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Phylogenetics of the Irano-Turanian taxa of *Limonium* (Plumbaginaceae) based on ITS nrDNA sequences and leaf anatomy provides evidence for species delimitation and relationships of lineages

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In a taxonomic and molecular phylogenetic study using nuclear ribosomal internal transcribed spacer (ITS) DNA sequences and anatomical data, the taxonomic status and relationships of Irano-Turanian *Limonium* spp. were investigated. The results of molecular phylogenetic analysis and anatomical synapomorphies showed that the Iranian *Limonium* spp. can be grouped into four major clades: (1) an unresolved clade including species of section *Pteroclados* as sister to all other *Limonium* spp.; (2) the *L. axillare* clade as sister to all Irano-Turanian and Mediterranean species; (3) a poorly supported clade consisting of species of section *Nephrophyllum*, *L. caspium*, *L. bellidifolium* and *L. iconium* of section *Limonium* subsection *Hyalolepidae* and the isolated species *L. sogdianum* (section *Siphonocalyx*) and *L. nudum* (section *Platyhymenium*); and (4) a well-supported clade including species of section *Limonium* subsection *Limonium*, part of section *Sarcophyllum* and *L. lilacinum* of section *Sphaerostachys*. The most diverse Mediterranean clade with many microspecies and apomictic taxa has no representatives in the Irano-Turanian area. The ITS results agree with distribution and some morphological and anatomical characters, giving strong support for separating *L. perfoliatum* and *L. reniforme* that have been considered conspecific in all recent taxonomic treatments. An updated key to all known Iranian *Limonium* spp., a synopsis of all species, with distribution maps, and descriptions and illustrations of Iranian species of section *Nephrophyllum* are provided.

ADDITIONAL KEYWORDS: Anatolia – Caryophyllales – endemism – flora of Iran – halophytes –Mediterranean – south-west Asian flora – taxonomy.

INTRODUCTION

The genus *Limonium* Mill. (Plumbaginaceae) is a cosmopolitan halophytic genus, with *c*. 350 species; it is most diverse in the Mediterranean area (Kubitzki, 1993). In the Middle Eastern deserts and salt marshes, this genus is represented in Anatolia by *c*. 22 species (Bokhari & Edmondson, 1982; Tan & Sorger, 1984, 1986; Yıldırımlı & Doğru-Koca, 2006; Dogan, Duman & Akaydin, 2008) and in the *Flora Iranica* area (including Iran, Afghanistan, western Pakistan and adjacent areas of Iraq and Turkmenistan) by 14 species (Rechinger & Schiman-Czeika, 1974). Additional species have been reported to occur in Iran in some post-*Flora Iranica* studies (Bokhari, 1982; Assadi, 1989; Akhani & Ghorbanli, 1993; Assadi, 2005). It is counter-intuitive that, in spite of a rich halophytic and xerophytic flora in the Middle East and Central Asia (Khan *et al*., 2006), *Limonium* is comparatively much less diverse than in the Mediterranean area. There are also several genera related to *Limonium* that have representatives in the Irano-Turanian area, but these have been subject to different generic interpretations in taxonomic treatments;

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these include: *Cephalorhizum* Popov & Korovin, *Dictyolimon* Rech.f., *Aeoniopsis* Rech.f., *Chaetolimon* Lincz., *Eremolimon* Lincz., *Goniolimon* Boiss., *Ikonnikovia* Lincz. *Popoviolimon* Lincz., *Neogontscharovia* Lincz., *Bamiania* Lincz., *Bukiniczia* Lincz. and *Vassilczenkova* Lincz. (Linczevski, 1971, 1979, 1985; Rechinger & Schiman-Czeika, 1974).

Some *Limonium* spp. in *Flora Iranica* were described by Rechinger as section *Nephrophyllum* Rech.f., which comprises two species *L. otolepis* (Schrenk) Kuntze and *L. reniforme* (Girard) Lincz. This section is characterized by round–reniform amplexicaul cauline leaves, reduced and ephemeral rosulate leaves and an obconical calyx with narrow limbs. *Limonium otolepis* has a Central Asian distribution ranging from Turkmenistan, through Kazakhstan, Kyrgyzstan and Tajikistan, to northern China in Gansu and northern Xinjiang (Linczevski, 1952; Pen & Kamelin, 1996). This species has been introduced into North America (Hickman, 1993; Smith, 2005). *Limonium reniforme* in its former circumscription has a similar range but extends into south-central Iran. Earlier morphological and geographical studies by the first author (H.A.) showed that these last populations of *L. reniforme* (*sensu* Rechinger & Schiman-Czeika, 1974) differ markedly from the northern populations in Iran by their sterile branches. The presence of such sterile branches caused Assadi (2005) to classify these plants as *L. otolepis*. In order to clarify this problem, we conducted more studies of *Limonium* in Iran, including detailed morphological, anatomical and molecular studies. The aims of this paper are to: (1) test the application of internal transcribed spacer (ITS) sequence data in reconstruction of phylogenetic relationships and as taxonomic markers for the Irano-Turanian lineages of *Limonium*; (2) test the congruence of morphological and molecular data with the traditional classification of the genus; (3) clarify the phylogeography of Iranian *Limonium* spp. and their putative origin; and (4) present an updated synopsis of the genus in Iran, an identification key and distribution maps.

MATERIAL AND METHODS

Morphological and taxonomical studies

Natural populations of these species have been investigated during several excursions throughout Iran since 1988 and to Turkmenistan during 1994, mostly by the first author (H.A.), but joined in 2007 by the second author (M.M.). Herbarium specimens from several herbaria in Iran and Europe (including B, IRAN, K, TARI, TUH, P and W; abbreviations following *Index Herbariorum*, (Thiers, 2009) and the private herbarium of the first author (Hb. Akhani, currently housed in the Halophytes and C_4 Plants Research Laboratory, School of Biology, University of Tehran), have been studied. An updated key to identification and a synopsis of all accepted species growing in Iran, distribution maps and descriptions of three species with new taxonomic status and their illustrations are provided, according to data obtained by the authors. Many type specimens have been examined by the first author in short herbarium visits since 1990 in B, G, K, P and W. However, we are unable to lectotypify most names, as these short visits did not have this as a primary aim.

Anatomical Studies

Anatomical studies were made on leaf epidermis, lamina and petiole cross sections. Forty-two samples belonging to 14 species were studied. Fresh leaves were fixed during field studies in FAA (one part formalin, one part glacial acetic acid, 18 parts 70% ethanol). The samples were transferred to 70% ethanol after 1 week. Using a razor blade, cross sections were cut from the middle of the leaf lamina and from the lower half of the petiole. Sections were stained in aqueous methylene blue/carmine and dehydrated through an ethanol series and xylene. The dehydrated samples were permanently mounted in Euparal. Epidermal characters were studied on herbarium samples following the method described by Bokhari (1972): leaves were soaked overnight in 10% potassium hydroxide (KOH) solution with a few drops of hydrogen peroxide (H_2O_2), washed with distilled water and allowed to stand in water with a few drops of H_2O_2 for 2 h. They were then thoroughly washed with water and placed in 'Eau de Javelle' for bleaching. After washing with distilled water, the upper epidermis became loosened and was easily peeled off. The epidermal peels were stained with toluidine blue. After thorough dehydration, the peels were mounted in Euparal. Sclereids were studied in both cross and longitudinal sections to get a three-dimensional view. Observations were made with a Nikon Optiphot-2 microscope, and photographs were taken with a Motic image plus 2.0 camera; measurements were made using a calibrated Motic image plus 2.0 software. Line drawings of the sclereids are included here.

DNA sequencing

Most samples in this study were collected during various excursions in Iran, Turkey, Uzbekistan, France and Italy by the first author. In most cases, leaves were collected in silica gel during field studies (Chase & Hills, 1991). Additional samples were taken from herbarium specimens. DNA was extracted using AccuPrep GMO DNA Extraction Kit according to the manufacturer's protocol. Amplification of the ITS region (ITS1 and ITS2 spacers plus the 5.8S gene)

used the ITS5 and ITS4 primers of White *et al*., (1990) and followed the protocol of Van den Berg *et al*. (2000). Amplified products were purified using NucleoSpin PCR purification columns in accordance with the manufacturer's protocols. Cycle sequencing reactions were performed using the BigDye Terminator Kit ver. 3.1 (Applied Biosystems Inc., ABI, Warrington, UK) following the ABI protocols. Cycle sequencing products were cleaned using Magnesil (Promega, Southampton, UK) on a Beckman Coulter robot (Biomek NX S8, Buckinghamshire, UK) following the manufacturer's protocols. Cleaned products were then sequenced on an ABI 3730 Genetic Analyser following the manufacturer's protocols.

Sequencing output files were edited and contigs assembled either by using Sequencher 4.0 (Genecodes, Ann Arbor, MI, USA) or PhyDe. Sequences were aligned using Muscle and manually improved following the guidelines of Kelchner (2000). Trees were produced using the maximum likelihood method (ML) with 1000 replicates in MEGA5 (Tamura *et al*., 2011). The Tamura Nei model (Tamura, 1992) with gamma rate (TN93+G) was found to fit best with the ITS data nucleotide matrix. The tree with the highest likelihood is generated. Initial tree(s) for the heuristic search were obtained automatically as follows. When the number of common sites was < 100, or less than 25% of the total number of sites, the maximum parsimony method was used; otherwise the BIONJ method with Markov linkage clustering (MCL) distance matrix was used. Bootstrapping was calculated according to Felsenstein's (1985) method. Maximum parsimony (MP) produced a similar topology with small differences in bootstrap support, which are not discussed in this paper.

RESULTS

Anatomical descriptions

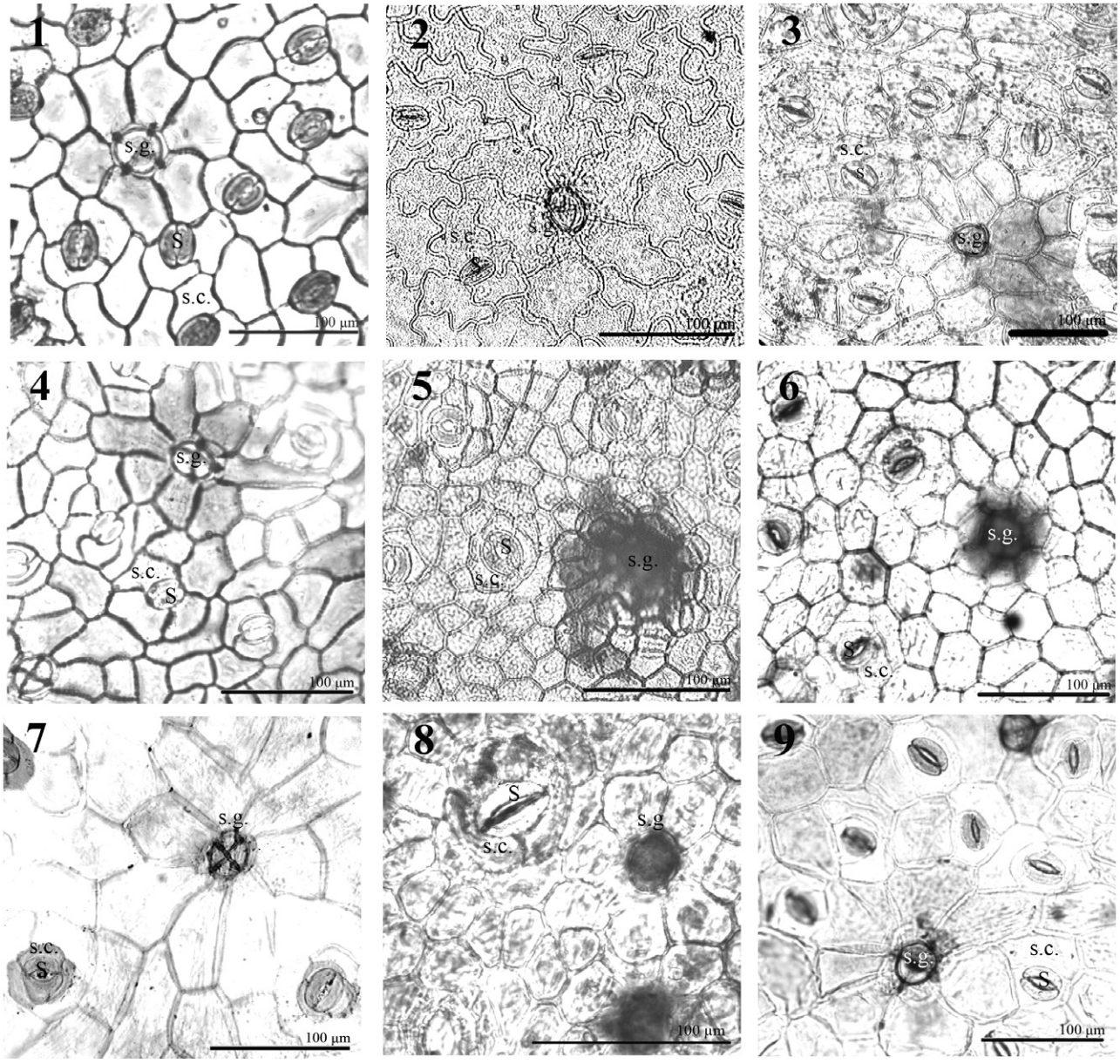
Epidermal cells and trichomes

The periclinal cell walls of the abaxial and adaxial leaf surfaces of Iranian *Limonium* spp. fall into two categories: (1) species with wavy or sinuous epidermal cells including *L. caspium* (Willd.) Gams, *L. nudum* (Boiss. & Buhse) Kuntze, *L. otolepis*, *L. perfoliatum* (C.A.Mey ex Boiss.) Kuntze, *L. reniforme* and *L. sogdianum* (Pop.) Ikonn.-Gal. (Table 1, Figs 1–4); and (2) species with entire epidermal cell walls including *L. carnosum* (Boiss.) Kuntze, *L. iranicum* (Bornm.) Lincz., *L. suffruticosum* (L.) Kuntze, *L. gmelinii* (Willd.) Kuntze, *L. meyeri* (Boiss.) Kuntze, *L. axillare* (Forssk.) Kuntze, *L. stocksii* (Boiss.) Kuntze and *L. lobatum* (L.f.) Kuntze (Table 1, Figs 5–9).

Stomata and salt glands: Stomata in all species are anisocytic with three subsidiary cells; rarely in

Table 1. The epidermal characters of basal leaves in Iranian *Limonium*. Data on subsidiary cells and cells around salt glands refer to their size in comparison with other epidermal cells

Species	Epidermal cells wall		Stomatal density (500 × 500 μm)		Subsidiary cells/epidermal cells	Cells around salt glands/ epidermal cells	Stomata level	Salt gland level
	Abaxial	Adaxial	Abaxial	Adaxial				
L. axillare	Entire	Entire	(39) 40.66 ± 1.52 (42)	(36) 39.6 ± 3.04 (43)	Similar	Similar	Sunken	Sunken
L. carnosum	Entire	Entire	(20) 21.5 ± 1.29 (23)	(24) 25.75 ± 2.21 (29)	Similar	Similar	Sunken	Sunken
L. caspium	Wavy	Wavy	(21) 24.62 ± 2.87 (29)	(18) 19.8 ± 1.78 (22)	Similar	Longer	At surface	At surface
L. iranicum	Entire	Entire	(22) 24.66 ± 2.59 (29)	(21) 26.28 ± 3.4 (31)	Similar	Similar	Sunken	Deeply sunken
L. lobatum	Entire	Entire	(23) 26.85 ± 2.47 (31)	(20) 21 ± 1.01 (23)	Smaller	Longer	At surface	At surface
L. gmelinii s.l.	Entire	Entire	(22) 26.16 ± 5.78 (41)	(15) 24.5 ± 7.27 (36)	Smaller	Longer	At surface	At surface
L. nudum	Wavy	Wavy	(26) 31.89 ± 2.65 (35)	(26) 27.33 ± 1.15 (28)	Similar	Longer	At surface	At surface
L. otolepis	Wavy	Sinuous	(16) 22.75 ± 3.77 (27)	(13) 17 ± 4.61 (21)	Similar	Longer	At surface	At surface
L. perfoliatum	Sinuous	Sinuous	(18) 20.2 ± 2.4 (24)	(20) 21.77 ± 1.56 (25)	Similar	Longer	At surface	At surface
L. reniforme	Sinuous	Sinuous	(19) 22.25 ± 2.81 (24)	(27) 27.5 ± 0.7 (28)	Similar	Longer	At surface	At surface
L. sogdianum	Wavy	Wavy	(27) 29 ± 1.41 (31)	(38) 42.4 ± 3.04 (46)	Similar	Longer	At surface	At surface
L. stocksii	Entire	Entire	(21) 21.6 ± 0.89 (23)	(15) 16 ± 0.81 (17)	Similar	Similar	Sunken	Sunken
L. suffruticosum	Entire	Entire	(16) 25.3 ± 8.73 (36)	(13) 20 ± 6.48 (32)	Similar	Similar	Sunken	Deeply sunken



Figures 1–9. Epidermal cells of adaxial leaf sides of *Limonium*. Fig. 1. *L. nudum* (*Akhani et al. 18804*). Fig. 2. *L. perfoliatum* (greenhouse cultivated plant, no voucher). Fig. 3. *L. caspium* (*Akhani et al. 18888*). Fig. 4. *L. sogdianum* (*Akhani & Memariani 19059*). Fig. 5. *L. iranicum* (*Malekmohammadi et al. 3826*). Fig. 6. *L. suffruticosum* (*Akhani & Joharchi 35188*). Fig. 7. *L. gmelinii* (*Akhani et al. 18946*). Fig. 8. *L. stocksii* (*Akhani 9750*). Fig. 9. *L. lobatum* (*Hekmatara 3978*). S., stomata; s.g., salt gland; s.c. subsidiary cells. Scale bars, 100 µm.

L. axillare, *L. carnosum*, *L. iranicum*, *L. perfoliatum* (C.A.Mey.ex Boiss.) Kuntze, *L. reniforme*, *L. sogdianum* and *L. suffruticosum* four and five subsidiary cells have been observed (Figs 2, 4, 5). Subsidiary cells in most species are the same size as other epidermal cells, with the exception of *L. gmelinii* and *L. lobatum*, in which they are smaller (Table 1, Figs 7, 9).

Stomata on the adaxial and abaxial lamina surface are almost the same size. Their density ranges from an average of 16 per 500 × 500 µm on the adaxial surface of *L. stocksii* to 40.6 on the abaxial side of *L. axillare* (Table 1). In the majority of species, stomatal density on the abaxial surface is higher than the adaxial surface (Table 1). Stomata and salt glands occur mostly on the same level as other epidermal cells, except in *L. axillare*, *L. carnosum*, *L. iranicum*, *L. stocksii* and *L. suffruticosum* where they are sunken (Table 1). Cells adjacent to the salt glands are

Table 2. Leaf anatomical characteristics of studied species of Iranian *Limonium*. Abbreviations and symbols used in position of sclerenchyma tissue: P, palisade; PS, between palisade and spongy tissues; S, spongy tissue; +, present; ±, scarcely present; –, absent

Species	Palisade tissue layers		Position of sclerenchyma cells	Sclereid type
	Abaxial	Adaxial		
L. axillare	4	3	P (+), SP (±), S (-)	Fusiform
L. carnosum	2 (midvein) 3 (blade)	2 (midvein), 3 (blade)	P (±), PS (+)	Fusiform
L. caspium	Absent	1	Absent	Absent
L. iranicum	2 (midvein), 3 (blade)	2 (midvein), 3 (blade)	PS (+), penetrating sometimes to palisade	Fusiform
L. lobatum	Absent	2	Absent	Absent
L. gmelinii	Absent	1–2 (midvein*), 3–4 (blade)	P (+), midvein (very rare)	Ramiform
L. nudum	Absent	1 (midvein), 2 (blade)	Absent	Absent
L. otolepis	Absent	0 (midvein), 1 (blade)	Absent	Absent
L. perfoliatum	Absent	1–2	Absent	Absent
L. reniforme	Absent	1–2	Absent	Absent
L. sogdianum	0 (midvein), 3 (blade)	3 (midvein), 4 (blade)	P (±), PS (+)	Fusiform
L. stocksii	3–4 layers	3 layers	PS (+)	Fusiform
L. suffruticosum	2 (midvein), 3 (blade)	2 layers	P (±), PS (+)	Fusiform

*Short palisade-like cells in midvein.

either the same size as other epidermal cells or remarkably larger; for example, in species with sinuous epidermal cells and *L. lobatum*, *L. gmelinii* and *L. sogdianum* (Table 1, Figs 1–4, 7, 9).

All species are glabrous except *L. lobatum*, which has unicellular, non-glandular and conical trichomes on midrib, secondary ribs and margins of leaves.

Leaf anatomy

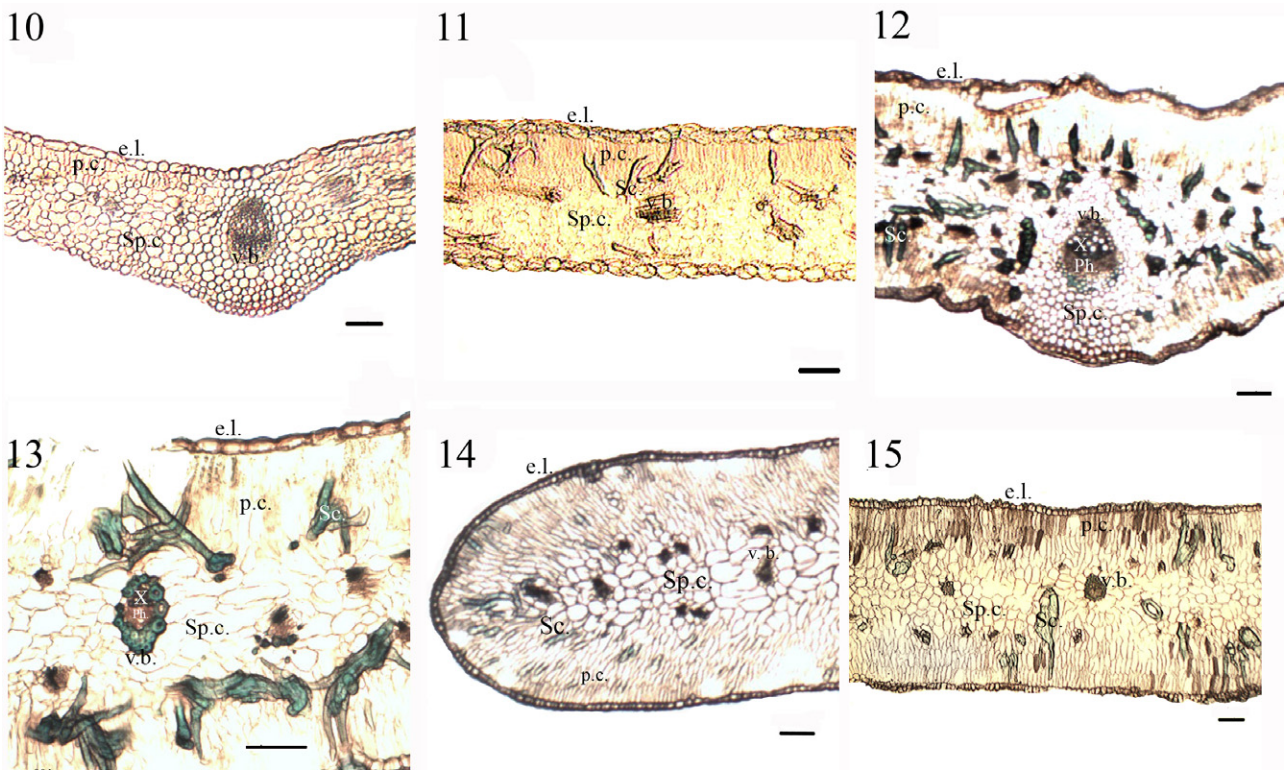
All species are characterized by having a one-layered epidermis followed by the palisade tissue. Based on number and position of palisade cells, the studied species can be grouped into three categories: (1) a bifacial group with one or two palisade layers occurring only in the adaxial leaf lamina, e.g. *L. caspium*, *L. nudum*, *L. otolepis*, *L. perfoliatum* and *L. reniforme* (Table 2, Fig. 10); (2) a sub-bifacial group with two or three palisade layers on the adaxial leaf lamina and a single-layered palisade tissue on the abaxial side (the palisade cells of the abaxial sides are shorter than those of adaxial side and therefore have an intermediate form between spongy cells and palisade cells such as *L. gmelinii*) (Fig. 11); and (3) an isobilateral group in which a more or less uniform palisade tissue consisting of two to four layers is present on both sides of the lamina, as in *L. axillare*, *L. carnosum*, *L. iranicum*, *L. sogdianum*, *L. stocksii* and *L. suffruticosum* (Table 2, Figs 12–15).

Arrangement of vascular bundles (VB) in leaf lamina and petiole cross sections is more or less similar (see below). An incomplete arc-like sclerenchymatous bundle sheath tissue covers the phloem in *L. carnosum*, *L. gmelinii*, *L. perfoliatum*, *L. stocksii* and *L. suffruticosum*, and a complete or partially complete sclerenchymatous tissue encircles the vascular bundles in *L. axillare*, *L. iranicum*, *L. otolepis* and *L. reniforme* (not illustrated).

Petiole anatomy

The outline of petiole transections of studied species are narrowly elliptic (*L. nudum*, Fig. 16) or arc-like to crescent-shaped (*L. capsicum, L. otolepis*, *L. perfoliatum* and *L. reniforme*, Figs 17, 18), semicircular–ovate (*L. sogdianum*, Fig. 19), circular to semicircular with intruded margin (*L. carnosum*, *L. iranicum* and *L. suffruticosum*, Figs 20, 21), more or less fusiform (*L. gmelinii*, Fig. 22, partially shown) or elliptic (*L. axillare* and *L. stocksii*, Figs 23, 24).

With regard to presence and position of palisade tissue in the petiole, Iranian *Limonium* can be grouped into four categories: (1) a bifacial group with one to three layers of palisade cells on the adaxial side of the petiole in *L. lobatum* (not shown), which might be small palisade-like cells as in *L. gmelinii* (Fig. 22); (2) a sub-bifacial category with two or three palisade layers on the adaxial side and a discontinuous layer of palisade-like tissue on the edges of abaxial side, as in *L. sogdianum* and *L. nudum*, (Figs 16, 19); (3) an isobilateral group with a well-developed and more or less uniform two to four layers of palisade tissue on both sides, as in *L. axillare*, *L. carnosum*, *L. iranicum*, *L. stocksii* and *L. suffruti-*



Figures 10–15. Leaf cross section of some representative *Limonium* species from Iran. Fig. 10. *L. perfoliatum* (*Akhani et al. 18808*). Fig. 11. *L. gmelinii* (*Akhani et al. 18946*). Fig. 12. *L. sogdianum* (*Akhani & Memariani 19059*). Fig. 13. *L. suffruticosum* (*Akhani & Joharchi 35188*). Fig. 14. *L. axillare* (*Malekmohammadi et al. 3974*). Fig. 15. *L. stocksii* (*Akhani 9750*). Sc., sclerenchyma; e.l., epidermal layer; v.b., vascular bundle; p.c., palisade cells; Sp.c., spongy cells; Ph., phloem; X, xylem. Scale bars, 100 ∝m.

cosum (Figs 20–21, 23–24); and (4) species lacking palisade tissue in petiole sections as in *L. caspium*, *L. otolepis*, *L. perfoliatum* and *L. reniforme* (Figs 17–18).

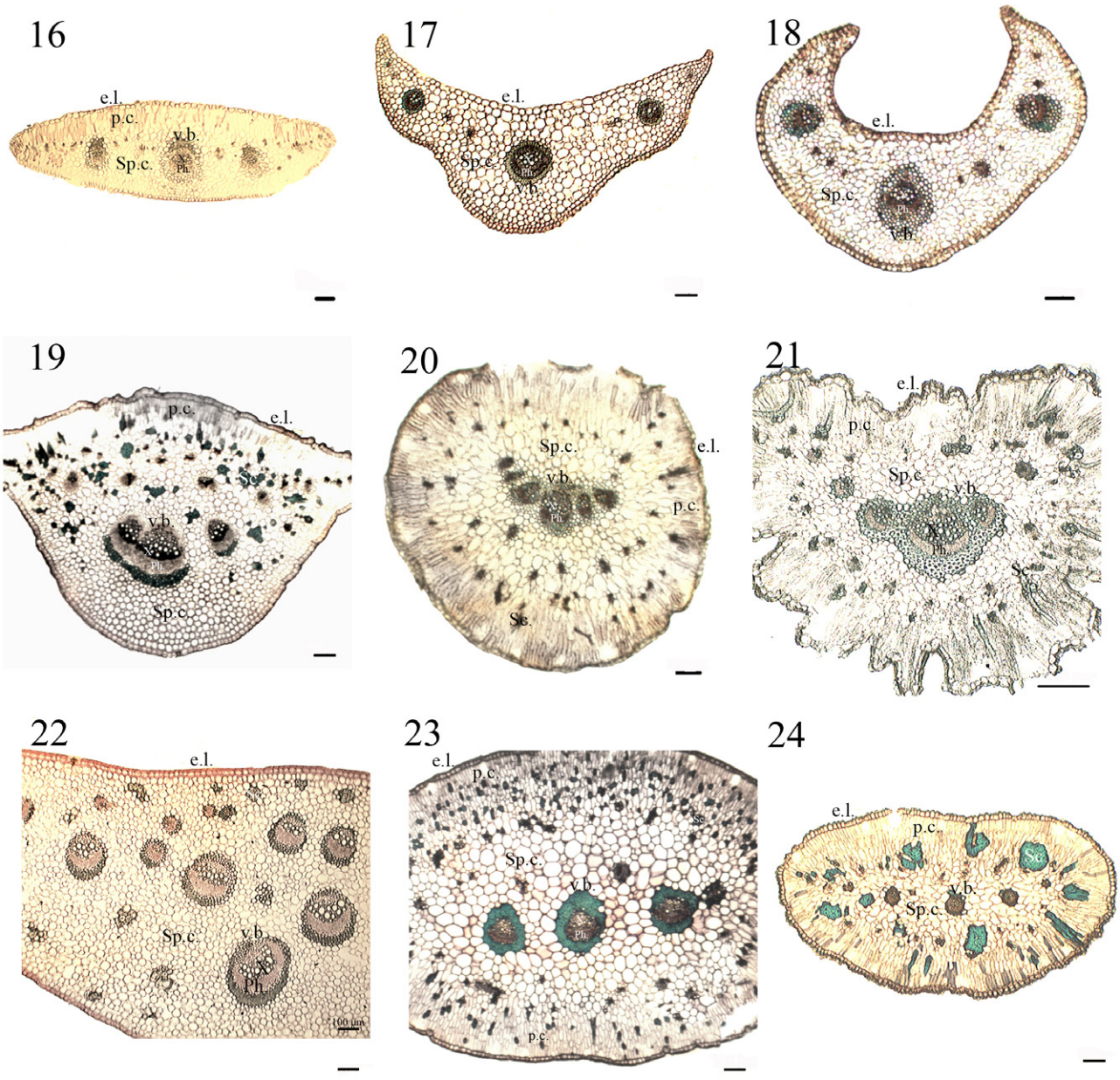
Vascular bundles in leaf and petiole

The general pattern of vascular bundle distribution in lamina and petiole is more or less similar. In *L. perfoliatum*, *L. caspium*, *L. otolepis, L. nudum* and *L. reniforme* there are three to five (rarely more) large vascular bundles arranged in a line with smaller accessory bundles between them (Table 3, Figs 10, 16–18). *Limonium sogdianum* is characterized by having one main vascular bundle in the middle with smaller accessory bundles nearby (Fig. 19). In *L. carnosum*, *L. iranicum* and *L. suffruticosum* there is a large vascular bundle in the centre associated with one to three smaller bundles on each side (Figs 13, 20, 21). In *L. gmelinii* there are several vascular bundles in the central part that are located irregularly and vary in size and orientation (Fig. 22). The related species *L. axillare* and *L. stocksii* are characterized by having three main vascular bundles in the middle and additional peripheral accessory bundles in the spongy tissue (Figs 14, 15, 23, 24).

Sclereids

Diffuse foliar sclereids occur only in *L. axillare*, *L. carnosum*, *L. iranicum*, *L. sogdianum*, *L. stocksii*, *L. suffruticosum* and *L. gmelinii*, which could be classified into two main groups using terminology suggested by Rao & Das (1981) (Figs 25–30).

Fusiform: This kind of sclereid is spindle-shaped, narrow at the end, without branches, straight or variously bent into C, V or S shapes, arranged vertically or horizontally. These are located in spongy and/or palisade tissue, as in *L. axillare*, *L. carnosum*, *L. iranicum*, *L. sogdianum*, *L. stocksii* and *L. suffruticosum* (Figs 25–28). There are differences including length, width and cell-wall thickness in different species: (1) in *L. axillare* they are mostly needle-like, straight, with thin and ± smooth cell walls, 300–600 μm in length, and with an average outer diameter of 20 μm in the middle. They occur singly in palisade tissue (Figs 23, 25); (2) in *L. stocksii* the cell walls of

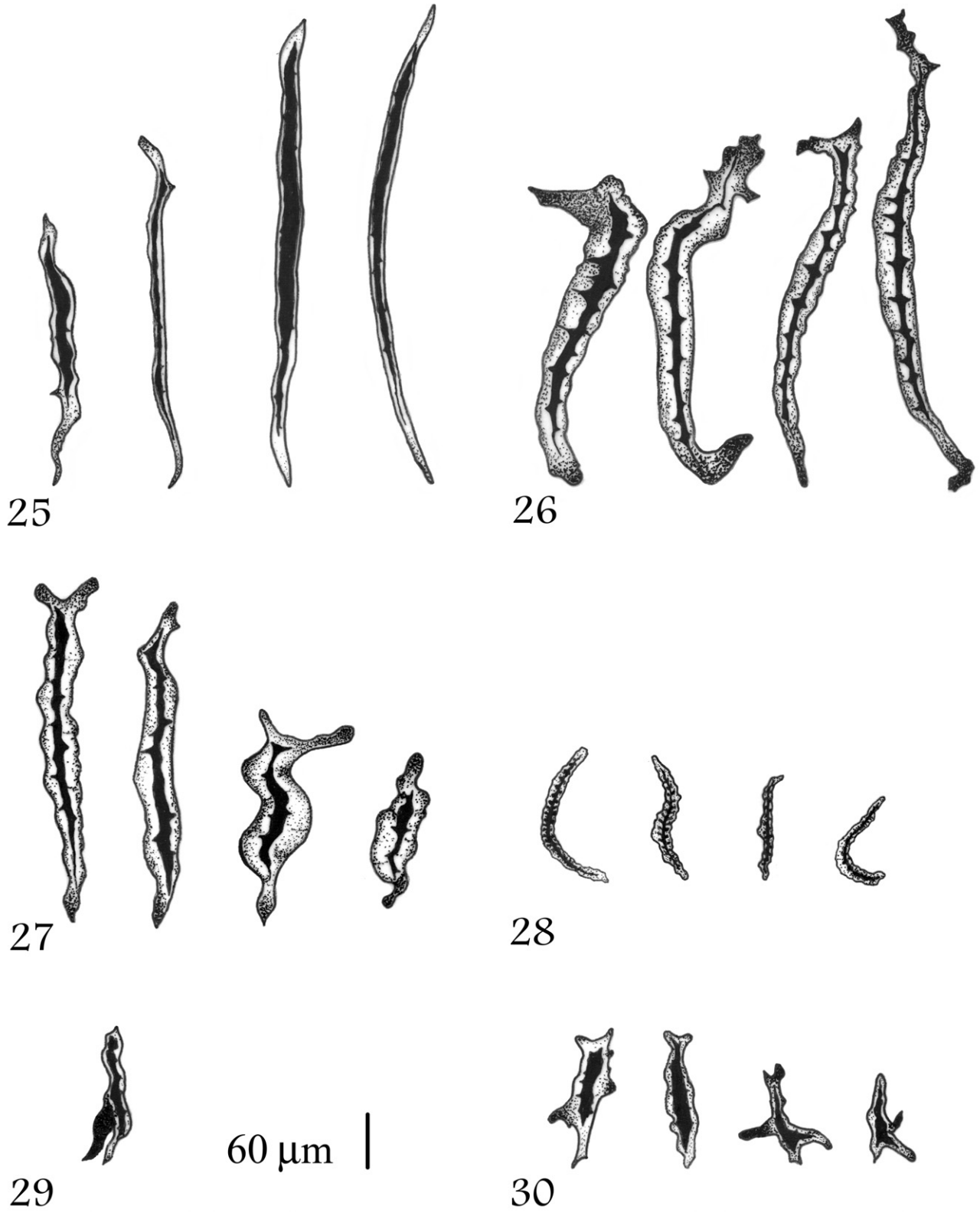


Figures 16–24. Petiole cross section of representative *Limonium* species from Iran. Fig. 16. *L. nudum* (*Akhani et al. 18804*). Fig. 17. *L. perfoliatum* (*Akhani et al. 18808*). Fig. 18. *L. caspium* (*Akhani et al. 18888*). Fig. 19. *L. sogdianum* (*Akhani & Memariani 19059*). Fig. 20. *L. iranicum* (*Malekmohammadi et al. 3809*). Fig. 21. *L. suffruticosum* (*Akhani & Joharchi 35188*). Fig. 22. *L. gmelinii* (*Malekmohammadi et al. 3827*). Fig. 23. *L. axillare* (*Malekmohammadi et al. 3974*). Fig. 24. *L. stocksii* (*Akhani 9750*). Sc., sclerenchyma; e.l., epidermal layer; v.b., vascular bundle; p.c., palisade cells; Sp.c., spongy cells; Ph., phloem; X, xylem. Scale bars, 100 µm.

sclereid cells are thickened and pitted and the length varies from 300 to 600 µm, with an average of 50 µm diameter in the middle; they occur both singly or in groups in the lamina, but are mostly seen in groups in the petiole (Figs 24, 26); (3) *L. sogdianum* is characterized by polymorphic sclereids with thickened cell walls, and length varies from 200 to 550 µm and an average of 70 µm outer diameter in the middle (Figs 19, 27); and (4) *L. carnosum*, *L. iranicum* and *L. suffruticosum* have fusiform sclereids mostly C, V or S- shape, rarely erect, with pitted and pointed appearance in the cell wall, 100–250 µm in length and with an average of 20 µm outer diameter in the middle (Figs 13, 20, 21, 28).

Table 3. Petiole anatomical characteristics of studied species of Iranian *Limonium*. Abbreviations and symbols used in position of sclerenchyma tissue: P, palisade; PL, palisade-like; PS, between palisade and spongy tissues; S, spongy tissue; +, present; ±, scarcely present; –, absent

Species	Palisade tissue layers		Arrangement of vascular bundles (VB)	Position of sclerenchyma cells
	Abaxial	Adaxial		
L. axillare	4	3–4	3 large VB in centre, some smaller VB in spongy tissue	P (+), PS (±), S (–)
L. carnosum	2 (midvein), 3 (blade)	2 (midvein), 3 (blade)	1 large VB, smaller VB in line with the main and dispersed in spongy tissue	P (±), PS (+)
L. caspium	0	0	3 large VB, small intercalary VB occur between them on the same line	Absent
L. gmelinii	0	0 (midvein), 2 (blade), 3 (edges)	Irregularly distributed in central part, secondary veins are horizontally derived from central bundles	P (+), PS (rare), S (+)
L. iranicum	2 (midvein), 3 (blade)	2 (midvein), 3 (blade)	1 large VB, smaller VB in line with the main and dispersed in spongy tissue	PS (+), penetrating sometimes to palisade
L. lobatum	0	2 PL	1 large, small VB dispersed in spongy tissue	Absent
L. nudum	0 (midvein), 2 (blade edges)	2	3 large VB, small intercalary VB occur between them on the same line	Mostly absent, rarely occur in S
L. otolepis	0	0	3 large VB, small intercalary VB occur between them on the same line	Mostly absent, rarely occur in S
L. perfoliatum	0	0	3 large VB, small intercalary VB occur between them on the same line	Mostly absent, rarely occur in S
L. reniforme	0	0	3 large VB, small intercalary VB occur between them on the same line	Mostly absent, rarely occur in S
L. sogdianum	0	2–3	1 large VB, smaller VB occur on the same line and are distributed on adaxial side of spongy tissue	P (–), PS (±), S (+) (only on adaxial side)
L. stocksii	3	2 (midvein), 3 (blade)	3 large VB in centre, some smaller VB in spongy tissue	P (–), PS (+), S (±)
L. suffruticosum	3	2	1 large VB, smaller VB in line with the main and dispersed in spongy tissue	P (–), PS (+), S (–)



Figures 25–30. See caption on next page.

Figures 25–30. Sclereid illustrations. Fig. 25. Fusiform sclereids in *L. axillare* (*Malekmohammadi et al., 3974*). Fig. 26. Fusiform sclereids in *L. stocksii* (*Akhani 9750*). Fig. 27. Fusiform sclereids in *L. sogdianum* (*Akhani & Memariani 19059*). Fig. 28. Fusiform sclereids in *L. iranicum* (*Akhani & Malekmohammadi 18842*). Fig. 29. Rhizoscelereids in *L. gmelinii* (*Akhani & Malekmohammadi 18852*). Fig. 30. Ramiform sclereids in *L. meyeri* (*Akhani & Malekmohammadi 18852*). Scale bar, 60 μm.

Rhizosclereids and ramiform sclereids: root-like sclereids, short, with two or three branches at one end only and thick and pitted cell walls are characteristic of palisade tissue in *L. gmelinii s.l.* (Fig. 29). Ramiform sclereids are similar to short rhizosclereids, with thick cell walls that are pitted but with forking in both ends. This type also occurs only in *L. gmelinii s.l.* (Fig. 30).

PHYLOGENETICS

New ITS sequences were provided in this study for 74 accessions belonging to 19 *Limonium* spp., one *Cephalorhizum* sp. and two *Psylliostachys* spp. Sequences of eight species were included from GenBank (accession numbers are provided in the Appendix). After trimming the ends of the matrix, the analysis involved 847 characters including 397 variable sites, among which 300 sites were potentially parsimony informative. The ML tree showing highest likelihood (ln = –4771.1757) is presented in Figure 31. Some important anatomical characters are shown or plotted on the tree with informal clade names. We apply the following descriptions for bootstrap percentage (BP): 50–74 poorly supported, 75–84 moderately supported and 85–100 well supported.

Apart from species of section *Pteroclados*, the remaining *Limonium* spp. (here called core *Limonium*) form a strongly supported clade (BP 99). The genera *Cephalorhizum* and *Psylliostachys* (outgroups) form a well-supported clade (BP 95). Internal relationships are largely resolved with five clades: (1) the *L. axillare* clade, sister to all other clades; (2) a moderately supported clade (BS 81) comprising species of section *Limonium* subsections *Dissitiflorae* Boiss. and *Steirocladae* Boiss. and *L. echioides* (subgenus *Limonium* section *Schizhymenium*) marked as 'Mediterranean clade'; (3) a poorly supported clade (BP 62) consisting species of section *Nephrophyllum* and *L. caspium*, *L. bellidifolium* (Gouan) Dumort and *L. iconium* (Boiss. & Heldr.) Kuntze of section *Limonium* subsection *Hyalolepidae*, *L. sogdianum* (section *Siphonocalyx*) and *L. nudum* (section *Platyhymenium*), all of which are collectively termed here the '*L. reniforme* clade'; (4) a well-supported clade (BP 91) including species of section *Limonium* subsection *Limonium*, part of section *Sarcophyllum* (*sensu* Rechinger & Schiman-Czeika, 1974) and *L. lilacinum* (Boiss. & Bal.) Wagenitz of section *Sphaerostachys* (*sensu* Bokhari & Edmondson, 1982), termed here the '*Limonium*-type clade'. This clade is subdivided into a *L. vulgare* subclade (BP 69) and *L. suffruticosum* subclade (BP 90).

DISCUSSION

PHYLOGENY

Our ITS tree includes almost all *Limonium* spp. in Iran, except *L. stocksii* (Rechinger & Schiman-Czeika, 1974); in addition, some endemic species from Turkey, some Mediterranean species, two species of *Psylliostachys* and one species of *Cephalorhizum* are included. The sampling includes representatives of main infrageneric taxa of *Limonium* from southwestern Asia according to Boissier (1848). ITS nuclear ribosomal DNA (nrDNA) provides enough variation for inferring phylogenetic relationships among major clades, but it also has good potential for being a useful molecular marker even among the most closely related species (see also Palacios, Rosselló & González-Candelas, 2000).

Our results confirm previous molecular studies based on plastid *rbcL*, *trnL* intron and the *trnL–trnF* intergenic spacer by Lledó *et al*. (2005); *Limonium*, as circumscribed in *Flora Iranica* and *Flora of Turkey* (Rechinger & Schiman-Czeika, 1974; Bokhari & Edmondson, 1982), is monophyletic. The situation in section *Pteroclados* requires more study (but see Lledó *et al*., 2011). Our results do not support splitting the genus into smaller genera, such as *Eremolimon*, as proposed by Linczevski (1979). Additionally, the independent status of *Cephalorhizum* and *Psylliostachys* as distinct from *Limonium* is strongly supported. However, additional sequences are required to clarify the relationships of some monotypic and oligotypic genera from Central Asia and Afghanistan, such as *Dictyolimon*, *Aeoniopsis*, *Chaetolimon, Ikonnikovia*, *Popoviolimon*, *Neogontscharovia*, *Bamiania*, *Bukiniczia* and *Vassilczenkova* (Linczevski, 1971, 1985), some of which are well supported as distinct in plastid trees (cf. Lledó *et al*., 2005).

The phylogenetic status of section *Pteroclados* remains unresolved. The sister position of this section to *Limonium* was only supported by 60 BP in the plastid analysis of Lledó *et al*. (2005), although the internal relationship of the two resulting groups (subsections *Odontolepideae* and *Pteroclados*) was strongly supported (100 BP). This section with distinctive winged stems comprises *c*. 15 species of

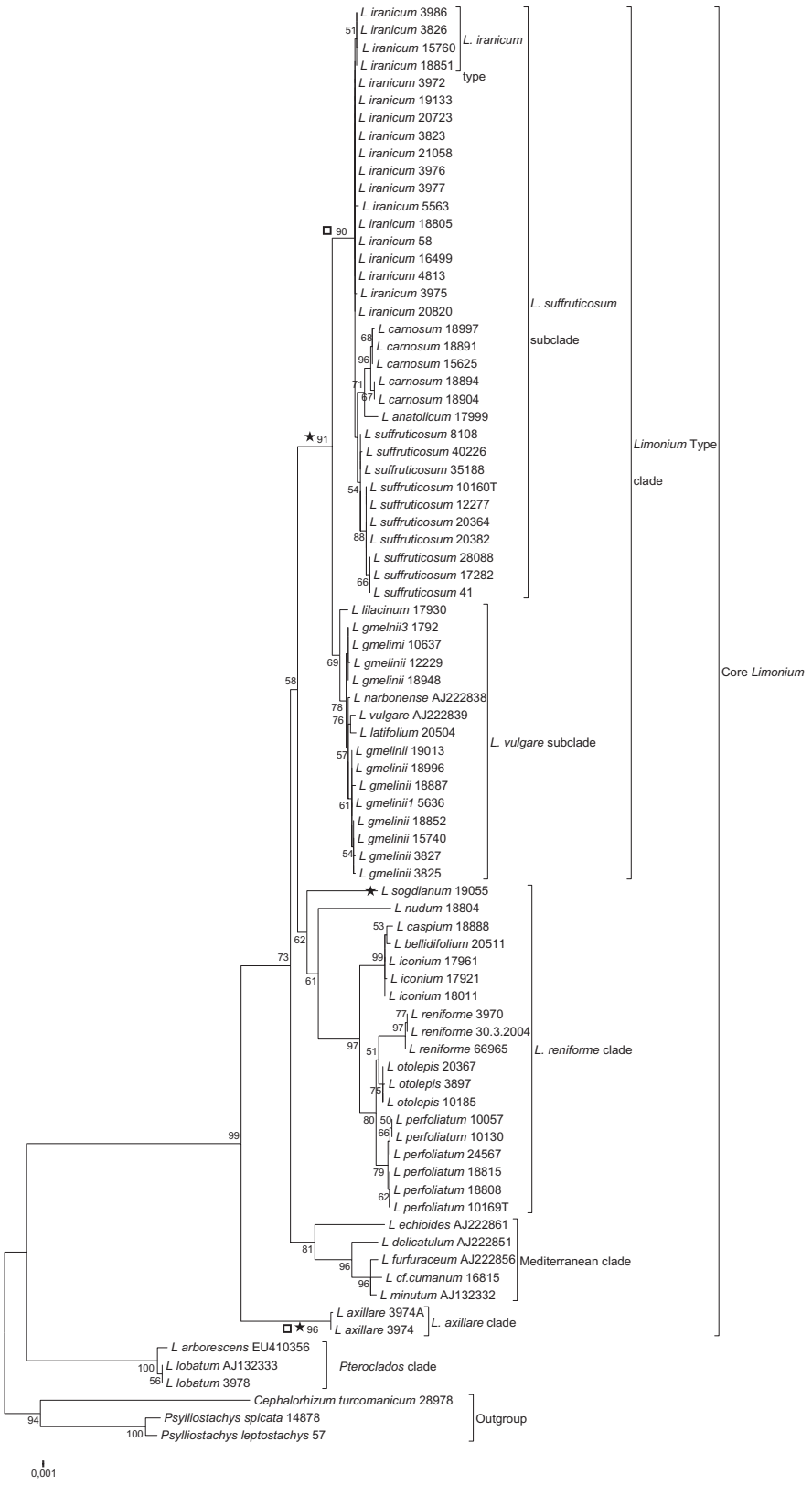


Figure 31. See caption on next page.

Figure 31. Maximum likelihood tree of Irano-Turanian lineages of *Limonium* obtained from analysis of the nuclear ribosomal internal transcribed spacers (nrITS) using TN93+G model (ln = –4771.1757). Numbers on branches are bootstrap percentages. An asterisk indicates occurrence of foliar sclereids and an empty square indicates presence of sunken stomata and isobilateral leaf anatomy.

annual herbaceous to shrubby species distributed from the Macaronesian to the Mediterranean and the Saharo-Sindian floristic regions (Karis, 2004). Anatomically, species of section *Pteroclados* subsection *Odontolepidae* contain no sclereids (see also Bokhari, 1970; Rao & Das, 1981) and have isobilateral leaf and bifacial petiole anatomy. This section is represented in southern Iran only by *L. lobatum*, the widespread annual species ranging from the Canaries through North Africa and the Mediterranean to southern Iran. The antiquity of extant species of some isolated groups of *Limonium*, such as species of sections *Pteroclados* and *Limoniodendron* in the Canaries and north-western Africa, was demonstrated based on morphological data by Karis (2004) and plastid phylogenetics by Lledó *et al*. (2005, 2011).

Limonium axillare is sister to the remaining species of the core-*Limonium* clade, which agrees with its position in analyses of plastid DNA sequences (Lledó *et al*., 2005). This species belongs to a small group of Saharo-Sindian species that were classified by Rechinger & Schiman-Czeika (1974) in section *Sarcophyllum* (Boiss.) Lincz. (including species of the *L. suffruticosum* subclade). *Limonium axillare* and its close relative *L. stocksii* are short shrubby species of hypersaline soils characterized by ± cushion habit and short flowering branches. They are restricted in their range in southern Iran along the shores of the Persian Gulf and Baluchestan. The most obvious anatomical feature separating *L. axillare* and *L. stocksii* from other species already classified in section *Sarcophyllum* is the presence of three main vascular bundles in petioles that are more or less the same size and separated by spongy tissue (Fig. 24). Furthermore, the leaf lamina has three main veins and petioles are flattened. In *L. iranicum*, *L. suffruticosum* and *L. carnosum*, the petiole cross section is characterized by three closely spaced bundles, of which the central one is larger than the laterals (Figs 20–21). The leaf lamina has a central midrib and the petioles are almost terete.

The Mediterranean species form a moderately supported clade (BP 81). Considering the unresolved relation with other clades, more studies are required, including a wider sampling of central and eastern Mediterranean taxa to clarify the origin of this rapidly diversifying lineage in the Mediterranean basin. Frequent apomixis and hybridization in this clade are further complications for resolving their phylogenetic relationships (Palacios *et al*., 2000; Lledó *et al*., 2005).

The '*L. reniforme* clade' is poorly supported (BP 62) and consists of endemic species of the Irano-Turanian area belonging to sections *Nephrophyllum* Rech.f. and *Platyhymenium* (Boiss.) Lincz. (according to *Flora Iranica*, Rechinger & Schiman-Czeika, 1974) or section *Limonium* subsection *Platyhymenium* (according to Boissier, 1848), in addition to species of the *L. bellidifolium* complex (*L. caspium* and *L. iconium*) and *L. sogdianum*. Except for *L. nudum* and *L. sogdianum*, all these species were classified in section *Limonium* subsection *Hyalolepidae* by Boissier (1848). *Limonium nudum* and *L. sogdianum* are successively sister to a strongly supported group (BP 97). Both species are isolated strictly Irano-Turanian species restricted to gypsum hills.

The synapomorphies of the wavy to sinuous epidermal cell walls link all species of *L. reniforme*-clade. However, the epidermal cells of *L. sogdianum* are slightly wavy (Fig. 4) compared with those of *L. perfoliatum* and *L. reniforme*, which are clearly sinuous (Fig. 2). Other characters, such as bifacial leaf anatomy, absence of palisade cells in petiole cross section and absence of diffuse sclereids, are additional synapomorphies linking members of this clade, except for *L. sogdianum*. This last species differs anatomically from other species of this clade by having diffuse sclereids that are uniquely straight, thickened and unbranched and arranged only on the adaxial side (Tables 3 and 4; Figs 12, 27). Linczevski (1979) transferred *L. sogdianum* and other species of section *Siphonocalyx* Lincz. to his new genus *Eremolimon* because of the tubulate calyx and erect or slightly dilated calyx limb with its peculiar habit. Neither morphology nor our molecular analysis supports its segregation.

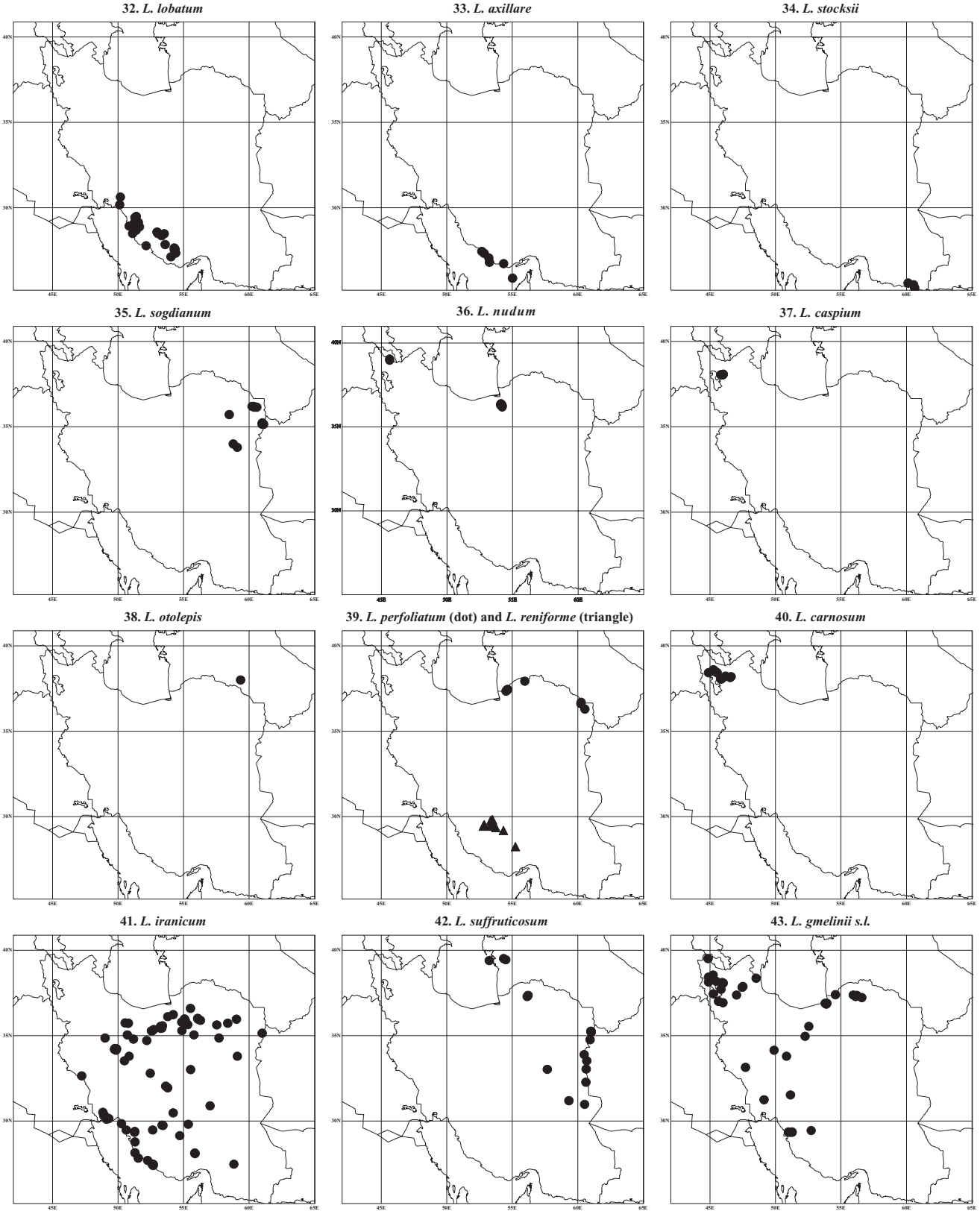
Limonium nudum is an isolated and geographically restricted species (Fig. 36). This is a typically unique plant among Iranian *Limonium* in having rosulate leaves and glomerate spikelets and large flowers (with petals up to 10 mm long).

The internal relationships of the *L. reniforme* clade show that three closely related western Irano-Turanian/Mediterranean species (*L. caspium*, *L. bellidifolium* and *L. iconium*) form a strongly supported group (BP 99), sister to three other closely related central Irano-Turanian species. The morphological and sequence differences between three species from Iran (*L. caspium*), Turkey (*L. iconium*) and France (*L. bellidifolium*) are minimal (see notes in taxonomic treatment).

Table 4. Comparison of morphological and anatomical characters of the three closely related species, *L. perfoliatum*, *L. otolepis* and *L. reniforme*. SD, stomatal density; SG, salt gland

Species / characters	*L. otolepis*	*L. reniforme*	*L. perfoliatum*
Height	40–50 (–90) cm	35–70 (–90) cm	50–95 (–150) cm
Sterile branches	Sterile branches numerous	Some lower branches sterile	Without sterile branches
Cauline leaves position	Only occurring on the lower nodes of main stem, rarely 1–2 small leaves present on nodes of lateral branches	Present on all nodes of main and lateral branches	Present on all nodes of main and lateral branches
Cauline leaf size	0.5–1.5 × 0.8–1.5 cm	0.5–2.5(–3.5) × 0.5–2.0(–3.0) cm	1.8–3.4 × 1.2–2.2 cm
Cauline leaf margin	Entire or slightly undulate	Entire	Entire and undulate
Length of inflorescence	17–30 cm	10–25 cm	24–70(–130) cm
No. of spikes per cyme	4–9	(1–)4–6	(5–)7–18
No. of flowers per spike	1(–2)	(1–)2	(2–)3
Outer bract size	0.5–1.0 × 1.0–1.5 mm	0.5–1.0 × 1.0–1.5(–1.7) mm	1.0–1.5(–1.7) × 1.0–1.5(–1.7) mm
Length of herbaceous part of outer bract	(0–)0.5 × 0–1 mm	(0–) 0.5–0.7 mm × (0–) 0.5–0.7 (–1.2)mm	1.0–1.5 mm × (0.2) 0.5–0.7 (1.0) mm
Middle bract length	0.5–1.0 mm × 0.5–1.0	(0.7-)1.0–1.5 × 1.0–1.2 mm	1.0–1.5 × 1.0–1.5 mm
Middle bract colour	Membranous, without nerve	Membranous with one or two brown nerves	Membranous usually with 1–2 narrow brown nerves
Inner bract length	1.5–2.0 × 2.0–2.5 mm	(1.5-)2.0–2.5 × 2.0–2.5 mm	2.5–3.0(-3.5) × 2.0–2.5 mm
Inner bract length of herbaceous part	1 mm	(1.0–) 1.5–2 mm	(1.7–)2.0–2.5(–2.7) mm
Bracteole shape	Obovate	Elliptic or orbicular rarely rhombic	Elliptic or broadly elliptic, rarely obovate
No. of bracteoles per spike	(0–)1	2–5(–7)	(1–)3–5(–8)
Calyx shape	Obconical	Obconical	Funnel form
Calyx length	2.0 mm	2.5–3.0 mm	(2.5–)3.5 mm
Calyx indumentum	Mostly with short or sometimes sparse long hairs on the basal 0.7 mm, hairs often confined to one side	Dense and short or more or less long hairs between nerves and on two nerves, other nerves glabrous or with short and lax hair, rarely calyx glabrous	Dense or sometimes lax long hairs on two or three of nerves, other nerves glabrous
Calyx diameter at apex	1.2–1.7 mm	(1.2–)1.5(–1.7) mm	2.0–3.0 mm
Calyx nerve	1.5 mm	2.0–2.5 mm	(2.0–)2.2–2.5(–3.0) mm
Length of calyx lobes	0.5 mm	0.5–0.7 mm	(0.5–)0.7–1.0 mm
Achene shape	Obovate	Fusiform	Obovate
Epidermal cells of leaf abaxial side	Wavy	Sinuous	Sinuous
SD* (abaxial)	30.28 ± 5.28	16.33 ± 2.88	25.77 ± 1.39
SD* (adaxial)	22.80 ± 5.77	20.33 ± 1.15	29.50 ± 2.25
SG* (abaxial)	3.16 ± 0.4	3.66 ± 0.57	4.55 ± 0.52
SG* (adaxial)	3.00 ± 0.87	3.33 ± 0.57	6.16 ± 1.47

* 500 × 500 μm.



Figures 32–43. Distributions of *Limonium* species in Iran.

In one cluster, all six samples of *L. perfoliatum* are grouped into two smaller sets each having three representatives. In one set, samples from the Golestan province and adjacent Turkmenistan are grouped, corresponding to the type locality of this species. The second set includes three samples from the north-easternmost parts of Iran. The sequences of the Golestan and Khorassan groups have two base pair differences. Morphologically, the populations from Khorassan are taller and their leaves are strongly undulate compared with those from Golestan. ITS sequence and morphological differences are compatible with subspecific rank for these geographically separated populations. However, because of the wide distribution of *L. perfoliatum* in Central Asia and Afghanistan, these questions should be addressed in a study including samples from across the entire range of the species.

In the second strongly supported cluster (BP 97), three accessions of *L. reniforme* (Girard) Lincz. (according to the circumscription accepted in this paper) are grouped apart from other species. The third cluster includes *L. otolepis* with a low support (BP 75). This result solves a complicated taxonomic problem, because the distinction between *L. reniforme* and *L. perfoliatum* has long been confused in the literature. *Limonium reniforme* (as *Statice reniformis* Girard) has been described from the saline depressions in Fars province (de Girard, 1844), and *L. perfoliatum* (*S. perfoliata*) was known from a saline depression in Hassan Kuli in the south-eastern lowlands of the Caspian Sea, a locality near the Iranian border in Turkmenistan (Karelin, 1839). This name was later validated by Boissier (1848), who also accepted Girard's species as var. *reniformis* (Girard) Boiss., although he later synonymized both names (Boissier, 1879). Ledebour (1849) also supported recognition of *S. reniformis*. In the standard floras of this area, these names have variously been used. Boissier (1879) accepted the name *Statice perfoliata* C.A.Mey. and considered *S. reniformis* L. a synonym. In the two main floras of the area, *Flora Iranica* (Rechinger & Schiman-Czeika, 1974) and *Flora of URSS* (Linczevski, 1952), the two species are considered conspecific and, based on priority, *L. reniforme* was accepted. More recently, Assadi (2005) erroneously applied *L. otolepis* to the populations of southern central Iran in Fars Province without providing any argument as to how populations of the *locus classicus* of *L. reniforme* can be attributed to *L. otolepis* described from Central Asia. As it is evident from molecular analysis (Fig. 31), morphological studies and distribution (Table 4, Figs 38–39, 44–46, and the taxonomic treatment below), these three taxa as treated here are distinct species.

The *Limonium*-type clade (BP 91) includes two main morphologically distinct complexes. The *L. vulgare* subclade (BP 69) includes broad-leaved hemicryptophyte and hygrohalophytic species, with a distribution spanning the Euro-Siberian, Mediterranean and Irano-Turanian areas. *Limonium lilacinum*, an endemic species from central Anatolia, is sister to other species. This is morphologically the most distinct species of this complex. *Limonium lilacinum* is characterized by more or less fleshy leaves with indistinct lateral veins and petioles with hyaline margin and a loose inflorescence (Bokhari & Edmondson, 1982). The anatomical studies of Bokhari (1970) showed that *L. lilacinum* has numerous clusters of sclereids dispersed in the lacunose spongy tissue of the petiole, which is different from *L. gmelinii* and related species. Accordingly, following Boissier (1848), Bokhari (1973) classified this species with another closely related Anatolian-Syrian species, *L. globuliferum* (Boiss. & Heldr.) Kuntze, in section *Sphaerostachys* (Boiss.) Bokhari.

In *Flora Iranica*, *L. meyeri* and *L. gmelinii* are distinguished by minor differences: the former with congested spikelets and the latter by loose inflorescences and cymes. However, in herbarium specimens it is always difficult to separate both species confidently. The molecular analysis gives a complicated topology in which most branches have only low support. The Iranian species are distributed into two clades: one clade includes samples from the northern sector of Iran (BP 50) and the other samples from central, southern and north-western parts of Iran (BP 61). The two Mediterranean and European representatives of the complex (*L. vulgare* Mill. and *L. narbonense* Mill.) are closely related and form a clade (BP 76), which is congruent with plastid analyses by Lledó *et al*. (2005, 2011). Despite several attempts, we were unable morphologically to separate the Iranian members of this complex and therefore prefer to treat them all under *L. gmelinii s.l.* The congested vs. loose inflorescence seems to be related to the age of collection and appears in both groups in the phylogenetic tree. This group needs additional investigation, including the microspecies described from Central Asian, Anatolia and the Mediterranean; for example, *L. vanense* Kit Tan & Sorger from eastern Anatolia (Tan & Sorger, 1984).

The *L. suffruticosum* clade is well supported (BP 90), but its internal relationships are not well resolved. In a large polytomy, three groups are distinguished: one includes all samples of *L. suffruticosum*, the second includes all specimens of *L. carnosum* with *L. anatolicum* Hedge as their sister, and the third includes four samples of *L. iranicum* from central Iran (Arak, Hamadan, Delijan and Esfahan); Arak is the *locus classicus* of *L. iranicum*. All other specimens of *L. iranicum* are unresolved and not related to either of the first two clades (above). *Limonium iranicum*, *L. suffruticosum* and

L. carnosum are widespread in Iran. They occur in almost all saline depressions and salt marshes of the Persian Gulf. Morphologically, these species are separable based on the treatment of *Flora Iranica* (see key below). Two other previously described species belonging to this complex are *L. gabrielii* (Bornm.) Rech.f., from Iranian Baluchestan between Nehbandan and Zahedan (Rechinger & Schiman-Czeika, 1974), and *L. failachicum* Erben & Mucina, which was recently described from Failacheh Island in Kuwait (Erben & Mucina, 2006). Two of the most isolated samples of *L. suffruticosum* are from the southernmost part of the range of this species, southern Khorassan (35188) and northern Baluchestan (8108), and in morphology and geography match *L. gabrielii*. This taxon is similar to *L. suffruticosum* and differs only in its tomentose calyx and pilose bracts and bracteoles. In *L. suffruticosum* the calyx is pilose, bracts are usually glabrous and bracteoles are always glabrous. Taking into account the molecular, geographical and morphological features, *L. gabrielii* could merit subspecific rank. *Limonium failachicum* is close and morphologically similar to *L. iranicum*. Study of the type of this species shows no reliable differences from the Iranian populations of the species along the Persian Gulf. Two sequenced samples collected from Ghabre Nakhoda (20723) and Deyreh Islands (20820) in the Persian Gulf belong to the large polytomy, in line with all other samples. They do not have unique sequence differences from other samples from southern Iran. However, further studies and plastid sequences are required to give a better picture of species delimitation and phylogenetic relationships in this complex.

Presence and shape of diffused sclereids have been considered to be important taxonomic characters in *Limonium* (Bokhari, 1970; Rao & Das, 1981). The phylogenetic tree shows that these are homoplastic characters occurring in all species of the *Limonium*-type clade, *L. sogdianum* belonging to the *L. reniforme* clade and the *L. axillare* clade (Fig. 31). These might be useful taxonomic characters to separate closely related species (e.g. *L. axillare* and *L. stocksii*, Figs 25, 26), but they should be used with caution. The presence of rhizosclerids and ramiform sclereids in *L. gmelinii s.l.* and the large variation in the form and size of sclereids in *L. sogdianum* are two examples (Figs 27, 29, 30).

Isobilateral leaf anatomy is another homoplastic character occurring in three clades of Iranian *Limonium* (Fig. 31). The presence of this character is congruent with sunken stomata in these species. Both features occur in xerohalophytic species of these clades, indicating putative adaptive value in coping with water stress and high temperature (Fahn & Cutler, 1992).

Biogeographical remarks

The sampling of *Limonium* from the Middle East in this paper is not sufficient to give a detailed phylogeographical interpretation, but it seems clear from these results that the Iranian species of *Limonium* have four phytogeographic origins.

1. Almost all species of the *L. reniforme* clade are Irano-Turanian species. *Limonium bellidifolium* occurs in the Mediterranean area and is closely related, and in a broad interpretation it is conspecific with *L. caspium*. In the results of Lledó *et al*. (2005), *L. bellidifolium*, *L. tetragonum* (Thunb.) Bullock (East Asia), *L. sinense* (Girard) Kuntze (China) and *L. tenellum* (Turcz.) Kuntze (China, Mongolia) form a clade. Except for *L. bellidifolium*, all these other species have eastern and central Asian distributions. Therefore, two possibilities with regard to their origin and diversification can be considered: either the Mediterranean distribution of this group might be secondary; or the migration of the Mediterranean ancestor into the Irano-Turanian area resulted in further divergence and speciation.
2. *Limonium lobatum* is the only Iranian representative of section *Pteroclados* subsection *Odontolepidae* (Karis, 2004). This is also the only annual species of *Limonium* in Iran. This section has a north-western African and Canarian centre of diversity, in which only *L. sinuatum* (L.) Mill. and *L. lobatum* have a widespread Mediterranean distribution. An extension of Mediterranean elements into western, south-western and northern Iran has already been reported in several groups: *Cercis siliquastrum* L., *Myrtus communis* L., *Jasminum fruticans* L., *Cupressus sempervirens* L., *Pteris cretica* L., *Hibiscus cannabinus* L., *Cistus salviifolius* L., *Caucalis platycarpos* L., *Convolvulus cantabrica* L., *Cynoglossum creticum* Mill., *Asteriscus spinosus* (L.) Sch.-Bip., *Petrorhagia prolifera* (L.) P.W.Ball & Heywood, *Vicia amphicarpa* Dorthes, *V. lutea* L., *Stipa bromoides* (L.) Dörfl., *Carex hallerana* Asso, *Daucus guttatus* Sm., *Laser trilobum* (L.) Borkh., *Orlaya daucoides* (L.) Greuter, *Fumana arabica* (L.) Spach, *Ononis pusilla* L., *Sternbergia lutea* (L.) Ker Gawl. ex Spreng., some species of *Orchis* L and halophytic communities of south-western Iran (Zohary, 1973; Akhani & Ziegler, 2002; Akhani & Deil, 2012).
3. *Limonium axillare* and the closely related *L. stocksii* are clearly isolated with an Afro-Arabian origin. They belong to *L.* subsection *Sarcophyllae p.p*. Restriction of these species to the frost-free zone of southern Iran with a tropical desert bioclimate close to sea shores indicates that this group is cold-sensitive. Field observations and greenhouse

cultivation indicate that these species have a continuous life cycle over the year. The presence of thick cuticle and sunken chalk glands are morphological traits that occur in *L. axillare* and *L. stocksii* in addition to species of the *L. suffruticosum* complex.

4. The biogeographic origin of the species belonging to core-*Limonium* (*L. iranicum*, *L. suffruticosum* and *L. gmelinii s.l.*) is more complicated because (1) these clades do not have strong support and (2) our sampling covers only part of this clade that is widely distributed over Eurasia. All these species are common in both inland and coastal saline soils.

In conclusion, ITS sequences provide useful taxonomic–phylogenetic data for studying sexual *Limonium* spp. and the results indicate that previous classifications of the genus in the literature require some alterations. It will be highly valuable to include plastid markers and extend this study into the southwestern and central Asian taxa of *Limonium*.

Taxonomic treatment

The taxonomic treatment here includes an updated key to all *Limonium* spp. accepted by us in Iran, a synopsis of all species with maps and descriptions and line drawings of the two species that are recircumscribed in this paper.

Key to species of *Limonium* in Iran

1. Annual herbs; stem and flowering branches with wing……1. *L. lobatum*
1. Perennial herbs or shrublets; stem and branches without wing……2
2. Perennial herbs; leaves in a rosette, with or without cauline leaves……3
2. Shrublets; leaves mostly cauline……9
3. Plants with many well-developed cauline, ± fleshy, rotundate–reniform and amplexicaul leaves……4
3. Plants without cauline leaves, often with scale-like reduced leaves on nodes……6
4. Stem without sterile branches; cauline leaves undulate at margins, basal cauline leaves auriculate……8. *L. perfoliatum*
4. Stem with sterile branches; cauline leaves entire, not auriculate……5
5. Sterile branches numerous; cauline leaves only on lower part of main stem, rarely on first to second nodes of lateral branches; spikes ± compact, 1–3 cm long, with four to nine spikelets (only cultivated or escaped from cultivation in Iran)……7. *L. otolepis*
5. Sterile branches scarce and laxly disposed, only on lower parts of lateral branches; cauline leaves on all nodes both main stem and lateral branches; spikes ± lax, 1–3 cm long, with two to six spikelets……9. *L. reniforme*
6. Sterile branches numerous, slender, occurring along the lower 2/3 of the plant height; inflorescence corymbose-paniculate; spikelets up to 5.5 mm long……6. *L. caspium*
6. Plants without sterile branches; combination of characters not as above……7
7. Basal leaves small, spathulate, up to 7 cm long; inflorescence subcapitate or spicate……8
7. Basal leaves large, obovate or spathulate–obovate, 8–38 cm long; inflorescence much branched, paniculate……13 *L. gmelinii s.l.*
8. Inflorescence subcapitate, at the end of dichotomous stem branches; calyx funnel-shaped, scarious parts of calyx pale violet; outer and middle bracts densely pilose……5. *L. nudum*
8. Inflorescence laxly spiciform, spikelets at intervals along spike; calyx tubular, scarious parts of calyx whitish; bracts glabrous……4. *L. sogdianum*
9. Flowering branches elongate, often longer than half of the plant height; leaves with single midrib……10
9. Flowering branches short, often shorter than one third of plant height; leaves with three main veins……12
10. Leaves with a scarious semicircular auricle at the base; inflorescence spicate; spikelets forming dense glomerules on elongated inflorescence branches, spikelets occurring only on lateral cymes……12. *L. suffruticosum*
10. Leaves without auricles; inflorescence paniculate; spikelets occurring on lateral and terminal cymes……11
11. Inflorescence shortly paniculate, cymes mostly condensed at the terminal branches of inflorescence; spikelets mostly 6.0–6.5 mm; calyx 5.5–6.0 mm long……10 *L. carnosum*
11. Inflorescence widely paniculate, cymes ± distanced along inflorescence branches; spikelets up to 5.5 mm long; calyx 3.0–4.0 mm long……11. *L. iranicum*
12. Leaves oblanceolate or spathulate–oblanceolate, acute or subacute at the apex; calyx funnel-shaped, with short hairs (0.5 mm) occurring only on the lower 1.5–2.0 mm of calyx tube; calyx lobes semicircular, rounded at apex, tube nerves ending below the base of calyx lobes……2. *L. axillare*
12. Leaves spathulate, rounded or obtuse at the apex; calyx obconical, with longer hairs (0.7 mm) occurring all along calyx nerves; calyx lobes triangular, acute at apex, tube nerves reaching the tip of calyx lobes……3 *L. stocksii*

SYNOPSIS OF IRANIAN SPECIES OF *LIMONIUM*

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

Distribution: Southern Spain, southern Greece, northern Africa, Syria, Palestine, Saudi Arabia, Iraq, southern Iran (Bushehr, Fars, Hormozgan, Khuzestan provinces, Fig. 32).

Note: L. lobatum is the only annual Iranian *Limonium* and a typical southern Mediterranean element occurring in southern and south-western Iran (Fig. 32). The species is easily distinguished by its annual life form, the winged stems and pedicel, horned middle bracts, pubescent leaves and coloured calyces bigger than corolla.

Limonium axillare (Forssk.) Kuntze
Rev. Gen. Pl.: 395. 1891. *Statice axillaris* Forssk., Fl. Aegypt.-Arab. 58.: 1775 [basionym]. *S. bovei* Jaub. & Spach, Ill. Pl. Or. 1: 157, t. 86. 1884. *L. wendelboi* Bokhari in Notes Roy. Bot. Gard. Edinburgh 40: 93. 1982.

Distribution: Egypt, Arabian Peninsula, Qatar and Iran (salty plains and Persian Gulf salt marshes in Bushehr and Hormozgan Provinces; Fig. 33).

Note: L. axillare is a rare plant restricted to Hormozgan and Bushehr Provinces (Fig. 33). Based on available data and field observations, its status according to IUCN (2001) has been evaluated as endangered in Iran. The species was not rediscovered in some of the previously known localities cited in the published literature (Rechinger & Schiman-Czeika, 1974).

Limonium axillare is closely related to *L. stocksii*. The main differences include the shape of calyx lobes, which are triangular in *L. axillare* and rounded in *L. stocksii*. However, the petiole anatomy of the former is characterized by individually dispersed needle-like sclereids, in contrast to the latter with fusiform sclereids that are mostly clustered (Figs 14, 15, 23, 24, 25–26).

Bokhari (1982) described the new species *L. wendelboi* Bokhari from southern Iran and compared it with *L. stocksii* based on the shape of sclereids. Earlier studies of *L. wendelboi* and *L. axillare* showed evidence for their synonymy (Akhani & Ghorbanli, 1993), and this is confirmed by detailed studies in this paper and comparison of material from North Africa and Saudi Arabia.

Limonium stocksii (Boiss.) Kuntze
Rev. Gen. 365. 1891. *Statice stocksii* Boiss. in DC. Prodr. 12: 664. 1848 [basionym]. TYPE: In Salsuginosis Prov. Scinde Indiae Borealis, *Stocks* (K!, G, W!).

Distribution: Afghanistan, western Pakistan and south-eastern Iran (Sistan-o Baluchestan Province, Fig. 34).

See notes under *L. axillare*.

Limonium sogdianum (Pop.) Ikonn.-Gal.
Trudy Bot. Inst. Akad. Nauk S.S.S.R. Ser. 1, Fl. Sist. Vyssh. Rast. 2: 268. 1936. *Statice sogdiana* Pop. in Bot. Geogr. Issled. V Turkest. 51: 1915 [basionym]. *L. piptopodum* Nevski in Tr. Bot. Inst. AN SSSR, Ser. I, 4. 313. 1937. *Eremolimon sogdianum* (Ikonn.-Gal.) Lincz. in Novosti Sist. Vyssh. Rast. 22: 206. 1985.

Distribution: Central Asia (Uzbekistan, Turkmenistan), north-eastern Iran in Khorassan province (Fig. 35).

Note: The habitat of *L. sogdianum* is restricted to the gypsum hills in the eastern parts of Khorassan Province. Associated species include *Salsola montana* Litw., *Asparagus breslerianus* Schult. & Schult.f., *Cleome quinquenervia* DC., *Kaviria tomentosa* (Moq.) Akhani, *Krascheninnikovia ceratoides* (L.) Gueldenst. and *Artemisia* sp.

Limonium nudum (Boiss. & Buhse) Kuntze
Revis. Gen. 2: 395. 1891. *Statice nuda* Boiss. & Buhse in Nouv. Mem. Soc. Nat. Mosc. 12: 184. 1860 [basionym]. SYNTYPES: Iran: Albursgebirge bei Radkann, Juli 1848; bei der Mineralquelle Gendäb auf steinigem Kalkboden in grosser Menge, 28 Juli 1848. Montibus Alborz, prope Pagum Radkann, Gendab, *Buhse 1039* (W!, K!, G-photograph!).

Distribution: Southern parts of Alborz in Semnan Province and Republic of Azerbaijan near Jolfa (Fig. 36).

Note: The locality of one of the syntypes near Gendab is located *c*. 70 km north-east of Semnan. There is another village named Kendab near Radkann, which is located in Golestan Province. Radkan area has been visited by the first author, without any evidence on the occurrence of this species. All localities where this species was found recently are on gypsum hills *c*. 15–20 km north of Damghan, *c*. 40 km from Gendab. The second locality 'An bergigen Orten bei Kaschan, Mai 1849. no. 1039.' cited in the original protologue and Rechinger & Schiman-Czeika (1974) is suspicious and probably incorrect. Kashan is a city located in Esfahan Province, *c*. 250 km far from Gendab. *Limonium nudum* has never been found in the Kashan area. The picture of the type specimen kindly provided by the authorities of Conservatoire and Jardin botaniques de la Ville de Genève (G) bears the locality of Gendab, 28.8.1948, Buhse 1039. It is

unlikely that two specimens bear the same number. Based on personal communication by Fernand Jacquemoud (G), there is no specimen of *L. nudum* in Boissier's herbarium collected by Buhse from Kashan.

The occurrence of *L. nudum* in Republic of Azerbaijan, near Jolfa is documented by a specimen collected by T. Heideman & H. Alive on 27.5.1932 (HAM).

Limonium caspium (Willd.) Gams
In Hegi, Ill. Fl. Mittleleur. 5, 3: 1880. 1927. *Statice caspia* Willd., Enum. Pl. Hort. Berol. 1: 336. 1809. Type: Regio Caspica. (LECTOTYPE: B-Willdenow!) [basionym]. *St. caspia* var. *urumiensis* Bornm. in Verh. Zool. Bot. Ges. Wein 60: 165. 1910. *L. bellidifolium* auct. non (Guan) Dumort.

Distribution: Central Asia, Dsungaro-Kashgar, Mongolia, Turkey and Iran (restricted to the surrounding area of the Uromieh Lake in eastern Azerbaijan, Fig. 37).

Note: L. bellidifolium and *L. caspium* have been variously interpreted in many taxonomic treatments of the Irano-Turanian and Mediterranean areas. Several authors considered *L. caspium* as a synonym of *L. bellidifolium* described from southern France (Bokhari & Edmondson, 1982; Assadi, 2005). Earlier in *Flora Iranica* (Rechinger & Schiman-Czeika, 1974), and later in the supplement of *Flora of Turkey* (Davis *et al*., 1988), the Irano-Turanian range of this complex was separated as *L. caspium*, which is said to differ from *L. bellidifolium* in its less developed sterile branches, outer bracts with herbaceous part in the middle, first inner bract (middle bract) obovate–oblanceolate and calyx tubular, as opposed to *L. bellidifolium* with dense sterile branches, membranous outer bracts and tubular–funnel-shaped calyx.

Comparison of Iranian plants with two specimens collected from southern France near the type locality of *L. bellidifolium* (France: Provence-Alpes-Cote d'Azur, near Port-Saint-Louis, 43°21′5″N, 04°52′28″E, sea level, 12.12.2008; *Akhani 20511*; ibid 1.10.1983, *Ponel s.n.*), provides additional differences, including slightly longer calyx (3.0–4.3 vs. 2.7–3.0 mm) and shorter and sparser calyx hairs in *L. caspium*. The ITS sequences of two species differ by eight nucleotide changes, which is compatible with the concept that they are distinct species.

Limonium otolepis (Schrenk) Kuntze
Rev. Gen. Pl. 2: 398. 1891. *Statice otolepis* Schrenk in Bull. Acad. Petersb. 1: 362. 1843 [basionym]. Figure 44.

Distribution: Turkmenistan, through Kazakhstan, Kyrgyzstan and Tajikistan, northern China in Gansu and northern Xinjiang. In Iran, known only as a cultivated plant for cut flowers.

Examined specimens: IRAN: Tehran: Flower shop in Tehran, 16.5.2008, *Malekmohammadi 3897* (Hb. Akh.); ibid. 25.6.2008, *3898* (Hb. Akh.); ibid. 20.7.2009, *Malekmohammadi 3899* (Hb. Akh.).

Additional specimens examined from outside Iran: KAZAKHSTAN: Golodnaja Steppe, 9.1915, Dimo and Popov (TARI). TURKMENISTAN: Charshanga District, Kelif, 7.6.1967, *Chopanov s.n.* (ASH, Hb. Akh.); Ashghabad Province (= Ashkhabadskia oblasti): 2 km north of Ashghabad, along Kara-Kum Canal, 16.9.1994. *Akhani 10185-T* (Hb. Akh.).

Note: This species is known in Iran only from cultivated plants offered for sale in flower shops. The report of this species from Fars province according to Assadi (2005) is attributable to misidentification of *L. reniforme* (see notes under *L. perfoliatum*).

Limonium perfoliatum (C.A.Mey. ex Boiss.) Kuntze
Rev. Gen. 2: 396 (1891). *Statice perfoliata* C.A. Mey. ex Boiss. in DC., Prodr. 12: 663. 1848 [basionym]. *Statice perfoliata* C.A.Mey. nom. nud. in Bull. Mos.: 167. 1839. Figure 45.

Description: Perennial herbs, 50–95(–150) cm tall; caudex 0.7–2.5 cm in diameter; stem sometimes branched from the base into two or three stems; current year stems (0.5–)1.5–2.5(–3.0) mm in diameter, green, glabrous, with salt glands, gland cavities indistinct, sterile branches absent. Basal leaves in a rosette, spathulate or spathulate–oblanceolate, mostly dying off during flowering time, trinerved, green, glabrous with salt glands, without gland cavities, sheathing at the base, (1.5–)2.5–5.5(–8.5) × (0.5–)1.0–2.0 cm, lamina (0.7–)1.0–2.0 cm long, petiole length excluding sheath (0.2–)1.0–3.0 cm and including sheath (0.7–) 1.5–3.5 cm, entire at margin, rounded or acutish–rounded at apex, attenuate at base. Cauline leaves more or less fleshy, arranged on nodes of main stem and lateral branches, decreasing in size towards the upper parts, green, glabrous, ± palmately veined, veins with dichotomous ends, with salt glands; lower half cauline leaves of main stem obovate or spathulate, rarely reniform, 1.5–3.5 × 1.2–2.2 cm, ± undulate at margin, rounded or rarely acute at apex, semiperfoliate or auriculate at base; upper half cauline leaves of main stem orbicular or reniform, 1.0–1.2(–2.2) × 0.2–1.0(–1.2) cm, strongly undulate at margin, perfoliate at base; cauline leaves of lateral branches orbicular or reniform, 0.1–0.7 × 0.1–1.2 cm, entire, sometimes slightly undulate. Inflorescence dense paniculate, 24–70 (–130) cm tall,

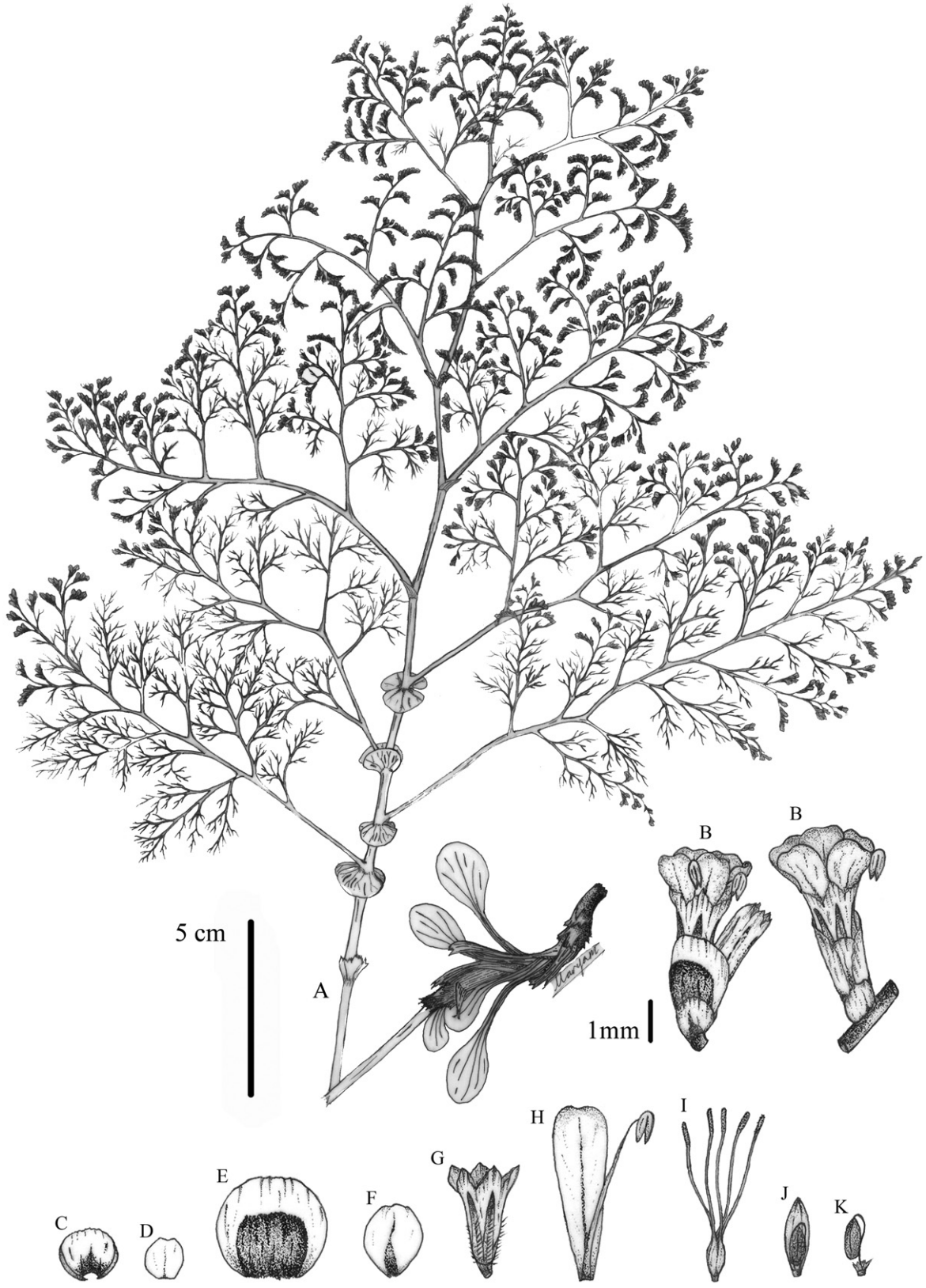


Figure 44. *Limonium otolepis*. A, habit. B, spikelet from two views. C, outer bract. D, middle bract. E, inner bract. F, bracteole. G, calyx. H, petal and stamen. I, gynoecium. J, fruit. K, seed. (*Chopanov 7.6.1967*).

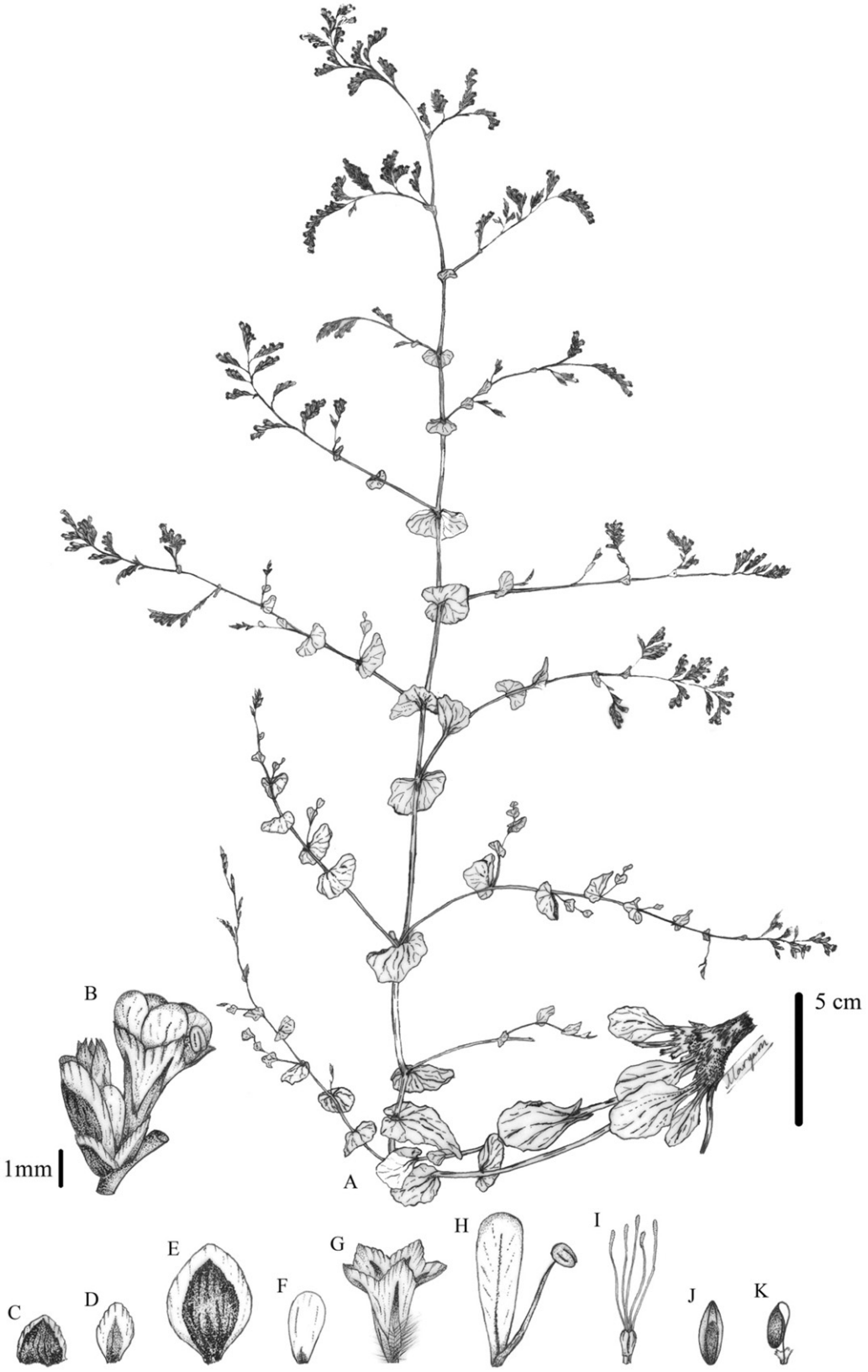


Figure 45. *Limonium perfoliatum*. A, habit. B, spikelet. C, outer bract. D, middle bract. E, inner bract. F, bracteole. G, calyx. H, petal and stamen. I, gynoecium. J, fruit. K, seed. (*Akhani et al. 18815*).

upper lateral branches 1.0–1.5(–2.0) cm tall; spikes unilateral, (five–) seven to 18 spikelets per spike, (two–) three-flowered. Outer bracts triangular or broad triangular, 1.0–1.5(–1.7) mm long, 1.0–1.5(–1.7) mm broad, herbaceous part brown with an apical and marginal 0.2–0.5 mm membranous band, glabrous, entire at margin, acute, rarely acuminate at apex, semiamplexicaul or amplexicaul at base; herbaceous part 1.0–1.5 mm long, (0.2–)0.5–0.7 mm wide, apex acute. Middle bracts elliptic or orbicular, rarely triangular–semicircular, 1.0–1.5 mm long, 1.0–1.5 mm wide, membranous, with one or two narrow brown nerves, glabrous, entire, rounded or abruptly acute, rarely retuse at apex, semiamplexicaul, rarely amplexicaul at base. Inner bracts elliptic or orbicular–elliptic, rarely obovate, 2.5–3.0(–3.5) mm long, 2.0–2.5 mm broad, herbaceous part brown with a 0.5–1.0 mm apical and 0.5–0.7 mm marginal membranous band, glabrous, entire, acutish–rounded or retuse, rarely truncate at apex, semiamplexicaul at base; herbaceous part (1.7–)2.0–2.5(–2.7) mm long, (0.7–)1.0(–1.5) mm wide, rounded, or abruptly acute, rarely truncate at apex. Bracteoles (two–)three to five(–eight) per spikelet, elliptic or broadly elliptic, rarely obovate, (1.5–)2.0–2.5 mm long, 1.0–1.5 mm wide, membranous with a narrow brown nerve, glabrous, entire at margin, rounded, or obtuse–rounded, rarely abruptly acute at apex, semiamplexicaul at base. Calyx funnel-shaped, (2.5–)3.0–3.5 mm long, limb 2.0–3.0 mm, base 0.5 mm and neck 1.0–1.5 mm in diameter, 5-lobed; nerves brown, 2–3 mm long, lobes and between nerves whitish, with dense or sometimes lax long hairs on two or three nerves, other nerves glabrous; calyx lobes (0.5–)0.7–1.0 mm, triangular. Corolla: petals oblanceolate, (3.0–)3.5–4.5 mm long, 1.0–1.2(–1.5) mm wide, glabrous, dark purplish or purplish, entire at margin, retuse or emarginate, rarely rounded at apex, slightly connate at the base. Filaments adnate to the base of petals, (2.0–)2.7–3.5(–4.0) mm long, in the middle 0.2–0.5 mm wide. Anthers 0.7–1.0 mm long, reddish or violet. Ovary elliptic to obovate, 0.7–1.0 mm long, upper half or one third granulate. Style 1.5–3.2 mm long, filiform, free from base. Stigma 0.5–0.7(–1.0) mm, filiform. Fruit elliptic or fusiform, upper half granulate, one-seeded, 2.0–2.5 mm long. Achene obovate, 1.2–1.5 mm long. Funicle 1.5–2.0 mm long.

General distribution: Afghanistan, Iran (Golestan and Khorassan Provinces, Fig. 39), Turkmenistan and Uzbekistan.

Examined specimens: IRAN: Golestan: Golestan, near the border of Turkmenistan, north-west of Alagol wetland, salty soils in *Tamarix* thickets, 37°23′27″N, 54°34′42″E, 10 m, 7.7.2007, *Akhani, Malekmohammadi & Toofani 18808* (Hb. Akh.); near Incheboroon, just close to Iran-Turkmenistan border, North Ajigol wetland, 37°26′18″N, 54°38′25″E, 12 m, 7.7.2007, *Akhani, Malekmohammadi & Toofani 18815* (Hb. Akh.); Gorgan: 47 km north of Pahlavi-Dezh, 13.5.1966, *Pobot 3377* (IRAN); Tangoly, 52 km north of Pahlavi-Dezh, sea level, 13.10.1977, *Hewer 4046* (TARI); 52 km from Gomishan to Inche-Boroon, –20 m, 1.11.1983, *Assadi & Abouhamzeh 43285* (TARI); Tangoly, near Ajigol salt lake, 0–10 m, 30.6.1988, *Akhani 4297* (Hb. Akh.); Maraveh-Tappeh, base of Atrak, 24.6.1956, *Scharif 33078* (IRAN). Khorassan: between Mashhad and Sarakhs, 18 km after Mazdavand to Sarakhs, 650 m, 16.8.1994, *Akhani & Zangui 10057* (Hb. Akh); between Sarakhs and Kalat, between Chahchaheh and main Mashhad–Kalat road, 750 m, 14.8.1993, *Mozaffarian 72280* (TARI); 9 km after Chahchaheh towards Kalat-e Naderi, in river bed, 600 m, 17.8.1994, *Akhani & Zangui 10130* (Hb. Akh); 10 km from Chahchaheh to Sanganeh (north-east of Mashhad), 600 m, 17.8.1994, *Akhani & Zangui 24567* (Hb. Akh. and FUMH); In declivibus argillosis a Mozduran boreo-orientem vs. *c*. 36°15′N, 60°34′E, inter Mashhad et Sarakhs, 900–1000 m, 25.5.1977, *Rechinger* 55671 (B).

Additional specimens examined outside Iran: TURKMENISTAN: Ashghabad Province (= Ashkhabadskia oblasti): 2 km north of Ashghabad, along the Kara Kum Canal, 16.9.1994, *Akhani 10169-T* (Hb. Akh.); soviet of the village Surkhi, Chodzhambaz District, Komsomol, nearby Amudarja River, 4.10.1970, *Sejfulin s.n.* (ASH, Hb. Akh.).

Note: L. reniforme, *L. perfoliatum* and *L. otolepis* are related Irano-Turanian species characterized by perfoliate leaves. See Table 4 for distinguishing characters of these species and discussion above on the history and reasons for recognizing *L. reniforme* and *L. perfoliatum* as separate species.

Limonium reniforme (Girard) Lincz
Fl. USSR. 18: 456. 1952. *Statice reniformis* Girard in Ann. Sci. Nat. Ser. 3 Bot. 2: 325. 1844 [basionym]. Figure 46. TYPE: Persia Australis, Shiraz, *Aucher-Eloy 5246* (LECTOTYPE: P!, ISOLECTOTYPE G!, K!, W).

Description: Perennial herbs, 35–70(–90) cm tall; caudex 1–2(–3) cm in diameter; stem pale green or green, glabrous, with salt glands, glands small and without cavities, branched from base into two or three (to ten) main stems, current year stems 1.0–1.5(–3.0) mm in diameter, sterile branches lax and just on the lower branches of the stem. Basal leaves in a rosette, spathulate, rarely oblanceolate, 3.0–4.0 (–7.0)

Figure 46. *Limonium reniforme*. A, habit. B, spikelet. C, outer bract. D, middle bract. E, inner bract. F, bracteole. G, calyx. H, petal and stamen. I, gynoecium. J, fruit. K, seed. (Akhani 7914).

cm × 0.5–1.5 cm, lamina (1.0–)2.0–2.5(–4.0) cm, petiole excluding sheath 1.0–2.5 cm and including sheath 1.5–3.0 cm, almost completely dying off about flowering time, trinerved, green, glabrous, with salt glands, without a cavity, entire, rounded, rarely abruptly acute at apex, attenuate at base. Cauline leaves ± fleshy, on the nodes of main stem and lateral branches, size decreasing upwards, ± palmately veined, veins at margin dichotomous, green or pale green, glabrous, with salt gland, without a cavity, cauline leaves of main stem reniform, rarely obovate, 0.5–2.5(–3.5) × 0.5–2.0(–3.0) cm, entire at margin, rounded at apex, semiamplexicaul at base; semiamplexicaul to ± perfoliate at base; cauline leaves of stem branches slightly fleshy, orbicular or transverse elliptic, 0.1–2.4 × 0.1–1.3 cm. Inflorescence panicle, 10–25 cm tall, upper fertile lateral branches of inflorescence 0.5–1.5 cm tall; spikes unilateral, ± lax, four to six spikelets per spike, spikelets (one–) two-flowered. Outer bracts triangular, or rarely semicircular, 0.5–1.0 mm long, 1.0–1.5(–1.7) mm broad, with an apical 0.2 mm and marginal 0.2–0.5 mm membranous band, sometimes without a fleshy part and completely membranous, brown, glabrous, entire, acute, rarely truncate at apex, semiamplexicaul, or amplexicaul at base; herbaceous part 0.5–0.7 mm long, 0.5–0.7(–1.2) mm broad, acute, rarely caudate at apex. Middle bracts triangular, elliptic, or orbicular, (0.7–)1.0–1.5 mm long, 1.0–1.2 mm broad, membranous with one or two narrow brown nerves, glabrous, entire, rounded or deeply retuse at apex, semiamplexicaul at base. Inner bracts orbicular, rarely transverse broadly elliptic, (1.5–)2.0–2.5 mm long, 2.0–2.5 mm broad, with an apical and marginal 0.5 mm membranous band, brown, glabrous, entire, rounded, or truncate, rarely emarginate at apex, amplexicaul at base; herbaceous part (1.0–)1.5–2.0 mm long, 1.0–1.5 mm wide, rounded, rarely truncate or praemorse at apex. Bracteoles elliptic, or orbicular, rarely rhombic, 1.2–1.5(–2.0) mm long, 1.0–1.5(–1.7) mm wide, membranous with a narrow brown nerve, glabrous, entire, rounded or acute, rarely obtuse at apex, semiamplexicaul at base, spikelets with two to five (to seven) bracteoles. Calyx obconical, sometimes obconical–funnel-shaped, five-lobed, 2.5–3.0 mm long, calyx limb (1.2–)1.5(–1.7) mm, base 0.5 mm and neck 1.0–1.5 mm in diameter; nerves 2.0–2.5 mm long, brown or reddish–brown; lobes and between nerves whitish, with dense and short to ± long hairs between and along two of nerves, other nerves glabrous or with short, lax hairs, calyx rarely glabrous; calyx lobes 0.5–0.7 mm long, triangular, or semicircular–triangular, rarely semicircular. Corolla; petals oblanceolate, rarely obovate, (2.5–)3.0–4.0 (–4.5) × 1.0–1.2(–1.5) mm, purplish, glabrous, entire, rounded, or slightly retuse at apex, slightly connate at the base. Filaments adnate to the base of petals, (2.0–)2.5–3.5(–4.0) mm long, up to 0.5 mm broad in the middle. Anthers (0.7–)1.0 mm long, pale yellow. Ovary obovate, 0.7–1.0 mm long, upper one third or one quarter granulate. Styles filiform, 1.5–3.0 mm long, free from base. Stigma filiform, 0.5 mm long. Fruit obovate, 2.2 mm long, upper half granulate. Achene fusiform, 1.5 mm long. Funicle 1.5 mm long.

Distribution: Endemic to southern–central saline depressions of Fars Province in Iran (Fig. 39).

Examined specimens: IRAN: Fars: Margin of Tashk Lake, 5 km south of Gomban, 1560 m, 17.11.1991, *Akhani 7914* (Hb. Akh.); Arsanjan, western shores of Tashk lake, between the villages Gomban and Katak, 1700 m, 27.11.1987, *Assadi & Akhani 61818* (TARI); Kalagh Djiro, south-west of Tashk lake, 1380 m, 2.7.1989, *Zehzad 66965* (TARI); between Arsanjan and Tashk, Chaharghanat, *c*. 1700 m, 7.6.1992, *Mozaffarian 71316* (TARI); 24 km after Arsanjan towards Gomban, before Charghanat Village, Sarcheshmeh Gomban, 29°48′17″N, 53°28′17.8″E, 1582 m, 4.12.2007, *Malekmohammadi, Khoshravesh & Mahdavi 3970* (Hb. Akh.); Maharlu Lake, 1600 m, 2.6.1973, *Bokhari 918* (SHIRAZ); Maharlu Lake, *c*. 20 km east of Shiraz, 1450 m, 7.10.1974, *Bokhari, Hedge & Wendelbo 14843* (TARI); in desert of Fengnnek near Schiraz, 29.6.1885, *Stapf 2172* (B); Bakhtegan Lake, near Kharameh, 1570 m, 4.10.1974, *Foroughi & Assadi 15036* (TARI); 10–18 km east of Kharameh, 26.10.1975, 1545 m, *Bokhari & Wendelbo 19006* (TARI); Ad lacum Niriz, *c*. 1400 m, VIII.1949, F. *Starmuehlner 21* (B); Neyriz, 10.7.1949, *Behboudi*, *33079* (IRAN); 103 km south-east of Darab towards Hajiabad, along salty river, 28°14′34″N, 55°14′41″E, 835 m, 25.11.2005, *Akhani, Dehghani & Doulatyari 18308* (Hb. Akh.); Darab, 13.4 km after fork to Ghalatooyeh, 55°14′N, 28°14′E, 750 m, 30.3.2004, *Khosravi & Tahari s.n.* (SHIRAZ); Senjunek near Shiraz 29.6.1885, *Stapf 2265* (K); south Iran, ad lacum salsum Nemek–Derja prope urbis Schiraz, 1.6.1842, *Kotschy 464* (K); Maharlu Lake near Shiraz, 5000 ft, 3.8.1939, *Davis 748* (B, K).

Note: See notes under *L. perfoliatum* and discussion. *Limonium reniforme* is an endemic restricted to margins of saline depressions in Fars Province around Tashk, Bakhtegan and Maharloo Lakes. This area is of great interest because of the presence of other halophytic local endemics, the most peculiar of which is *Hypericopsis persica* Boiss., an isolated species of south-western Asian Frankeniaceae (Chrtek, 1972). Recent anatomical studies and molecular evidence show that this species belong in

Frankenia L. (Olson, Gaskin & Ghahremani-nejad, 2003). *Salicornia persica* Akhani and *S. perspolitana* Akhani are other species described from the same area (Akhani, 2008).

Limonium carnosum (Boiss.) Kuntze
Rev. Gen. Pl. 2: 395 (1891). *Statice carnosa* Boiss. in DC. Prod. 12: 663. 1848 [basionym]. TYPE: Aderbidjan [Azerabaijan], Persiae bor. Prope Khoi, *Aucher-Eloy 2505* (LECTOTYPE G!). *S. suffruticosa* var. *typica* Trautv. in Bot. Sada. 7, 2: 504. 1881, non Trautv. 1867. *S. suffruticosa* var. *carnosa* (Boiss.) Kusn. in Mat., Fl. Kavk. 4, 1: 222. 1903.

Note: Limonium carnosum is a vicariant of the widely distributed *L. iranicum* in north-western Iran (Fig. 40). This species can easily be distinguished from the latter by longer (4.5–5.0 mm) and funnelform calyx (in *L. iranicum* the calyx is 3.0–3.5 mm long and its shape is usually tubulate). Furthermore, the spikelets of *L. carnosum* are more condensed and are borne at the end of inflorescence branches. The character of glabrous vs. pilose calyx used to distinguish *L. carnosum* from *L. iranicum* by Assadi (2005) cannot be confirmed here. Several specimens, including plants near the type locality (*Akhani et al. 18891*, *18904*, *18894*, *19046*, *Assadi 60977*, *Zehzad 83/1089*) have a pilose or shortly pilose calyx. Considering the calyx characters, two specimens collected from Ghahavand in Hamedan and Semnan Provinces (*Assadi 61097*, *Assadi & Hamdi 85415*) were misidentified as *L. carnosum* by Assadi (2005). Specimens with a glabrous calyx in *L. iranicum* occur in Semnan province (*Mirjalili 20729*, *Akhani & Salimian 15335*, *Akhani 16499*, *Akhani & Ghobadnezhad 15777*).

Limonium iranicum (Bornm.) Lincz.
Fl. URSS. 18: 461. 1952. *Statice leptophylla* Schrenk var. *iranica* Bornm. in Beih. Bot. Centrbl. 22, 2: 140 1907 [basionym]. TYPE: Sultanabad, Strauss ad Teramis, 4.8.1809. *Th. Strauss s.n.* (LECTOTYPE B!, ISOLECTOTYPE B!, W!, G, JE).

Distribution: Iran (Bushehr, Esfahan, Fars, Hamedan, Hormozgan, Ilam, Kerman, Khorasan, Ostan-e Markazi, Qom, Semnan, Tehran, Yazd. Provinces, Fig. 41), Iraq.

Note: Limonium iranicum is the most frequent *Limonium* sp. in central and southern Iranian saline deserts and salt marshes. It is closely related to *L. leptophyllum* (Schrenk) Kuntze and *L. suffruticosum*. In most parts of Iran, there is no difficulty in distinguishing *L. suffruticosum* and *L. iranicum* using leaf and inflorescence characters (see key above). However, in some parts of Iran (e.g. Khorassan Province) where they occur together it is difficult to separate them, probably because of hybridization.

The southern Iranian populations of *L. iranicum* differ from central Iranian plants in their clearly woody base, smaller flower segments, denser inflorescence and longer life cycle. Because of the arid tropical climate of southern Iran and absence of low winter temperatures, many plant species including *L. iranicum* persist nearly throughout the year. Therefore, they appear as a subshrub with more developed woody parts. Erben & Mucina (2006) described *L. failachicum* as an endemic species from Kuwait (Failacheh Island). In a study of type specimen (Kuwait, Failaka, east part of the island, 5 km from the port, 2 m, very salty area, 4.X.1981, *Rawi 10838* (MSB 86094!) and plants collected from Dara Island (*Akhani & Pahlevani 20820*), *c*. 100 km north-east of Failakeh, we found no reliable differences between these populations. In our molecular results they fall in an unresolved polytomy (Fig. 31). One alternative option would be to combine the southern Iranian plants and *L. failachicum* as a subspecies of *L. iranicum*, but we prefer to conduct more studies before making this decision.

Limonium suffruticosum (L.) Kuntze
Rev. Gen. Pl. 2: 396.1891. *Statice suffruticosa* L., Sp. Pl. 276. 1753 [basionym]. *L. gabrielii* (Bornm.) Rech.f. in Flora Iranica 108: 10. 1974. *St. gabrielii* Bornm. in Repert. Spec. Nov. Regni Veg. 36: 170. 1934.

Distribution: Afghanistan, Iran (Golestan, Khorasan, Sistan-o Balochestan, Yazd, Fig. 42), Mongolia, south-eastern Russia, Siberia, Turkmenistan.

Note: Limonium suffruticosum extends from Central Asia through eastern parts of Iran (Fig. 42). The southernmost populations of *L. suffruticosum* collected from southern Khorassan (*Gabriel 10*; *Mobayen 8108*; *Akhani & Joharchi 17313*; *Foroughi 10562*; *FOS 8109*) differ from other plants studied in having broader leaves, a tomentose calyx, hairs on bracts and bracteoles that are tomentose on the outer bracts and a slightly shorter corolla, 4.5 mm long, vs. narrower leaves, shortly pilose calyx tube, and slightly longer corolla, 5.5–6.0 mm long. The southern populations match *L. gabrielii* (*Gabriel 10*, W!). The position of this taxon as a subspecies or a distinct species is under further investigation.

Limonium gmelinii (Willd.) Kuntze
Rev. Gen. Pl. 2: 395. 1891. *Sensu lato. Statice gmelinii* Willd., Sp. Pl. 1: 1524. 1797 [basionym]. TYPE: USSR, in Siberia locis salsis a Jaico ad Angaram Usque,

Gmelin 6174 (HOLOTYPE: B-Willd.!). Incl. *L. meyeri* (Boiss.) Kuntze, Revis. Gen. Pl. 2: 395. 1891. *St. meyeri* Boiss. in DC., Prodr. 12: 645. 1845. *St. gmelinii* Willd. var. *laxiflora* Boiss., l. c. 646.; *S. obovata* Ledeb., Fl. Ross. 3: 468. 1849.

Distribution: Central Asia, Balkans, Caucasia, Crimea, Central Europe, Iran (Ardebil, Azarbaijan-e Gharbi, Azarbaijan-e Sharghi, Bushehr, Esfahan, Fars, Golestan, Khorasan, Khuzestan, Kohkiloye va Boyer Ahmad, Lorestan, Mazandaran, Ostan-e Markazi, Tehran Provinces, Fig. 43).

Note: Limonium gmelinii and *L. meyeri* belong to a widely distributed species complex occurring in the Mediterranean, Euro-Siberian and Irano-Turanian areas (including *L. vulgare* Mill, *L. narbonense* Mill. and *L. latifolium* (Sm.) Kuntze). In Iran, populations of these two species occur in most parts of the country. Rechinger & Schiman-Czeika (1974) separated them using the densely arranged spikelets in *L. gmelinii* and loose spikelets in *L. meyeri*, as in the *Flora of Turkey* (Bokhari & Edmondson, 1982). We found that dense and loose inflorescences can occur in the same population (e.g. *Akhani 12228*, *12229*, collected from Golestan National Park). Apparently plants growing in areas with more water produce much longer and looser inflorescence branches (the *meyeri*-form). Those growing in drier soils usually develop smaller and denser inflorescence (the *gmelinii*-form). Furthermore, younger plants have looser inflorescences than older plants. Boissier (1848), who originally described *L. meyeri*, later reduced it in *Flora Orientalis* (Boissier, 1879) to a variety of *L. gmelinii*, which seems to be more applicable based on present knowledge.

Analysis of ITS sequence data (Fig. 31) separated several accessions into two major groups that are distinct geographically: one group includes plants from north-eastern Iran and northernmost parts of Azerbaijan (close to the Aras River). They are characterized by hairs on the calyx only on the basalmost 1–3 mm and leaves that are spathulate or spathulate–oblanceolate. The second group includes populations from central Iran and near the Uromieh Salt Lake in north-eastern Iran that are characterized by hairs on the calyx nerves and oblanceolate leaves. In this latter group, two subgroups can be distinguished based on our analysis. One includes only the central and southern Iranian populations and the second only plants occurring in saline soils near Uromieh Salt Lake in eastern and western Azerbaijan, but morphologically these two are not easily distinguished. A revision of the whole group across the Mediterranean, Euro-Siberian and Irano-Turanian area using detailed morphological and molecular analysis is required to solve the taxonomic problems of this species complex.

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APPENDIX

List of species used in phylogenetic analysis of *Limonium* in Iran with their classification according to Boissier (1848), and post-Boissier classification, vouchers and GenBank accession numbers. Boissier's special infrasectional rank is considered, as for other authors, as subsection. The cases indicated by '*L.* SUBSECT.' showed that the species was classified under a subsection of section *Limonium*. Voucher details of two species described in taxonomic part are not repeated. They are indicated by an asterisk after collector and herbarium number

Name	Boissier's sections and subsections (sub *Statice*)	Sections or subsections of later authors	Voucher and/or origin and [DNA accession no.]
Cephalorhizum turcomanicum Pop.		*Cephalorhizum*	Khorasan: Kalat Naderi Archangan, km 10, 1100 m, 1.vi.1997, *Faghihnia & Zanguei 28978*-FUMH [JX983658]
L. anatolicum Hedge	–	*Sarcophyllum*‡	Turkey-Aksaray: 10 km east of Eskil towards southern saline shores of Tuz Gölü Lake, high salty soils, 38°25′5″N, 33°2952″E, 914 m, 28.viii.2004, *Akhani et al. 17999* [JX983724]
L. axillare (Forssk.) Kuntze	*L.* subsect. *Sarcophyllae*	*Sarcophyllum*†	Bushehr, Bidkhoon, Nayband National Park, 27°27′28″N, 52°40′31E, 7.xi.2007, *Malekmohammadi et al. 3974* [JX983660, JX983661]
L. arborescens (Brouss. ex Webb & Berthel.) Kuntze	*Pteroclados* subsect. *Nobiles*		(Brockington *et al*., 2008) EU410356
L. bellidifolium (Gouan) Dumort			France: Provence-Alpes-Cote d'Azur, near Port-Saint-Louis, 43°21′5″N, 04°52′28″E, sea level, 12.xii.2008, *Akhani 20511* [JX983722]
L. carnosum (Boiss.) Kuntze	*L.* subsect. *Sarcophyllae*	*Sarcophyllum*†	Azerbaijan Sharghi: *c*. 20 km west of Marand, 2 km south of Koshksaray towards Arland, 38°25′57″N, 45°33′39″E, 1260–1300 m, 15.ix.2007, *Akhani et al. 18894* [JX983727]; 22 km south of Evoghli, in salty flats along the road towards Marand, 38°33′13″N, 45°19′22″E, 1034 m, 15.ix.2007, *Akhani et al. 18904* [JX983728]; *c*. 30 km West Tabriz, 5 km West Qezel Dizej towards Alishah, 38°5′35″N, 45°56′56″E, highly saline soils, 1310 m, 14.ix.2007, *Akhani 18891* [JX983729]; Azerbaijan Gharbi: 10 km south of Khoy towards Salmas, salty hills and saline flats beside Khoy industrial centre, 38°25′N, 44°54′E, 1197 m, 17.ix.2007, *Akhani et al. 18997* [JX983726]; East Azerbaijan: 10 km south-west of Sarab on the road towards Asbforoushan, 8.ix.2001. *Akhani 15625* [JX983725].
L. caspium (Willd.) Gams	*L.* subsect. *Hyalolepidae*	*Limonium*†	Azerbaijan Sharghi: 22 km west of Tabriz, 11 km west of Mayan-e Olia, saline flats near Qezel Dizej, 38°04′29″N, 46°00′31″E, 1318 m, 14.ix.2007, *Akhani et al. 18888* [JX983721].

APPENDIX *Continued*

Name	Boissier's sections and subsections (sub *Statice*)	Sections or subsections of later authors	Voucher and/or origin and [DNA accession no.]
Limonium cf. *cumanum* (Ten.) Kuntze			Italy: Naples (Napoli), south-east of Naples, *c*. 10 km south-west of Salerno, Amalfi, 11.v.2003, *Akhani 16815* [JX983717].
L. delicatulum (Girard.) Kuntze	*L.* subsect. *Dissitiflorae*	*L.* subsect. *Dissitiflorae*§	Palacios *et al*. 2000: Spain: Alicante (AJ222851)
L. echioides (L.) Miller	*Schizhymenium*	*Schizhymenium*‡	Palacios *et al*., 2000: Spain: Alicante (AJ222861)
L. furfuraceum (Lag.) Kuntze	*L.* subsect. *Steirocladae*	*L.* subsect. *Steirocladae*§	Palacios *et al*., 2000: Spain: Alicante (AJ222856)
L. gmelinii (Willd.) Kuntze *s.l.* (Group A)	*L.* subsect. *Genuinae*	*Limonium*†‡	Azerbaijan Gharbi: 40 km north-west of Poldasht, 10 km west of Shotloo towards Aghghol, 39°30′43″N, 44°50′18″E, 788 m, 16.ix.2007, *Akhani et al. 18948* [JX983715]; Khorassan: Jajarm to Chamanbid, Shurek, 20.ix.1998, *Faghihnia & Zangui 31792-FUMH* [JX983713]; Khorassan: Golestan National Park: near Cheshmekhan, 14.x.1995, *Akhani 12229* [JX983714]; north-west of Bojnurd, Shahrabad, 800 m, 28.viii.1983, *Joharchi & Zangui 10637* [JX983716].
L. gmelinii (Willd.) Kuntze *s.l.* (Group B)	*L.* subsect. *Genuinae*	*Limonium*‡	Arak: *c*. 18 km north-east of Arak, saline lands near the southern margin of Arak salt lake, 34°12′10″N, 49°55′8″E, 1686 m, 27.viii.2007, *Akhani & Malekmohammadi 18852* [JX983691]; 25 km from Delijan towards Esfahan, Roud-e Shour bridge, 33°47′33″N, 50°50′42″E, 1861 m, 3.x.2007, *Malekmohammadi et al. 3827* [JX983685]. Kohkiloye va Boyerahmad: 35 km east of Lordegan, 21.ix.2001, *Akhani 15740* [JX983692]; Azerbaijan Sharghi: 23 km north of Ajabshir, on the eastern salt marshes of Orumieh lake, 37°42′34″N, 45°50′25″E, 1296 m, 18.ix.2007, *Akhani et al. 19013* [JX983688]; 22 km west of Tabriz, 11 km west of Mayan-e Olia, saline flats near Qezel Dizej, 38°4′42″N, 46°00′53″E, 1318 m, 14.ix.2007, *Akhani et al. 18887* [JX983690]; 8 km south-west of Sarab, on the road towards Asbforoushan, 8.ix.2001, *Akhani 15636* [JX983686]; Azerbaijan Gharbi: 10 km south of Khoy towards Salmas, salty hills and saline flats beside Khoy industrial centre, 38°25′N, 44°54′E, 1197 m, 17.ix.2007, *Akhani et al. 18996* [JX983689]; Bushehr: 10 km to Dalaki from Borazjan, Cheshme Googerdi, 29°20′35″N, 51°15′49″E, 2.x.2007, *Malekmohammadi 3825* [JX983687].
L. iconium (Boiss. & Heldr.) Kuntze	*L.* subsect. *Hyalolepidae*	*Limonium*‡	Turkey: Aksaray: salt flats south of Tuz Gölü Lake, 17 km from Yenikent towards Sultanhani, 38°15′56″N, 33°38′51″E, 938 m, 27.viii.2004, *Akhani et al. 17961* [JX983719]; Ankara: 28 km north of Şereflikochisar towards Ankara, north of Tzu Gölü Lake, saline soils around Mogan Gol Lake, 39°8′50″N, 33°19′4″E, 895 m. 27.viii.2004, *Akhani et al. 17921* [JX983720]; Konya: west of Tuz Gölü Lake, 8 km north-west of Gölyazi, 38°37′3″N, 33°9′16″E, 920 m, 28.viii.2004, *Akhani et al. 18011* [JX983718].

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Name	Boissier's sections and subsections (sub *Statice*)	Sections or subsections of later authors	Voucher and/or origin and [DNA accession no.]
L. iranicum (Bornm.) Lincz.	*L.* subsect. *Sarcophyllae*	*Sarcophyllum*†	Arak: *c*. 18 km north-east of Arak, saline lands near the southern margin of Arak salt lake, 34°12′10″N, 49°55′8″E, 1686 m, 27.viii.2007, *Akhani & Malekmohammadi 18851* [JX983704]; Bushehr: Kangan–Asalooyeh road, 45 km before Asalooyeh, after Akhtar village, 27°41′32″N, 52°15′16.5″E, 13 m, 7. xii.2007, *Malekmohammadi, Khoshravesh & Mahdavi 3972* [JX983707]. Esfahan: 26 km south–south-east of Delijan, 22.ix.2001, *Akhani 15760* [JX983705]; 25 km from Delijan towards Esfahan, Rude Shur bridge, 33°47′33″N 50°50′42″E, 1861 m, 3.x.2007, *Malekmohammadi et al. 3826* [JX983706]; Fars: 30 km south-east of Arsanjan, near Tashk Lake, 27.ix.1991, *Khademian 58* (Shiraz University Herbarium) [JX983696]; Hormozgan: Bandar-Abbas towards Haji-Abad, between Sarchahan and Gahkom, 28°5′35″N, 55°52′10″E, 663 m, 9.xii.2007, *Malekmohammadi et al. 3977* [JX983700]; Bandar Lengeh–Bandar Khamir road, 63 km after Bandar Lengeh, 22 km before Dejgan village, left side of the road, sandy soil, 29°48′59″N, 55°21′05″E, 6 m, 8.xii.2007, *Malekmohammadi, Khoshravesh, Mahdavi 3976* [JX983701]; Bandar-e Emam Hasan, behind Emam Hasan police station, coastal area, 29°50′36″N, 50°15′18″E, 3 m, 30.ix.2007, *Malekmohammadi & Kazemi 3823* [JX983709]. Ilam: *c*. 5 km south-west Dehloran, 6.viii.1989, *Akhani 5563* [JX983699]; Tehran, east of Hassan Abad, after Key Ghobad village, 13.ix.1987, *Akhani 4813* [JX983695]; Khorassan: 10 km from Ghaen to Gonabad, 1450 m, 5.x.1991, *Joharchi & Zangui 21058* [JX983702]; Khuzestan: Persian Gulf, Khore Musa, 20 km south-west of Bandare Khomeini, Ghabre Nakhoda Island, 30°18′21″N, 48°54′41″E, 10.iii.2010, *Akhani & Pahlevani 20723* [JX983711]; north-west of Persian Gulf, Dayreh Island, sandy and saline soils, 30°6′N, 49°6′E, 7–8.v.2010, *Akhani & Pahlevani 20820* [JX983712]; Semnan: 37 km north-east Torud, along a river 11 km north-east of Razeh, Cheshmeh Morrah, 35°35′38″N, 55°20′2″E, 1218 m, 9.xi.2007, *Akhani et al. 19133* [JX983710]; 18 km north of Damghan towards Cheshmeh Ali, saline and gypsum hills, 36°13′22″N, 54°12′28″E, 1402 m, 6.vii.2007, *Akhani et al. 18805* [JX983697]. Bushehr: Bidkhon, Nayband National Park, 27°27′28″N, 52°40′31″E, 7.xii.2007, *Malekmohammadi et al. 3975* [JX983708]; Semnan: 28 km east of Khors towards Chajam, south of Kavire Haji Ali Gholi, 14.xi.2002, *Akhani 16499* [JX983698]; Hamadan: east of Ghahavand, 3 km from Ghahavand towards Boyaghchi, left side of the road, beginning of the road of Haji Abad, 34°51′N, 49°0′E, 1637 m, 31.viii.2008, *Malekmohammadi et al. 3986* [JX983703].

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Name	Boissier's sections and subsections (sub *Statice*)	Sections or subsections of later authors	Voucher and/or origin and [DNA accession no.]
L. lilacinum (Boiss. & Bal.) Wagenitz		*Sphaerostachys*‡	Turkey: Ankara: 28 km north of Şereflikochisar towards Ankara, north of Tzu Gölü Lake, saline soils around Mogan Gol Lake, 39°8′50″N, 33°19′4″E, 895 m. 27.viii.2004, *Akhani et al. 17930* [JX983693].
L. latifolium (Sm.) Kuntze			Mediterranean coast of France: Provence–Alpes–Cote d'Azur, 10 km west of Fos-sur-Mer, Etange de Caban, 43°25′16″N, 04°48′38″E, sea level, 12.xii.2008, *Akhani 20504* [JX983694].
L. lobatum (L.f.) Kuntze	*Pteroclados* subs. *Odontolepidae*	*Pteroclados*†‡	Fars: 39 km south-west of Jahrom, Mobarak Abad village, 1.iv.2008, *Hekmatara 3978* [JX983659].
L. lobatum (L.f.) Kuntze	*Pteroclados*	*Pteroclados*†‡	Palacios *et al.*, 2000: Almería (AJ132333)
L. minutum (L.) Chaz.	*L.* subsect. *Steirocladae*	Subs. *Steirocladae*§	Palacios *et al*., 2000; Spain: Baleares (AJ132332)
L. narbonense Mill.	*L.* subsect. *Limonium*	sub. *Limonium*	Palacios *et al*., 2000: Spain: Valencia (AJ222838)
L. nudum (Boiss. & Buhse) Kuntze		*Platyhymenium*†	Semnan: 18 km north of Damghan towards Cheshme Ali, saline and gypsum hills, 36°13′22″N, 54°12′28″E, 1402 m, 6.vii.2007, *Akhani et al. 18804* [JX983672]
L. otolepis (Schrenk) Kuntze	*L.* subsect. *Hyalolepidae*	*Nephrophyllum*†	*Malekmohammadi 3897** [JX983682]; *Akhani 10185-T** [JX983683]; Uzbekistan: Kyzylkum, *c*. 15 km north-east of Chingil'dy (Shingeldi), near Karaktau station, near Noorbulak village, 41°2′2″N, 64°29′39″E, 100 m, 26.x.2009, *H. Akhani 20367* [JX983684].
L. perfoliatum (C.A.Mey ex Boiss.) Kuntze	*L.* subsect. *Hyalolepidae*	*Nephrophyllum*†	*Akhani 10169T** [JX983680]; *Akhani et al. 18808** [JX983679]; *18815* [JX983678]*; *Akhani & Zangui 10130* [JX983681]*; *24567* [JX983677]*; *10057* [JX983676]*
L. reniforme (Girard) Lincz.	*L.* subsect. *Hyalolepidae*	*Nephrophyllum*†	*Malekmohammadi et al. 3970* [JX983674]*; *Khosravi & Tahari s.n*. (30.iii.2004) [JX983675]*; *Zehzad 66965* [JX983673]*
L. sogdianum (M.Pop.) Ikonn.-Gal.	–	*Eremolimon*¶	Khorassan: Between Neyshabur and Kashmar, 70 km south of Neyshabur, gypsum hills near Chelpu, 35°37′23″N, 58°31′48″E, 1846 m, 24.x.2007, *Akhani & Memariani 19055** [JX983723]

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Name	Boissier's sections and subsections (sub *Statice*)	Sections or subsections of later authors	Voucher and/or origin and [DNA accession no.]
L. suffruticosum Kuntze	*L.* subsect. *Sarcophyllae*	*Sarcophyllum*†	IRAN: Khorassan: Petergan, Cheshme shirin, 21.x.1996, *Rafei & Zangui* 28088 [JX983666]; 143 km east of Qaen towards Afghanistan border, west of Daqe Petergan, 33°31′29″N, 60°39′12″E, 644 m, 31.viii.2003, *Akhani & Joharchi 17282* [JX983667]; 45 km east of Torbategan, between Gale-Hamam and mallu-Olia, 29.iv.2003, collector? *41* (FUMH) [JX983668]; Golestan National Park, south Mirza-Baylu flats, near Armadlu village, 1200 m, 15.xi.1996, *Akhani 12277* [JX983669]; Yazd: 50 km from Tabas to Yazd, 1000 m, 20.x.1982, *Assadi & Abouhamzeh 40226* (TARI) [JX983662]; Khorassan: Birjand, between Mahirud and Estakhr deraz, 1100 m, 3.ix.2003, *Joharchi 35188* [JX983665]; Sistan va Baluchestan: Kavire Lut, Deh-e Salm, 9.xi.1972, 1100 m, *Mobayen 8108* (TUH) [JX983663]. TURKMENISTAN: Balkhan Province: *c*. 14 km south-east of Nebet-Dagh, 12.ix.1994, *Akhani 10160T* [JX983664]. UZBEKISTAN: Kyzylkum, *c*. 15 km north-east of Chingil'dy (Shingeldi), near Karaktau station, near Noorbulak village, 41°2′2″N, 64°29′39″E, 100 m, 26.x.2009, *Akhani 20364* [JX983671]; *c*. 100 km north of Bukhara, Ayagakitma saline lake, highly saline soils near the lake marshes, 40°39′30″N, 64°29′37″E, 148 m, 26.x.2009, H. *Akhani 20382* [JX983670].
L. vulgare Mill.	*L.* subsect. *Limonium*		Palacios *et al*., 2000: Spain: Cantabria (AJ222839)
Psylliostachys leptostachya (Boiss.) Roshk	*Psylliostachys*	–	Fars: Maharlu, 15.iv.1993, *Elmi 57* (Shiraz University Herbarium) [JX983657].
Psylliostachys spicata (Willd.) Nevski	*Psylliostachys*	–	Khuzestan: W Shoosh, along Karkhe River, 1.iv.2001, *Akhani 14878* [JX983656]

†Rechinger & Schiman-Czeika, 1974.
‡Bokhari, 1973.
§Palacios *et al*., 2000.
¶Linczevski, 1985.