JASIONE (*CAMPANULACEAE*) ANATOMY IN THE IBERIAN PENINSULA AND ITS TAXONOMIC SIGNIFICANCE

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The stem and leaf anatomy of the ten species of *Jasione* L. (*Campanulaceae*) in the Iberian Peninsula were investigated; their infra-specific taxa were also studied. The species differ from each other anatomically and can be identified by their anatomical characters. The anatomical evidence supports the taxonomic treatment that will be published in the forthcoming *Flora iberica* Volume 14. The possible relations between the anatomy and the ecology of these plants are discussed. Specialized small multicellular structures (trichoids) present on the leaf surface, whose interest has not previously been recognized, are described and their possible function discussed.

Keywords. Anatomy, *Campanulaceae*, Iberian Peninsula, *Jasione*, taxonomy.

Introduction

The genus *Jasione* L. (*Campanulaceae*) has c.12 species throughout Europe and the Mediterranean area. The greatest morphological variation occurs in the Iberian Peninsula, where its classification is especially difficult. There are scarcely any reliable morphological characters and many apparently distinctive ecological variants abound. Numerous poorly defined taxa have been described in the past as a result of over-emphasizing particular character states. *Jasione montana*, *J. laevis*, *J. sessiliflora* and *J. crispa* are the commonest and most widespread species. Within each, there is great polymorphism and some of their variants can even break down the dividing line between the species. In addition to the difficulties of the taxonomy of the genus, its nomenclature is extremely confusing, with far too many names being applied within the group in the Iberian Peninsula. Such aspects have been revised in a nomenclatural paper (Sales & Hedge, 2001).

The taxa recognized here are those of the account by Sales & Hedge in *Flora iberica* Volume 14: *J. foliosa* Cav. (fo); *J. mansanetiana* R. Roselló & J.B. Peris (ms); *J. montana* L. var. *montana*, var. *bracteosa* Willk., var. *latifolia* Pugsley, var. *gracilis* Lange (mo); *J. penicillata* Boiss. (pe); *J. corymbosa* Poir. (co); *J. laevis* Lam. (la); *J. maritima* (Duby) Merino var. *maritima*, var. *sabularia* (Cout.) Sales & Hedge (mr); *J. crispa* (Pourr.) Samp. subsp. *crispa* (cr), subsp. *tristis* (Bory) G. López (tr), subsp. *mariana* (Willk.) Rivas-Mart. (mn), subsp. *tomentosa* (A. DC.) Rivas-Mart. (to); *J. cavanillesii* C. Vicioso (ca); *J. sessiliflora* Boiss. & Reut. (se). These taxa differ

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substantially from those recognized in previous accounts (Tutin, 1976; Greuter *et al.*, 1984).

Seven taxa are restricted to the Iberian Peninsula: *J. mansanetiana*, *J. montana* var. *bracteosa*, *J. penicillata*, *J. crispa* subsp. *tristis*, *J. crispa* subsp. *mariana*, *J. crispa* subsp. *tomentosa*, and *J. cavanillesii*. *Jasione foliosa*, *J. corymbosa* and *J. sessiliflora* also occur in NW Africa; *J. laevis* grows as far east as W Germany; *J. maritima*, confined to the north and north-west coastal line of the Iberian Peninsula, also stretches over to France as far as N Gironde; *J. montana* var. *montana* is the most widespread taxon and grows throughout Europe to Scandinavia and east to European Turkey. About four other taxa occur in SE Europe (Tutin, 1976).

The present research studies the previously poorly or unknown stem and leaf anatomy of *Jasione* in the Iberian Peninsula, and investigates its potential as a complement to the morphological characters already available.

Material and Methods

The present study is entirely based on the examination of leaves and stems from herbarium material. The techniques used for reviving herbarium material for sectioning and clearing are basically the same as those used by Bokhari (1970), but with some modifications.

Leaves and part of stems were soaked overnight in 5% KOH solution. Next morning the material was thoroughly washed with water and placed in FAA containing 1% glycerol. The material was fixed in FAA for at least 12h, before sectioning or clearing. Hand-sections were taken because this is the most rapid and cheapest technique for examining large numbers of specimens in a short time. Sections were bleached for 2–3min on a slide in a drop of household bleach and then thoroughly washed with water before staining. A suitable stain for examining revived herbarium material is 2% safranin dissolved in ethanol. Thoroughly washed sections were stained in a drop of safranin for about 2min. Excess stain was removed with ethanol and sections were mounted in Euparal. For the sake of uniformity, leaves were sectioned in the middle region and leafy stems of comparable age were selected for anatomical study. In perennial species, old parts of stems were also sectioned to study the formation of cork and bark.

Leaves were cleared for comparative anatomy of vein-endings, nature of adaxial and abaxial epidermis, trichomes and structure of trichoids. For clearing, leaves were placed in bleach for at least 24h. They were taken out of the bleach and boiled in water for about 5min in a beaker. The water was allowed to cool before the cleared leaves were taken out. These leaves were placed in safranin for staining in a petri dish for 12h. The stained leaves were washed with ethanol and then mounted in Euparal. It is preferable to clear, stain and mount at least two leaves in order to study adaxial and abaxial surfaces. All slides are in the herbarium of the Royal Botanic Garden Edinburgh (E) for future reference. The specimens examined are listed in the Appendix.

RESULTS

Stem anatomy

There is a single layer of EPIDERMIS having cutinized walls, which give strength to slender stems. Epidermal cells have smooth walls, but in *J. mansanetiana* cell walls are raised externally (Fig. 1A). STOMATA are invariably present in the epidermis, suggesting that cortex in the stem is photosynthetic. In old stems, the guard cells of stomata become lignified so these stomata are non-functional. In some species of *Jasione*, such as *J. montana* and *J. maritima*, the stem is prominently winged (Fig. 1B). In other species, wings are variously developed but smooth-surfaced stems have not been observed. CORK has been observed in older stems of *J. crispa* subsp. *tristis* and *J. maritima* (Fig. 1C). In the latter species and *J. mansanetiana* there are also a number of brachysclereids in the cork (Fig. 1D). Thick-walled macrosclereids have been observed in leaf bases of *J. crispa* var. *sessiliflora* from Morocco (Fig. 1E). CORTEX is generally parenchymatous and remains so even when the wood is well developed. However, in *J. crispa* subsp. *tomentosa* and *J. sessiliflora*, patches of cortical cells become lignified (Fig. 1F). The characteristic feature of *Jasione* stem is the presence of a conspicuous ENDODERMIS in which the casparian bands are indistinct (Fig. 1B,G,H).

In the young stem, the PHLOEM forms a continuous slender ring but the XYLEM is in separate strands (Fig. 1A). In all species, wood is formed in older stems of annual as well as perennial species. WOOD is usually very well developed in perennial species (Fig. 1C,D), but in some taxa, such as *J. crispa* subsp. *crispa*, *J. crispa* subsp. *tristis*, *J. foliosa* and *J. penicillata*, poorly developed wood has been observed. In species with well-developed wood, vessels are arranged in radial rows accompanied by exceptional development of fibres (Fig. 1B,C,F). In *J. maritima* and *J. mansanetiana*, the older part of the stem with cork has various arrangements of vessels in the wood. They may be in radial rows, solitary, or in groups of twos, threes or fours, accompanied by well-developed parenchymatous and fibrous tissue (Fig. 1D). PITH in all species (Fig. 1A–D,H) except *J. sessiliflora* (Fig. 2A) is parenchymatous and usually disintegrates in the middle resulting in hollowing of stems. In many specimens of *J. sessiliflora*, pith cells are sclerified.

Sclereids

As far as we have been able to determine, there is no record in the literature of stem sclereids in *Jasione.* We have observed only brachysclereids in cork of *J. maritima* (Fig. 1D). In *J. sessiliflora*, the majority of the specimens studied have sclereids in the pith. These sclereids have been examined in cross- and longitudinal sections of stem, the latter better revealing their true nature. The morphology and distribution of these sclereids can be broadly classified into three types:

i. *Thin-walled macrosclereids*. These are sclerified cells of pith in the peripheral region. They have a heavily lignified cell wall, but a large lumen, and appear rounded in cross-section, whereas the ordinary pith cells are polygonal in outline. In a longitudinal section these sclereids are like other pith cells in shape and size but are easily distinguished by their lignified walls and comparatively narrow lumen (Fig. 2A).

ii. *Thin-walled and thick-walled macrosclereids*. A combination of the thin- and thick-walled macrosclereids has been observed in some specimens. These two types of sclereids are interspersed and could be easily identified by their lignified walls and lumen. The thin-walled macrosclereids have the same nature as already described above, but thick-walled macrosclereids have very thick lignified walls resulting in extreme narrowing of lumen as seen in cross- (Fig. 2B) and longitudinal sections (Fig. 2C).

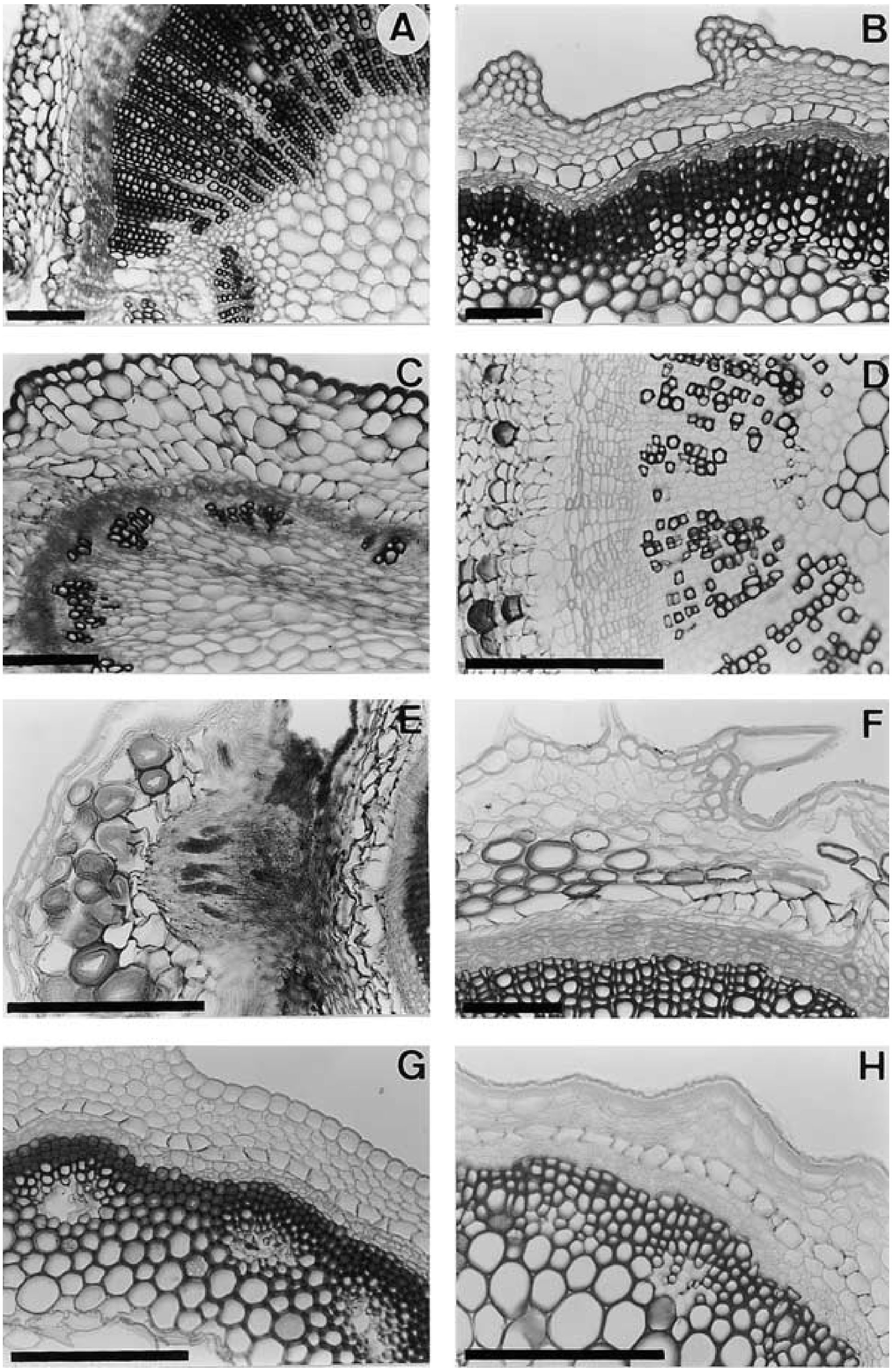
iii. *Thick-walled macrosclereids and thick-walled brachysclereids*. Both these types have very thick lignified walls and have a narrow lumen so they are indistinguishable in cross-section of stem. Their true nature becomes clear only in longitudinal section. These two types of sclereids are not interspersed. The thick-walled macrosclereids are longer than ordinary pith cells and are found in the inner region of pith, whereas thick-walled brachysclereids are similar to ordinary pith cells in size and are located in the outer pith region (Fig. 2C).

Leaf anatomy

There is considerable intraspecific variation in the structure of the lamina. In all the species examined, both the adaxial and abaxial EPIDERMAL CELLS in cross-sections are more or less oval in shape but are unequal in size (Fig. 2D,G,H). In the majority of species, the adaxial and abaxial epidermal cells are subequal in size but in some taxa, such as *J. laevis*, *J. sessiliflora*, *J. cavanillesii* and *J. crispa* subsp. *tomentosa*, the adaxial epidermal cells are distinctly 1.5–2 × larger than the abaxial epidermal ones (Fig. 2G). As seen in face view in cleared leaves, most of the adaxial epidermal cells have smooth walls and are polygonal in shape (Fig. 2E), but the abaxial epidermal cells are wavy in outline in most of the species. In *J. penicillata*, *J. cavanillesii* and *J. mansanetiana* both adaxial and abaxial epidermal cells are distinctly wavy in outline (Fig. 2F). In all species there is a distinct cuticle on the outer epidermis. In *J. montana*, *J. cavanillesii* and *J. crispa* subsp. *tomentosa*, in addition to cuticle, the inner and radial walls of adaxial epidermal cells are also cutinized. The epidermal cells at the leaf edge, especially towards the apex, are variously thickened (Fig. 4).

STOMATA are at the level of the epidermis cells (Fig. 2G) or slightly raised (Fig. 2H) and, in general, are more numerous towards the apex than towards the leaf base.

FIG. 1. Transverse sections of stems in *Jasione* showing wings, epidermis, cork with lignified cells and brachysclereids, endodermis, xylem, phloem and pith; bar = 0.1mm. A, *J. mansanetiana*, young stem; B, *J. montana*; C, *J. maritima* var. *sabularia*; D, *J. mansanetiana*; E, *J. sessiliflora*, stem and leaf base; F, *J. crispa* subsp. *tomentosa*; G, *J. laevis*; H, *J. foliosa*.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The stomata are anomocytic and are irregularly scattered on the adaxial and abaxial epidermis. There are usually more stomata on the adaxial than on the abaxial epidermis, but in *J. laevis* and *J. cavanillesii* stomata are mostly confined to the abaxial epidermis and are rare or absent on the adaxial epidermis.

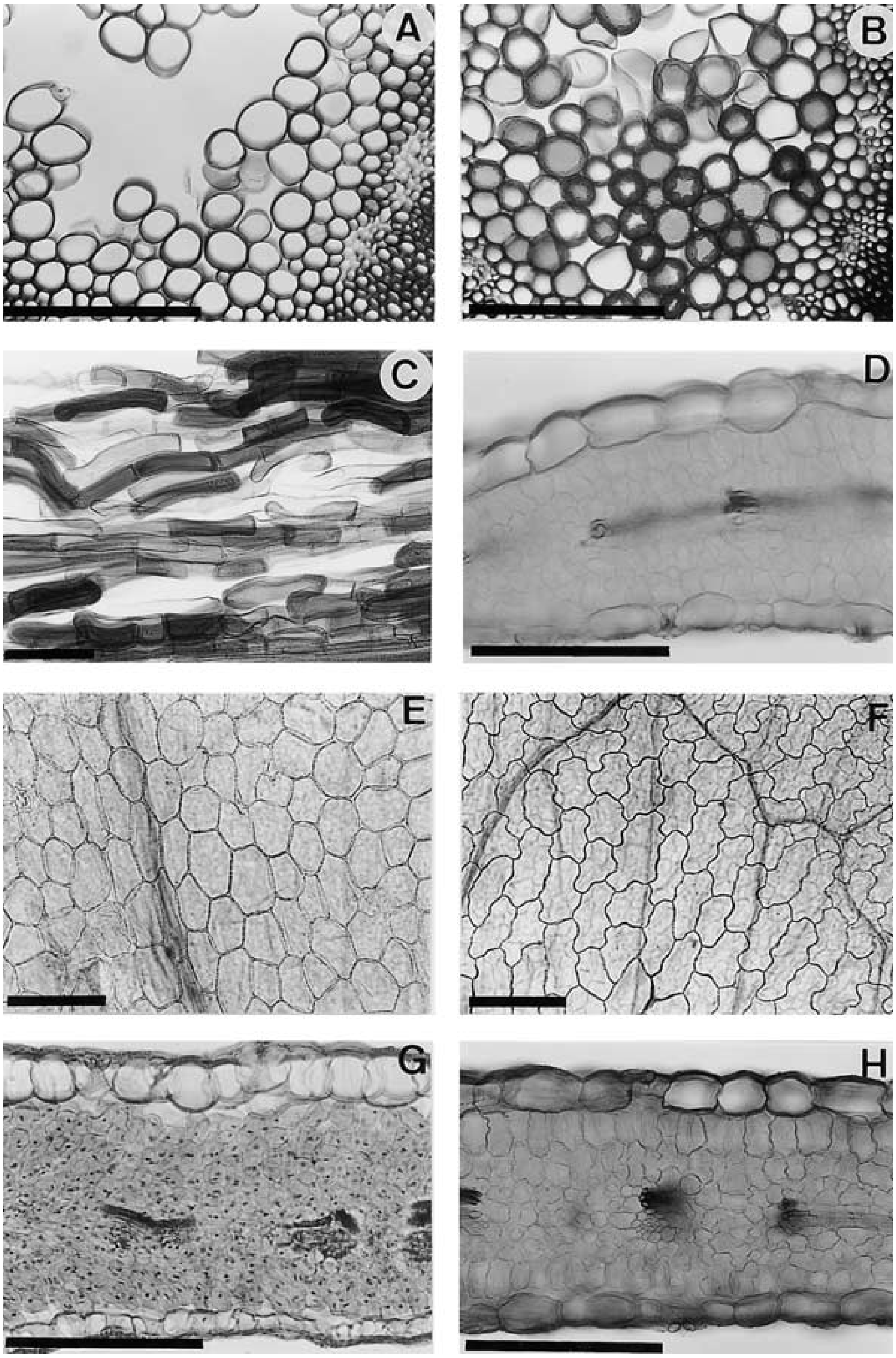
MESOPHYLL is the general tissue between upper and abaxial epidermis. It is a specialized photosynthetic tissue and may be differentiated or not into palisade and spongy tissue. In most species of *Jasione* mesophyll is undifferentiated and is composed of almost rounded cells with distinct intercellular spaces (Fig. 2G). In species with differentiated mesophyll, the palisade is made up of squarish to circular cells and is mostly confined to the adaxial surface of the leaf; the spongy mesophyll is of rounded cells. This type of mesophyll has been observed in *J. crispa* subsp. *tristis* and *J. crispa* subsp. *mariana*. There is considerable variation in the structure of the mesophyll of both *J. maritima* and *J. sessiliflora*. In some specimens, a single layer of palisade of isometric cells is present on both the adaxial and abaxial surfaces (Fig. 2H); in other specimens palisade may be confined to the upper side or mesophyll is undifferentiated (Fig. 2G). It is presumed that in the early growth period leaves did differentiate mesophyll in these species, but more extensive work is required before any generalization can be made. *Jasione penicillata* is the only species with a special type of mesophyll. In cross-section its leaves show an undulate outline and alternating regions with differentiated and undifferentiated mesophyll. Areas with differentiated palisade mesophyll of longer cells are present on both adaxial and abaxial leaf surfaces with a middle region of spongy mesophyll; in between the areas with undifferentiated mesophyll, cells are typically rounded with intercellular spaces.

HAIRS are unicellular and are extensions of the epidermal cells; they may be present on the margins or on the leaf surface (Fig. 3A). In *J. mansanetiana*, retrorse short marginal hairs have been observed. VEINLET RETICULUM may be with (Fig. 3B) or without veinlet endings (Fig. 3C). In the marginal parts of leaves there are free veinlets ending without forming a reticulum (Fig. 3D). MIDRIB usually starts branching from the leaf base, but in *J. mansanetiana* the midrib and two lateral veins run parallel for a third of the leaf before branching (Fig. 3E).

Trichoids

These are specialized structures found adaxially on leaves apically (Fig. 3F) and often also marginally (Fig. 3G,H) in our *Jasione* species. They are multicellular with a well-developed vascular supply at the base (Fig. 3G) and a number of functional

FIG. 2. Stem (A–C) and leaf (D–H) anatomy in *Jasione*; bar = 0.1mm. A, *J. sessiliflora*, transverse section; B, *J. sessiliflora,* transverse section, thickened cells can be macrosclereids or brachysclereids, the difference being only observed in C; C, *J. sessiliflora* longitudinal section; D, *J. maritima*, transverse section; E, *J. crispa* subsp. *tristis*, adaxial view; F, *J. cavanillesii*, adaxial view; G, *J. sessiliflora*, transverse section; H, *J. maritima*, transverse section.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stomata scattered on their surface (Fig. 3H). Their development starts in very young leaves and they are fully developed and functional in mature leaves. Their structure and function is not properly understood. It has been suggested by Prof. A. Weber (Vienna, personal communication) that these are secretory structures, which are functional in young and expanding leaves and supply water whenever needed, but which in mature leaves become non-functional. However, the presence of a distinct vascular supply and functional stomata on their surface clearly suggests that these are functional even in mature leaves. The non-functional stomata, as seen in older stems, have thick cutinized or lignified walls, but in trichoids the stomata have thin walls of guard cells and are just like the stomata of leaves, so there is no doubt that these are functional stomata. The trichoids were considered hydathodes at first. Structurally, however, these trichoids are different from hydathodes that secrete excess water through a pore or pores, but not through stomata. SEM study of trichoids at different stages of their development is required to understand their detailed structure and possible function.

Discussion

During the course of the preparation of the *Jasione* account for *Flora iberica* Volume 14, a very large number of specimens was studied from the total range of the taxa involved. The taxonomic conclusions resulting from this study differ substantially, as already indicated, from previous treatments, especially on the attribution of taxonomic ranks and nomenclature. The new proposed taxonomy recognizes the areas of major morphological continuity between taxa by attributing only the varietal rank to the most significant variants within the very polymorphic *J. montana*. Also at varietal rank is the supposedly very distinctive Portuguese endemic, *J. maritima* var. *sabularia*, that scarcely differs from the plants growing along the north coast of Spain and W France (*J. maritima* var. *maritima*). The geographical confinement of the endemics, sometimes rather extreme (e.g. *J. cavanillesii*, *J. mansanetiana* – known from a single gathering, *J. penicillata*), and the variation in altitude suggest a substantial variation in ecology (Table 1). The present anatomical investigation sought to provide a new perspective of the relations between the different taxa involved, between them and their environment, and would be an acid test to the taxonomic treatment used in the *Flora iberica* account.

Table 2 provides a synopsis of the distinctive anatomical characters and can be used as a key for identification. Specimens of all the Iberian species have been examined anatomically and it seems that endomorphic characters can be used in

FIG. 3. Leaf anatomy in *Jasione* showing hairs, veinlet reticulum and trichoids with vascular tissue (G) and stomata (H); bar = 0.1mm. A, *J. montana*; B, *J. mansanetiana*; C, *J. montana*; D, *J. maritima*; E, *J. mansanetiana*; F, *J. crispa* subsp. *tomentosa*; G, *J. maritima* var. *sabularia*; H, *J. montana*.

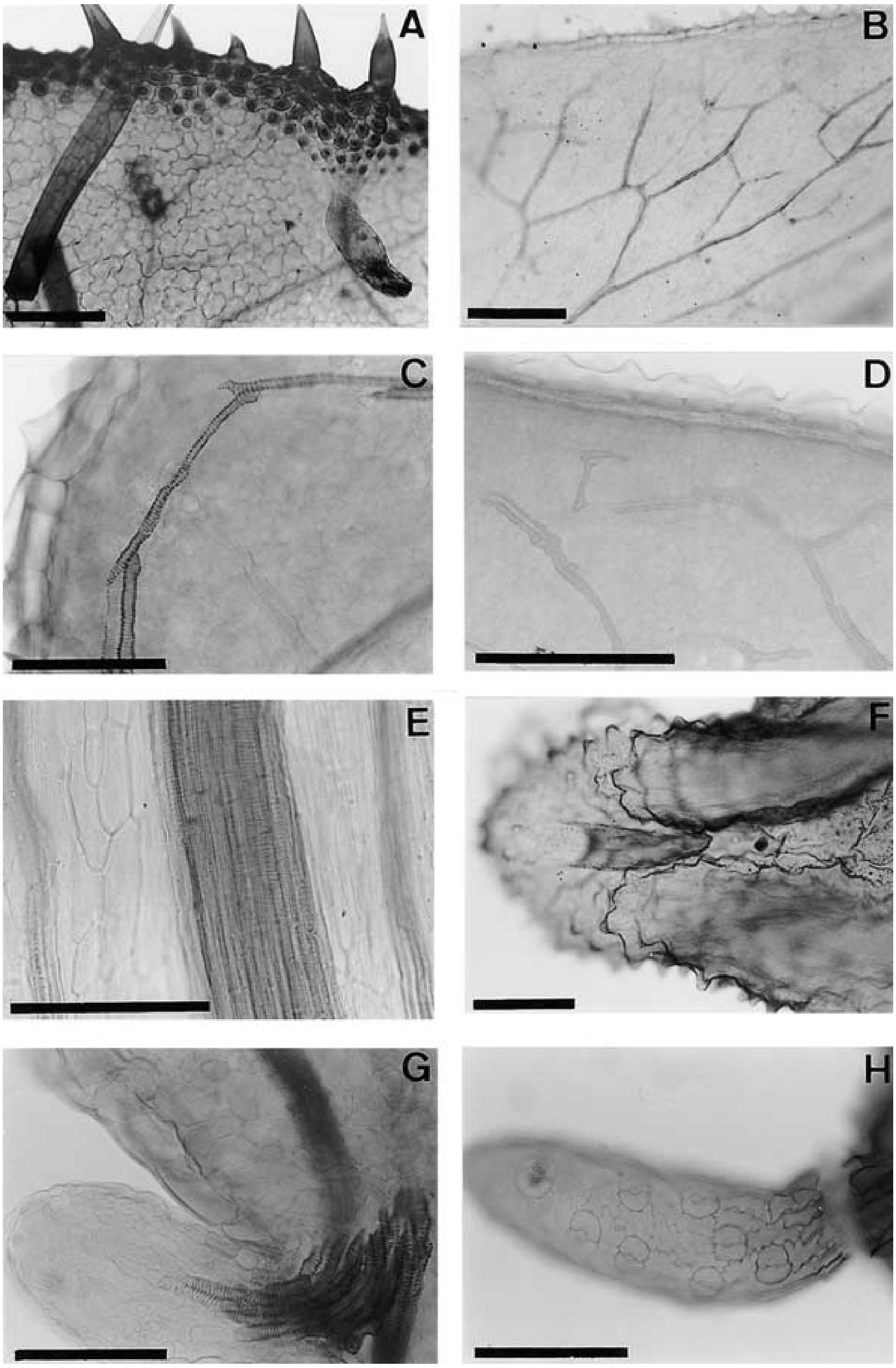
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TABLE 1. Comparison between the classification of *Jasione* by Tutin (1976) and the taxonomic conclusions in the light of the present anatomical analysis

Tutin (1976)	Present anatomical data
J. montana	*J. montana*
[*J. montana* subsp. *echinata*]	*J. montana*
[*J. blepharodon*]	*J. montana*
J. penicillata	*J. penicillata*
J. corymbosa	*J. corymbosa*
J. lusitanica A. DC. sensu Tutin	*J. maritima*
[*J. lusitanica* sensu A. DC.]	*J. montana*
J. crispa subsp. *crispa*	**crispa*
amethystima	**amethystina*
centralis	**crispa*
serpentinica	*J. sessiliflora*
mariana	**mariana*
maritima	*J. maritima*
sessiliflora	*J. sessiliflora*
tomentosa	**tomentosa*
cavanillesii	*J. cavanillesii*
J. laevis subsp. *laevis*	*J. laevis*
carpetana	*J. laevis*
rosularis	*J. montana*
J. foliosa subsp. *foliosa*	*J. foliosa*
minuta	*J. foliosa*

*, taxa of unclear anatomical affinities.

conjunction with morphological ones in distinguishing closely related species. In no way do they contradict the taxonomic treatment in the *Flora* account. In fact they are compatible with the rather iconoclastic views of the genus presented there. Also, they disagree in a number of aspects from the taxonomic treatment given by Tutin (1976) (Table 1).

Jasione mansanetiana is quite similar morphologically to *J. foliosa*, but can be easily distinguished from it on anatomical characters, such as wavy leaf epidermis on both sides, retrorse short hairs on the leaf margin and parallel veins in the lower third of leaf lamina in *J. mansanetiana*.

Jasione montana and *J. laevis* are very similar in many morphological characters, but have distinctive anatomical characters. In *J. montana* adaxial and abaxial leaf epidermal cells are subequal in size, but in *J. laevis* upper epidermal cells are 2 × larger than the lower epidermal cells. In *J. montana* stomata are present in adaxial and abaxial epidermis. In *J. laevis* stomata are rarely present in adaxial epidermis and are confined to abaxial epidermis. Wings on the stem when fully developed are mostly curved in outline in *J. montana*, but smaller and straight in *J. laevis*.

Jasione penicillata is a distinct species in habit and morphological characters, and this is supported by endomorphic characters, such as poor development of wood in stem, wavy leaf epidermis on both leaf surfaces, and alternating differentiated and undifferentiated mesophyll in the same leaf.

There is no anatomical character that distinguishes *J. maritima* var. *maritima* from *J. maritima* var. *sabularia*. But *J. maritima* is quite distinct from other species in having brachysclereids in the cork of old wood and the development of two layers of palisade tissue on the adaxial and abaxial side of its fleshy leaves.

None of the subspecies of *J. crispa* are distinguishable on anatomical characters. That is the reason for the uncertain taxonomic rank given on exclusively anatomical data and indicated by * in Table 1. *Jasione crispa* subsp. *tomentosa* also shares some common anatomical characters with *J. sessiliflora* and shows an affinity with this species. Both have rounded pith cells, undifferentiated mesophyll, development of lignified patches in cortex and a distinct endodermis even after formation of wood. *Jasione crispa* subsp. *mariana* and *J. crispa* subsp. *tomentosa* have some common anatomical characters, such as adaxial leaf epidermal cells 1.5–2 × larger than abaxial epidermal cells, well-developed wood, and endodermis distinct even when wood is formed.

Jasione cavanillesii, which is related to *J. crispa* subsp. *crispa* and has also been treated as a subspecies of *J. crispa*, is quite distinct in endomorphic characters, such as poor development of wood, adaxial epidermal cells 2 × larger than abaxial epidermal cells and both epidermal cells wavy in outline. Therefore, on the basis of morphological characters in conjunction with endomorphic ones, it can be regarded as a distinct species.

Jasione crispa subsp. *serpentinica* (= *J. sessiliflora*) has been recognized as a separate taxon mainly on the grounds of its very thick, papillose and whitish leaf edge. However, such a feature is present in different degrees virtually throughout the genus. The papillae are ornate (Fig. 4A,B) or smooth (Fig. 4C,D). To associate their morphology with any ecological requirement seems irrelevant. In fact, such a feature is present in most widespread species of the genus (*J. montana*, Fig. 4B) and in the species with the flattest leaf blades (*J. foliosa*, Fig. 4C,D). Also, the so-called *J. crispa* subsp. *serpentinica* is in no way different anatomically from *J. sessiliflora*. They both form a distinct unit separate from the four subspecies considered here in *J. crispa* s.l. by the non-parenchymatous pith and the presence of sclereids in the stem (Table 2).

Jasione corymbosa, a sand-dune annual sometimes regarded as a subsp. of *J. montana*, is also quite distinct in endomorphic characters, such as almost wingless, angular stem, poor development of wood and differentiated mesophyll.

Some of the anatomical characters are quite variable within a taxon. In *J. maritima* and *J. sessiliflora* differentiated and undifferentiated leaf mesophyll has been noticed in specimens of the same species; for that reason, in these species such a character is not useful for taxonomic purposes. Stem sclereids have been observed in the pith of a majority of specimens of *J. sessiliflora*. It is difficult to explain the presence or absence of sclereids in the same species. The age of the plant, and especially the kind of environment during plant development, may play an important role in

TABLE 2. Synopsis of the anatomical characters of the Iberian taxa of *Jasione*. *Jasione foliosa* (fo); *J. mansanetiana* (ms); *J. montana* L. var. *montana*, var. *bracteosa*, var. *latifolia*, var. *gracilis* (mo); *J. penicillata* (pe); *J. corymbosa* (co); *J. laevis* (la); *J. maritima* var. *maritima*, var. *sabularia* (mr); *J. crispa* (Pourr.) subsp. *crispa* (cr), subsp. *tristis* (tr), subsp. *mariana* (mn), subsp. *tomentosa* (to); *J. cavanillesii* (ca); *J. sessiliflora* (se)

		Species												
Characters		fo	ms	mo	pe	co	la	mr	cr	tr	mn	to	ca	se
A.	Stem epidermal cells raised externally	B	A	B	B	B	B	B	B	B	B	B	B	B
B.	Stem epidermal cells not raised externally													
A.	Stem prominently winged	B	B	A	B	B	B	A	B	B	B	B	B	B
B.	Stem not prominently winged													
A.	Cortex parenchymatous when wood is well developed	B	B	B	B	B	B	B	B	A	B	B	B	B
B.	Cortex not parenchymatous when wood is well developed													
A.	Cork present	B	B	B	B	B	B	A	B	A	B	B	B	B
B.	Cork absent													
A.	Pith parenchymatous	A	A	A	A	A	A	A	A	A	A	A	A	B
B.	Pith not parenchymatous													
A.	Pith cells polygonal	A	A	A	A	A	A	A	A	A	A	B	A	B
B.	Pith cells rounded													
A.	Sclereids present in the stem	B	B	B	B	B	B	A	B	B	B	B	B	A
B.	Sclereids not present in the stem													
A.	Leaf adaxial and abaxial epidermal cells subequal in size	A	A	A	A	A	B	A	A	A	A	B	B	B
B.	Leaf adaxial epidermal cells 1.5–2 × larger than abaxial epidermal cells													

A. Leaf adaxial epidermal cells with straight walls	A	B	A	B	A	A	A	A	A	A	A	B	A
B. Leaf adaxial epidermal cells with wavy walls													
A. Inner and radial walls of adaxial epidermal cells of leaf cutinized	B	B	A	B	B	B	B	B	B	B	A	A	B
B. Inner and radial walls of adaxial epidermal cells of leaf not cutinized													
A. Leaf stomata on both epidermises	A	A	A	A	A	B	A	A	A	A	A	B	A
B. Leaf stomata only on the abaxial epidermis													
A. Leaf mesophyll differentiated into palisade and spongy tissue	B	B	B	B	B	B	B	B	A	A	B	B	B
B. Leaf mesophyll undifferentiated													
A. Leaf undulate in cross-section with alternating regions of differentiated and non-differentiated mesophyll	B	B	B	A	B	B	B	B	B	B	B	B	B
B. Leaf not undulate and without regions of differentiated and non-differentiated mesophyll													
A. Leaf margin with retrorse marginal hairs	B	A	B	B	B	B	B	B	B	B	B	B	B
B. Leaf margin without retrorse marginal hairs													
A. Leaf midrib branching from leaf base	A	B	A	A	A	A	A	A	A	A	A	A	A
B. Leaf midrib branching only one-third above leaf base													

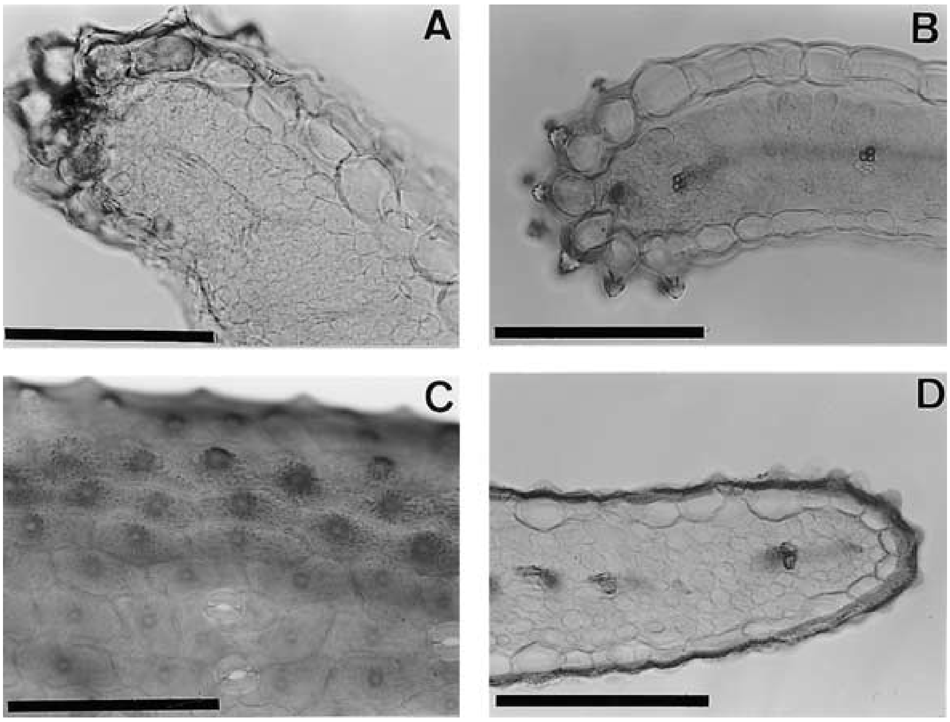

FIG. 4. Leaf anatomy in *Jasione* showing the epidermal cells at the leaf margin; bar = 0.1mm. A, *J. sessiliflora*, transverse section; B, *J. montana* var. *montana*, transverse section; C, *J. foliosa*, surface view; D, *J. foliosa*, transverse section.

sclerification of tissue. The relation between environment and anatomical variation within a taxon may be clarified by a study of plasticity in which seeds of the same population were grown in different conditions. The factors that can be more limiting to the success of *Jasione* (Table 3) seem to relate to water availability and shade possibly versus temperature, and these should be investigated in such an experiment.

On the whole, the anatomical characters do not show obvious adaptive features to the environment, in particular as far as coping with water stress. Characters that may be connected with environment, such as position of leaf stomata, shape of pith cells, wall of adaxial epidermal cells (Table 2), do not seem to be linked to particular habitats and seem to occur randomly in the genus (Table 2). Species that must withstand quite high temperatures, e.g. *Jasione penicillata*, do not show anatomical features particularly adaptive in relation to others that occupy rather mesophytic environments, e.g. *J. laevis.* Therefore, in designing a plant experiment on plasticity it must be borne in mind that in *Jasione* adaptations seem to be, not surprisingly (see Turesson, 1922), more of a physiological nature rather than structural.

Some anatomical features seem to be linked to particular taxa. Sclereids present in the stem of *J. crispa* subsp. *mariana* may play a role in providing rigidity to the stem

TABLE 3. Synopsis of some ecological characters of the Iberian taxa of *Jasione*. For abbreviations of taxa names see Table 2. Other abbreviations: crev, crevices; edf, edge of forest; grn, granite; lmst, limestone; mdw, meadow; msnd, maritime sand dunes; rdr, ruderal; roc, rocks; slt, slate; snd, sand; ultr, ultrabasic soil; wal, walls; woo, woodland

	Characters	
Taxon	Altitude (m)	Ecology
fo	1200–2400	crev, lmst
ms	400–700	wal, lmst
mo	0–1700(–1900)	rdr, mdw, edf
pe	500–2000	snd, lmst
co	s.l.	msnd
la	(860–)1330–2600	grn, lmst, slt, snd, mdw, woo
mr	s.l.	msnd
cr	1600–2600	grn, lmst, slt, mdw
tr	1700–3470	slt, roc
mn	300–700	crev, lmst
to	1000–1400	snd
ca	1650–2460	crev, roc, slope
se	600–2030	grn, ultr, snd

of this chasmophytic, often pendent, species. But in some species, e.g. *J. sessiliflora*, it is difficult to see any link between the presence of sclereids and habit or environment. The presence of stomata only on the abaxial epidermis in *J. laevis* may indicate that the species rests its adaptations on more ‘conventional’, morphological, features.

Facultative autogamy has been described as an efficient mechanism for generating ecotypic populations in various plant groups (Turesson, 1922, 1925; Davis & Heywood, 1963; Smith, 1981), explaining some of the variation in populations. However, in *Jasione* the reverse situation, cross-pollination with occasional autogamy, has been reported (Kirchner, 1897; Leins & Erbar, 1990). These are issues that need further investigation.

From the taxonomic point of view it is interesting that the taxa treated in the *Flora iberica* account at varietal rank (that is, within *J. montana* and *J. maritima*) cannot be separated on anatomical grounds. On the other hand, the anatomical evidence, although diagnostic, does not support grouping of taxa above variety level. For example in *J. crispa* (Table 2), subsp. *tristis* differs from the other subspecies in three characters, as many as the characters that separate e.g. *Jasione foliosa* and *J. maritima*, two very distinct species in morphological, ecological and distributional terms. Therefore, it is impossible to point out relationships based solely on anatomical characters.

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Appendix

Specimens examined.

J. cavanillesii. SPAIN. Santander: Espinama: camino de Peña Vieja, *Castroviejo & Valdés* (MA 427002); Espinama, Garganta de Hoyo Grande, Montserrat, *Laínz & Villar* (JACA 292688). Leon: Cabaña Veronica, *Garcia Gonzalez* (JACA 485985).

J. corymbosa. SPAIN. Granada: Torrox, iv 1903, *Domingo s.n.* (G); Estepona, *Bernardi* 13883 (G).

J. crispa subsp. **crispa**. SPAIN. Gredos, *Rivas Goday* (MAF 85778). Gredes, *R.M.* [probably Rivas Martinez] (MAF 03285). León: Llanaves de la Reina, *Rivas Martinez* (MAF 125171). *Sine loc.*: (MAF 151058).

J. crispa subsp. **mariana**. SPAIN. Badajoz: Castillo de Alange, *Zubizarreta* 34536 (MA 579819; MA 581060); cerca de Garlitos, *Pérez Chiscano* (MA 560764). Cáceres: Cuarcitas de Monfragüe, Torrejón el Rubio, *Pérez Chiscana* (MA 560765). Jaén: Aldeaguemada, Sierra Morena, *Aran & Tohá* (MA 545692).

J. crispa subsp. **tomentosa**. SPAIN. Castellón: Monte Pina, Bernal, *Muñoz & Pedrol* (MA 459338); Monte Pina, *Mateo & Puche* (MA 431979). Jaén: Sierra Quintana, *Ferdández &*

Cano (MA 430422); La Carolina, *Castroviejo* (MA 430963). Toledo: Navahermosa, Sierra Fria, Marcos, *Gómez et al.* (MA 430392).

J. crispa subsp. **tristis**. SPAIN. Granada: Sierra Nevada: *Defferrard* 4274 (G 271921); 27 vi 1973, *Fernandez-Casas s.n.* (G); vii 1853, *Ayasse* (G); *Jacquemoud & Jeanmonod* 3266 (G 177718).

J. foliosa. SPAIN. Jaén: Sierra del Pozo, picos Cabañas, *Fernández Casas* (MA 418761). Murcia: illeg., *Caridad Telma* (MA 541938).

J. laevis. SPAIN. Lugo: Sierra de Ancares, Peñarrubia, *Castroviejo et al.* (MA 432035). Burgos: Espinosa de los Monteros, *Izuzquiza* (MA 472249). León: puerto de Ancares, *Carrasco et al.* (MA 542760). Gerona: collada de Tosas, *Fernández Casas* (MA 416947). Asturias: puerto de Leitariegos, *Castroviejo* (MA 433558). León: Riano to Potes, Puerto de San Glorio, *Sales & Hedge* DNA 98:14 (E).

J. mansanetiana. SPAIN. Castellón: Argelita/Espadilla, *Roselló & Peris* (VF 17061) – holotype of *J. mansanetiana*.

J. maritima var. **maritima**. FRANCE. Gironde: Cap Ferret, iv 1882, *Foucaud s.n.* (LY): Après, bassin d'Arcachon, *Brochon & Neyraut* 2519 (LY). Ychoux (Landes): près du ruisseau Barade dans Brastey, 11 vi 1899, *Neyraut s.n.* (LY). *Sine loc.*: 22 vi 1890, *Brochon & Neyraut s.n.* (LY); 28 vi 1896, *Foucaud s.n.* (LY).

SPAIN. La Coruña: Muros to Cabo Finisterra, Mar de Lira beach, *Sales & Hedge* DNA 98:49, 98:50, 98:53, 98:57 (all at E); Finisterre, *Lacaita* 32283 (BM – holo. *J. montana* subsp. *maritima* var. *imbricans* J. Parnell).

J. maritima var. **sabularia**. PORTUGAL. Beira Litoral: Ovar, Furadouro beach, *Sales & Hedge* DNA 98:88, 98:89, 98:91, 98:94, 98:97, 98:100 (all at E).

J. montana s.l. SPAIN. Orense: Lovios, Sierra Santa Eufemia, *Castroviejo* 9256 bis (MA 431970). Huelva: Almonte, Reserva Biológica de Doñana, Coralles de Santa Olalla, Barra, *Costa et al.* 2174 (MA 432005).

J. montana var. **sabularia**. SPAIN. Orense: Park of Serra do Xurés, Torneiros to Portela do Homen, *Sales & Hedge* DNA 98:100 (E).

J. montana var. **montana**. SPAIN. La Coruña: Cabo Fisterra, *Sales & Hedge* DNA 98:59 (E).

J. montana 'cornuta'. MOROCCO: Chaonia, Guicer, *Pitard* 1866 (G); Tiflet, *Lewalle* 14063 (G 464434).

J. penicillata. SPAIN. Málaga: Mijas, Sierra de Mijas, *Fernández Casas* (G 135920); Mijas, Cerro Castillejo, *Fernández Casas* (G 197778, MAF 116113); Tejeda supra Canillas, vi 1837, *Boissier* (G – lecto. *J. penicillata*); Sierra de Ronda, 9 vii, *Reverchon* 1889: 194 (G); Sierra Almijara, 23 vi 1935, *Modesto Laza Palacios* (MAF 03258); Pinar de Cómpeta, *Rivas Goday* (MAF 101554).

J. sessiliflora. MOROCCO. MA: Jebel Hebri, *Davis* 55073 (E); GA: Imlil, *Davis* 55538 (E); GA: Tizi-Oukaimeden, *Davis* 55403 (E).

PORTUGAL. Trás-os-Montes e Alto Douro, Bragança: Ouzilhão, Bairro da Ameã, *Sales & Hedge* DNA 98:7 (E); Carrazedo, *Sales & Hedge* DNA 98:5 (E); Carrazedo, *C. Aguiar* 4351 (E), *C. Aguiar* 2627, *C. Aguiar* 2211; Espinhosele, *A. Carvalho*, 1796; Rabal, Moagem, *C. Aguiar* 644 (all at Herb. Esc. Sup. Agrária de Bragança); Alimonde, *Sales & Hedge* DNA 98:6 (E); Montezinho Park, *Sales & Hedge* DNA 98:8, 98:9, 98:10 (all at E); Soeira versus Penoiços, *Silva & Teles* 8251 (LISE). Minho: Gerês Natural Park, Pedra Bela viewpoint, *Sales & Hedge* DNA 98:68, 98:69, 98:70, 98:71, 98:72 (all at E). Beira Alta: Serra de Estrela, Penhas da Saúde to Manteigas, *Leadlay & Petty* 355 (BM). *Sine loc.*: *Cuatrecasas* (MAF 03297).

SPAIN. Logroño: Valbanera, *Losa* (MAF 03298). Burgos: Silos, *Rivas Goday* (MAF 94462). Ávila: Piedralaves, *Montserrat & Rebollar* (JACA 32683); Sierra de Gredos, Mombeltran, vi 1928, *Wilmott* (BM); Sierra de Gredos, Barranco de las Escalernelas, Herb. *Lacaita* 410/27 (G). León: Cistierna to Riano, vii 1927, *Wilmott* (BM). Valladolid: Traspinedo-Sardon de Duero, *Montserrat* (JACA 330374). Guadalajara: El Pedregal (JACA 473181). Madrid: Pinar San Rafael, ann. 1841, *Reuter s.n.* (G – lecto. *J. sessiliflora*); Guadarrama, *Reuter s.n.* (G); Sn. Bernardino, 18 vi 1854, *Bourgeau s.n.* (G). Ourense: Carballeda, *Valdés-Bermejo et al.* (G 339193). *Sine loc.*: Herb. *Quatrecasas* (MAF 94016).