 cm from the tip, wings inconspicuous and up to 1 mm wide or sometimes more conspicuous and up to 2.5 mm wide, generally \pm abaxial to cauline leaves. Leaf blade (30–)60–250 \times (18–)25–140 mm, elliptic to obovate,

entire, base attenuate or sometimes shallowly sinuate, seemingly glabrous but marginally with few single hairs, tips aristate, petiole (20–)40–90 mm. Inflorescences much-branched, rather lax, diaspore branches up to 13 mm long, \pm adaxial–abaxial wings up to 4 mm wide, middle (lateral) up to 1.5 mm wide, extensions up to 6 mm long, subulate to flat. Diaspores with 1–4 spicules, bract mucronate, pubescent or glabrous, but with ciliate margin, α 1-prophyll entire, mucronate, pubescent, with ciliate margin, β -prophyll with a dorsal ridge and a fin-like wing apically, apically flat, coarsely veined beneath, pubescent or glabrous but with a ciliate margin, α 2-prophyll rounded to truncate, lateral wings 1 or 2. Unequal. Calyx infundibuliform, conspicuous, primary ribs epilobal, not reaching lobe tips, glabrous, bluish. Corolla white.

Taxonomic note: *Limonium arborescens* attains 2 m in height and is the tallest of all *Pteroclados* species. It has been claimed to be conspecific with the very similar but shorter *L. fruticans*, which also occurs on Tenerife at nearby localities. Apart from height there are some morphological differences between the two species: *L. arborescens* has leaves with or without a conspicuous whitish margin and blade midveins with no or few collateral bundles, generally \pm abaxial stem wings, and a thicker layer of parenchyma cells between the fibre ring and the chlorophyllous peripheral cells of the main stem. By contrast, *L. fruticans* has conspicuously whitish-margined leaves, one or two rings of collateral bundles in the blade midveins, generally adaxial and abaxial stem wings, and fewer layers of parenchyma cells between the fibre ring and the peripheral chlorophyllous cells of the main stem. For comparison with *L. preauxii* and *L. sventenii* see taxonomic notes under those species. *Limonium perezii* is found in the same clade in the cladograms, but is not likely to be confused with *L. arborescens* because it is much smaller and has the clearly aristate cauline leaves and spicule bracts.

Distribution: *Limonium arborescens* grows along the north-west coastline on Tenerife. It is grown in greenhouses (e.g. Bergius Botanic Garden, Stockholm) and for example on Gran Canaria, but the natural populations are truly endangered.

Ecological zone: Coastal desert. Status in IUCN red data list: E (endangered).

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APPENDIX

List of examined specimens. If different specimens under a certain taxon are separated by a comma they are from the same locality, as judged from the label. In such cases, when the exact position includes additional somewhat varying information, this is supplied.

L. arborescens. Masson s.n., [1777] (S). Tenerife: Webb s. n. (K); Below Tangué Bajo, near Garachico, leg. ignot., 1906 (K); Between San Juan de la Rambla and Realejo, 100 m, Sventenius 155, 1944 (S); La Dehesa de los Frailes, Bourgeau Pl. Can. 65, 1845 (K); La Longera, G. Mann 2509 (K); Barranco Castro, Okpon 19, 1969 (K).

L. bourgaei. Lanzarote: Famara, Bourgaeu Pl. Can. 564, 1846 (isotype of *Statice bourgaei* Webb ex Boiss.), and 335, 1845 (K).

L. brassicifolium ssp. *brassicifolium*. La Gomera: Bolle s. n. (S); Agulo, Risquete, 400 m, Anderberg *et al.* 88, 1976 (S); between Agulo and Hermigua, Santesson 26768, 1976 (S); Risco de Agulo and Risco de las Sulas, Lugar de Agulo, R. P. Murray s. n., 1899 (K); Agulo, 200 m, Burchard Pl. Can. Exs. 6, 1921 (S).

L. brassicifolium ssp. *macropterum*. El Hierro: Sabina, Bourgeau Pl. Can. 951, 1845 (isotype of *Statice macroptera* Webb & Berth., K), Murray s. n., 1899 (K), Bermejo, 500 m, Burchard Pl. Can. Exs. 400, 1924 (S), El Golfo, Perrandière s. n., 1855 (S), 6–700 m, Bornmüller Pl. Exs. Can. 2778, 1901 (S).

- L. fruticans*. Tenerife: Bourgeau Pl. Can. 1497, 1855 (K); Buenavista, El Fraile, Asplund 1263, 1933 (K, S), Bourgeau Pl. Can. 565 (K); Teno just west of Punta del Fraile, 75 m, Anderberg *et al.* 18, 1976 (S); El Fraile, between Buenavista and Teno, Murray s. n., 1899 (K); Cuertes Negras de los Silos, 200 m, D. Bramwell 1335, 1969 (K); Punta de Teno, Wikström *et al.* 88, 1994 (S).
- L. imbricatum*. Tenerife: Buenavista, Bourgeau 1496 (K) and Burchard Pl. Can. Exs. 211, 1925; La Hon-dura, Tacoronte, Bourgeau Pl. Can. 566 (K) and Burchard Pl. Exs. Can. 321, 1911 (K); Islet off Garachico, 1945, Prior s. n. (K); El Roque, Garachico, Sventenius 156, 1940 (S); Buenavista, Puerto Buen Jesus, Asplund 1015, 1933 (S).
- L. lobatum*
Algeria: Oued Chelif, 10 km S Ksar-es-Boukhari, Anderberg 413, 1980 (S); Biskra, between Maglouf and Djebel Snia, Chevallier s. n., 1896 (S); Chelif, St.-Cyprien, Chevallier s. n., 1894 (S).
Egypt: Wadi Ramle – Wadi Maddoar junction, 45 km from Matruh, Wanntorp & Sjödin 2225, 1969 (S);
Greece: Korinth, Hagios Theodoros, Samuelsson & Zander 456, 1931 (S).
Iran: Fars, Bushehr, Kangan, 20 m, 21°50'N 52°04'E, Mohisen s. n., 1992 (S), Tangestan, Abad, 55 m, 29°02'N 51°15'E, Keshtkar s. n., 1995 (S).
Israel: Jordan Valley, Dinsmore 10508, 1935 (S); north side of Dead Sea, Wall s. n., 1933 (S)
Morocco: Beni Bulaki, Ker-Ker, 600 m, Font-Quer 350, 1929 (S); Between Marrakech and Tamladet, 500 m, Samuelsson 6648, 1936 (S).
- L. macrophyllum*. Tenerife: Webb s. n., 1845 (K), Bolle s. n. (S); Il Tablero, Jimenez s. n., 1899 (K); Anaga, Bourgeau Pl. Can. 1499, 1855 (K), Tablero, Asplund 1316, 1933 (S), Tafada, 650 m, Sventenius 157, 1955 (S); Bajamar, Risko, 2–300 m, Bornmüller Pl. Exs. Can. 2777, 1901 (S); Valle de Afur, Tablero, 600 m, 1921, Burchard Pl. Can. Exs. 3 (S); Taganana, Perrandière s. n., 1855 (S); La Longera, Mann s. n., 1803 (K).
- L. mouretii*. Morocco: Moyen-Atlas, Ifrane, Tizguit, 2000 m, Gattefossé 806, 1937 (K, S), Daiet Achlef, 2000 m, Gattefossé s. n., 1931 (S), Bekrit, Kenoual valley, 1800 m, Jehandiez 643, 1924 (K).
Cult.: Kew, Stearn s. n., 1938 (K).
- L. perezii*. Tenerife: Masca, Perez s. n., July 1907 and August, 1907 holotype and isotypes (K), Stork s. n., 1962 (S), Gran Andén, 800 m, Sventenius 159, 1945 (S), Tarbucho, 800 m, Burchard Pl. Can. Exs. 4, 1923 (S).
- L. preauxii*. Gran Canaria: Barranco de Fataga, Mirador de la Yegun, 27°48'N, 15°35'W, Swenson 541, 2001 (UPS); Angostura, 700 m, Kunkel s. n., cult in K, 504.66, 1967 (K); Barranco Angostura, 600 m, Kunkel Exs. Sel. Fl. Can. 62 (BM).
- L. puberulum*. Lanzarote: Famara, R. P. Murray s. n., 1892, 1400', 1902 (K), Burchard Pl. Exs. Can. 327, 1911 (K), and 450 m, Pl. Can. Exs. 12, 1924 (S); El Risco, 500 m, Hummel s. n., 1961 (S).
- L. redivivum*. Gran Canaria: Cult in Tarfeira Bot. Garden, originally from Los Organos, Valle Hermoso, La Gomera, Melville & D. Bramwell 72/10 (K).
- L. sinuatum* ssp. *sinuatum*. Morocco: Haut-Atlas, Amsmiz, 1100–1700 m, Balls s. n., 1871 (K).
Australia: South Australia, Kingston, corner Agnes St. & Strickland S, 36°50'S 139°52'E, Gibbons 454, 1985 (S).
Cyprus: Salamis, Larsen 432, 1963 (S), Famagusta, Hultén s. n., 1963 (S).
Greece: Attica, de Heldreich 1175, 1891 (S).
Israel: Zikhron Ya'aqov, Tantura, Aaronsohn & V. Täckholm 321, 1935 (S).
Lebanon: Saïda, Alonzo 338, 1934 (S).
Spain: Malaga, Fuengirola, Wrehler s. n., 1953 (S); Malaga, Nerja, Kretzhmer 44/32, 1932 (S).
Syria: Nakoura, Samuelsson 1191, 1932 (S).
- L. sinuatum* ssp. *baumierianum*. Morocco: Goulimine, Ifni, Maire & Wilczek 381, 1935 (S); Anti-Atlas, Jbel Bani, at river Dra between Foug-el-Hassan and Tindouf, Maire & Wilczek 495, 1935 (S); Anti-Atlas, Taghjicht, 600 m, Maire 3072, 1935 (S), Akka, Beaumier s. n., 1872 or 1873 (K).
- L. sinuatum* ssp. *bonduellei*
Morocco: Djebel el Maiz, 1000 m, Samuelsson 6864, 1936 (S); Quarzazat, 3900', Balls B2625, 1936 (S);
Algeria: Beni-Isghen, Chevallier s. n., 1902 (S); 15 km north of Ghardaïa, Anderberg 457, 1980 (S);
Cult. Belgium, Pepinster, Mairlot s. n., 1908 (S).
- L. spectabile*. Tenerife: Masca, 'El Guelgue', 500 m, Sventenius 160, 1940 (S).
- L. sventenii*. Gran Canaria: Galdar, Montana Amurga (cult. at Santa Lucia de Tirajana), Stearn 1150 (BM).
- L. vulgare*
Denmark: Jylland. Aalborg, Netzel s. n., 1896 (S).
England: North Somerset, between Burnham and Highbidge, White 1057, 1884 (S).
Germany: Borkum (island), Krummel 2523, 1885 (S).
Portugal: Estremadura, Nazaré, Rainha 2519, 1953 (S).
Sweden: Skåne, Vellinge, Bernstorp, Berggren s. n., 1898 (S); Halland, Galteskär s. n., 1898 (S).