

Taxonomic Significance of Leaf Indumentum Characteristics of the Genus *Biscutella* (Cruciferae)

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Source: *Folia Geobotanica & Phytotaxonomica*, Vol. 27, No. 4 (1992), pp. 401-417

Published by: Springer

Stable URL: <https://www.jstor.org/stable/25130307>

Accessed: 05-09-2019 17:09 UTC

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Taxonomic Significance of Leaf Indumentum Characteristics of the Genus *Biscutella* (Cruciferae)

KEYWORDS

Biscutella, *Cruciferae*, Trichomes, Indumentum, Taxonomy, SEM, Europe

ABSTRACT

Leaf indumentum characteristics of 52 taxa of the genus *Biscutella* are examined by hand lens, stereo- and scanning electron microscopy. Hairs occur on all vegetative organs of all taxa except *B. laevigata* subsp. *lucida* which is completely glabrous and shining. Trichomes are simple unicellular and attenuate but are variable in structure, size and distribution both within and between species. Eight types of indumenta are recognized and these include hispid/hirsute, puberulent, tomentose, villous and velutinous. Each type varies in abundance from sparse to dense within the genus. In a few cases, indumentum is species-specific; for example, the whitish tomentose hair covering of *B. frutescens* distinguishes this species from the remaining species of the genus. In other taxonomically important species affinities are indicated. The occurrence of indumentum is discussed in relation to the various roles usually ascribed to this feature.

INTRODUCTION

Trichomes and indumenta are widely used in taxonomic studies. As simple tools of morphology they are useful because of the relative ease with which they may be examined and because of their almost universal occurrence, particularly in some groups of higher plants such as the Pteridophytes and Angiosperms (PAYNE 1978). In the *Cruciferae*, trichomes and indumenta are commonly employed as taxonomic characters at every level of

classification (PRANTL 1891, PAYSON 1922, SCHULZ 1936, ROLLINS and SHAW 1973, ROLLINS and BANERJEE 1975, 1976).

However, there is no satisfactory and generally acceptable morphological classification of the various trichome and indumentum types despite the large volume of previous work or probably because of it (BEHNKE 1984); and certainly to some extent due to its wide historical background. Consequently, the systematic utility of these simple but important characters has been partially obscured by inadequate and frequently overlapping definition of terms.

In the course of a taxonomic and biosystematic study of the genus *Biscutella* L., the trichomes and indumenta of the leaf have been critically examined as part of the multidisciplinary study-approach (OLOWOKUDEJO and HEYWOOD 1984, OLOWOKUDEJO 1985, 1986a, b, c, d, e, f; 1987). *Biscutella* is a taxonomically difficult group because it lacks "good" characters which can be used for defining its species precisely. Previous taxonomic studies of the genus by DE CANDOLLE (1811, 1821), JORDAN (1864), ROUY and FOUCAUD (1895), MALINOWSKI (1910), MACHATSCHKI-LAURICH (1926), GUINEA (1963) and GUINEA and HEYWOOD (1964) among others, differ in the number and circumscription of taxa. Apart from their inclusion in taxonomic keys and general descriptions, the indumentum and trichomes of *Biscutella* leaves have never been studied in detail. The present study is aimed at exploring the taxonomic significance of these morphological features which have been successfully applied in the classification of taxa and demonstration of species relationships in several other plant genera and families.

MATERIAL AND METHODS

Specimens of *Biscutella* species in the following herbaria were studied: B, BC, BCC, BCF, BM, G, GDA, GJO, GZU, HBG, KC, LINN, LY, MA, MAF, RNG and W. Standard herbarium abbreviations follow HOLMGREN et al. (1981).

This was augmented by living natural populations of some taxa which were sampled during field investigations in Spain in 1978. Fruits and seeds obtained from these trips and also from the *Cruciferae* Seed Bank of Professor C. Gómez-Campo (GÓMEZ-CAMPO 1972) and those of known wild origin received from other collectors and Botanic gardens were cultivated in the greenhouses and experimental grounds of the School of Plant Sciences, University of Reading. All cultivated taxa are listed in the Appendix 2 together with the accession number of Botanic Gardens (BG) from which the seeds were obtained. Collectors' names and numbers are also included in the case of samples provided by individuals or groups.

MORPHOLOGICAL EXAMINATION

About 10 - 100 specimens of each taxon were examined by the hand lens, stereo- and light- microscopes. The trichome structure, indumentum type and distribution of both adaxial and abaxial surfaces of basal and cauline leaves were recorded. Representative specimens of each taxon studied are in Appendix 1.

SCANNING ELECTRON MICROSCOPY

Two to six representative leaf samples were examined depending on the geographical spread of each species. Each leaf was rehydrated by boiling in water for 5-10 minutes and then fixed in formalin-acetic-alcohol (FAA) for 12-24 hrs. It was washed in distilled water and dehydrated by passing through 50%, 70%, 80%, 90%, 95% and 100% ethyl alcohol series and then stored in a dessicator.

An area about 5 mm² was removed from a standard central position of each leaf and attached to a labelled stub using double-sided adhesive tape. All samples were then coated with gold in a Polaron E-500 sputter coating unit and scanned in a JEOL JSM - T20 scanning electron microscope operated at an accelerating voltage of 12.5 KeV in the Electron Microscopy Unit, Department of Botany, University of Reading. Electron micrographs were made at different magnifications of 50x to 900x.

USE OF TERMINOLOGIES

It has been deemed necessary to define the various terminologies employed in this study because of the frequently overlapping and generally confusing definition of hairs and indumentum in the literature. The definitions given below are modified from LAWRENCE (1951), JOHNSON (1975), and PAYNE (1978).

The indumentum is defined as the collective trichome cover of a given plant surface. Pubescence is regarded as a synonym and therefore can be used interchangeably. Trichomes are the basic building blocks from which indumenta are made and may be arranged on plant surfaces to form different kinds of indumenta.

The various types of trichomes and indumenta observed in *Biscutella* are defined as follows:

Trichome types or attributes

Attenuate:	With a long gradual taper.
Bosseled:	Covered with knobs or small protuberances or bosses.
Curly:	With several bends or curvatures; tortuous; sinuous.
Contorted:	Twisted; irregularly sinuate; spiral.
Pedestal:	The unicellular or multicellular raised base to which hairs are attached.
Setiform:	Shaped as a bristle.

Indumentum types

Ciliate:	Fringed with conspicuous hairs on the margin.
Ciliate-dentate:	Having teeth fringed with hairs.
Glabrate:	Nearly glabrous.
Glabrous:	Lacking trichomes, not hairy.
Hirsute:	With long, rather stiff trichomes.
Hispid:	With long, very stiff bristles or trichomes.
Puberulent:	With very short hairs; minutely and finely pubescent.
Tomentose:	Densely woolly or with soft, matted, wool-like trichomes.
Velutinous:	Velvety with a covering of short, silky hairs.
Villous:	With long, soft, curly but not matted hairs.

RESULTS

Leaf indumentum characteristics of the genus are summarised in Table 1 where taxa are arranged according to the classification of GUINEA and HEYWOOD (1964). Scanning electron micrographs of indumentum and trichome types of some species are shown in Plate 22-24. Abaxial and adaxial surfaces usually possess the same type of trichome and indumentum, except in a few cases where the abaxial surface may be hairy and the adaxial glabrous or glabrate (e.g. *B. lamottii*).

Trichomes are found on all vegetative organs of most species but are particularly abundant on the leaves where they are aggregated to form different types of indumentum. The only important exception is *B. laevigata* subsp. *lucida* (Plate 24A) which has completely glabrous and shining leaves which, however, may be ciliate in some cases. The leaves of some populations of *B. laevigata* subsp. *laevigata* are also glabrous but may be occasionally ciliate dentate. The trichomes found in the remaining taxa are simple, unicellular and attenuate. They are usually with swollen bases (Plate 23C) or seated on pedestals of several epidermal cells (Plate 22A, B, D). There is intra- and inter-specific variation in trichome structure, size and distribution. Setiform hairs occur in some populations of *B. valentina* (Plate 22E), *B. scaposa*, *B. flexuosa*, *B. apricorum* and *B. mediterranea* (Plate 22D). The hair surface in these species are ornamented with knobs or small protuberances, that is, they are bosselated or tuberculate (Plate 22F). In *B. sempervirens* the hairs may be contorted (Plate 23A, B) and covered with tubercles and striae. In some cases the tubercles or bosses are restricted to the mid region of the trichome (Plate 22D) while the base and top are smooth, or the trichome may be tuberculate throughout. The density of the tubercles varies both within and between species. The size also varies considerably even on a single trichome. On the other hand the hairs of *B. frutescens* are soft, curly and smooth (Plate 23E). It is quite common to find relatively long hairs intermixed with very short ones on the same leaf surface as is clearly illustrated in *B. vincentina* (Plate 22C).

Five main types of indumentum are found within the genus as summarised in Table 1. *B. laevigata* is the most variable species for this character since all the 5 indumentum types can be found among the 12 subspecies investigated. Subspecies *varia*, *geustphalica*, and *subaphylla* have puberulent indumentum i.e. the leaves are usually finely pubescent and the hairs are often short and minute. This type of indumentum also occurs in subspecies *kernerii* and *tenuifolia*, some specimens of which may bear tomentose and villous indumenta types respectively (Table 1). The leaves of subspecies *gracilis* may be densely tomentose or velutinous. The trichome cover of the remaining taxa, i.e. subspecies *laevigata*, *austriaca*, *tirolensis*, *angustifolia* and *illyrica*, is either hispid or hirsute or both. Some totally glabrous populations occur in subspecies *laevigata* while in subspecies *austriaca* subglabrous or ciliate dentate specimens are of frequent occurrence. The only totally glabrous taxon with shiny leaves is subspecies *lucida*. Figure 3A shows the smooth epidermal surface and several stomata which are clearly visible with the SEM.

Among the remaining species of the genus, tomentose indumentum occurs in *B. vincentina*, *B. sclerocarpa*, *B. arvernensis* and *B. guillonii*. The whitish tomentose indumentum of *B. frutescens* is unique within the genus. In addition to the tomentose trichome cover, some specimens with puberulent indumentum are found in *B. divionensis*, *B. controversa* and *B. neustriaca*. Both tomentose and villous indumenta occur in *B. sempervirens*, a widespread and morphologically variable species. The leaves of *B. variegata*, *B. megacarpaea* and *B. foliosa* are finely pubescent. However, long and rather stiff hairs may be mixed with the relatively shorter and softer ones on the same surface. Moreover subglabrous leaves may occur in a rosette of densely pubescent leaves. The leaf indumentum of *B. cuneata*, *B. eriocarpa*,

B. lyrata, and *B. didyma* is predominantly puberulent. The villous indumentum of *B. glacialis* is quite distinctive and is the most important character linking it with some populations of *B. sempervirens*, its closest relative.

In the remaining 23 species the leaf indumentum is either hispid or hirsute or both. It is often difficult to distinguish between these two indumenta types as defined by PAYNE (1978), and are therefore regarded as synonymous here. Occasionally glabrous or subglabrous leaves, in which trichomes are restricted to the margins (ciliate) or major veins, are found among densely hispid or hirsute specimens e.g. *B. lamottii*, *B. coronopifolia*, *B. apricorum*, *B. intermedia* and *B. valentina*. Finely tomentose leaves also occur in a few specimens of *B. gredensis* and *B. cichoriifolia*. As shown in Table 1, the density of trichomes also varies considerably both within and among species.

DISCUSSION

The family *Cruciferae* represents a prominent example of a higher taxon in which different classifications have considered trichome and indumentum characters at almost every level. Although the various hairs and indumenta observed within the genus *Biscutella* show no correspondence to already established infrageneric groupings based on other features, yet they indicate taxonomically important group affinities and in a few cases are species-specific.

The whitish tomentose indumentum of *B. frutescens* distinguishes this species from all others in the genus and is therefore of practical taxonomic significance. This correlates with a diagnostic combination of other characters possessed by this species (OLOWOKUDEJO 1987). The puberulent/subglabrous leaves of *B. variegata*, *B. megacarpaea* and *B. foliosa* indicate the close morphological similarity of these species which OLOWOKUDEJO (1986a) has earlier regarded as conspecific. The variable indumenta recorded for the various subspecies of *B. laevigata* further reinforces the observations of HEYWOOD (1964) that it is indeed a polymorphic species. The various indumenta types do not follow any trend within this species complex and are therefore not correlated with the level of ploidy (OLOWOKUDEJO and HEYWOOD 1984). Generally species that have been shown to be morphologically variable usually have more than one type of indumentum e.g. *B. laevigata*, *B. sempervirens*, *B. valentina* and *B. coronopifolia*.

The villous indumentum of *B. glacialis* and some populations of *B. sempervirens* indicates the close relatedness of these two species. Some plants of *B. sempervirens* which are small in stature and have villous hair covering are sometimes confused with *B. glacialis*. These plants are, however, distinguishable from *B. glacialis* by a combination of other characteristics and have been recognised as a variety by OLOWOKUDEJO (1986b). *B. glacialis* is also one of the few species in which indumentum density correlates with a number of other attributes employed in recognising two varieties within the species (OLOWOKUDEJO 1986c). The indumentum characteristics of *B. coronopifolia*, *B. intricata*, *B. polyclada*, *B. granitica*, and *B. pinnatifida* are very similar. This agrees with the results of earlier studies, based on fruit morphology (OLOWOKUDEJO 1985), nectary structure (OLOWOKUDEJO 1986d) and petiole anatomy (OLOWOKUDEJO 1987), that these taxa constitute one variable species with many variants which are all linked with the more common forms. The present observation on the hair coverings does not support continued separation of these taxa. The necessary nomenclatural changes have been proposed by OLOWOKUDEJO (1986a). *B. microcarpa* also shares the same type of indumentum with *B. baetica*, the only species to which it is related within the genus. The only two species, *B. auriculata* and *B. cichoriifolia*, which have been elevated to the rank of a subgenus (OLOWOKUDEJO 1986e) also possess similar indumentum.

Table 1. Summary of leaf indumentum characteristics of *Biscutella*

Taxa	Indumentum type	Density of hairs
Section <i>Biscutella</i>		
Series <i>Laevigatae</i> MALIN.		
<i>B. laevigata</i> L.		
subsp. <i>laevigata</i>	Hispid/Hirsute/Glabrous	Dense to sparse
subsp. <i>austriaca</i> (JORD.) MACH.-LAUR.	Hispid/Subglabrous	Dense to sparse
subsp. <i>kemeri</i> MACH.-LAUR.	Puberulent/Tomentose	Dense
subsp. <i>gracilis</i> MACH.-LAUR.	Tomentose/Velutinous	Dense
subsp. <i>tenuifolia</i> (BLUFF et FINGERH.) MACH.-LAUR.	Villous/Puberulent	Dense
subsp. <i>guestphalica</i> MACH.-LAUR.	Puberulent	Dense
subsp. <i>varia</i> (DUMORT.) ROUY et FOUC.	Puberulent	Dense
subsp. <i>subaphylla</i> MACH.-LAUR.	Puberulent	Dense
subsp. <i>tirolensis</i> (MACH.-LAUR.) HEYWOOD	Hispid	Dense
subsp. <i>angustifolia</i> (MACH.-LAUR.) HEYWOOD	Hirsute/Hispid	Dense to sparse
subsp. <i>illyrica</i> MACH.-LAUR.	Hispid	Dense to sparse
subsp. <i>lucida</i> (DC) MACH.-LAUR.	Glabrous	---
<i>B. scaposa</i> SENNEN ex MACH.-LAUR.	Hirsute/Hispid	Dense to sparse
<i>B. flexuosa</i> JORDAN	Hirsute	Dense to sparse
<i>B. variegata</i> BOISS. et REUTER	Puberulent/Subglabrous	Dense to sparse
<i>B. megacarpaea</i> BOISS. et REUTER	Puberulent/Subglabrous	Dense to sparse
<i>B. foliosa</i> MACH.-LAUR.	Puberulent/Subglabrous	Dense to sparse
<i>B. gredensis</i> GUINEA	Hispid/Tomentose	Dense to sparse
<i>B. neustriaca</i> BONNET	Puberulent/Tomentose	Dense
<i>B. frutescens</i> COSSON	Tomentose, whitish	Dense
<i>B. vincentina</i> (SAMP.) ROTHM. ex GUINEA	Tomentose	Dense
<i>B. sempervirens</i> L.	Tomentose/Villous	Dense
<i>B. glacialis</i> (BOISS. et REUTER) JORDAN	Villous	Dense to sparse
<i>B. brevifolia</i> ROUY et FOUC.	Hirsute	Sparse
<i>B. cuneata</i> (FONT QUER) FONT QUER ex MACH.-LAUR.	Puberulent	Sparse
<i>B. rotesii</i> FOUC.	Hispid	Sparse
<i>B. lamottii</i> JORDAN	Hispid/Glabrous (abaxial)	Dense to sparse
<i>B. sclerocarpa</i> REVEL	Tomentose	Dense
<i>B. arvernensis</i> JORDAN	Tomentose	Dense
<i>B. divionensis</i> JORDAN	Tomentose/Puberulent	Dense
<i>B. controversa</i> BOREAU	Tomentose/Puberulent	Dense
<i>B. brevicaulis</i> JORDAN	Hirsute/Hispid	Sparse
<i>B. coronopifolia</i> L.	Hispid/Hirsute/Subglabrous	Dense to sparse
<i>B. intricata</i> JORDAN	Hispid/Hirsute	Dense to sparse
<i>B. apricorum</i> JORDAN	Hispid/Subglabrous	Sparse
<i>B. granitica</i> BOREAU ex PERARD	Hispid/Hirsute	Dense to sparse
<i>B. pinnatifida</i> JORDAN	Hispid/Hirsute	Sparse

Taxa	Indumentum type	Density of hairs
<i>B. polyclada</i> JORDAN	Hispid/Hirsute	Sparse
<i>B. lusitanica</i> JORDAN	Hispid	Dense to sparse
<i>B. mediterranea</i> JORDAN	Hispid/Hirsute	Dense to sparse
<i>B. nicaeensis</i> JORDAN	Hirsute/Hispid	Sparse
<i>B. intermedia</i> GOUAN	Hispid/Hirsute/Subglabrous	Sparse
<i>B. guillonii</i> JORDAN	Tomentose	Sparse
<i>B. valentina</i> (L.) HEYWOOD	Hispid/Hirsute/Subglabrous	Dense to sparse
Series <i>Lyratae</i> MALIN.		
<i>B. microcarpa</i> DC	Hirsute	Sparse
<i>B. baetica</i> BOISS. et REUTER	Hirsute	Sparse
<i>B. eriocarpa</i> DC	Puberulent	Sparse
<i>B. lyrata</i> L.	Puberulent	Sparse
<i>B. didyma</i> L.	Puberulent	Sparse
<i>B. radicata</i> COSSON	Hirsute	Sparse
Section <i>Iondraba</i> REICHENB.		
<i>B. auriculata</i> L.	Hispid/Hirsute	Sparse
<i>B. cichoriifolia</i> LOISEL.	Hispid/Tomentose	Dense to sparse

One of the most interesting observations in this study is the discovery that the indumentum and trichome types found in the adult plants of some species were already noticed in the juvenile leaves of 3-4 week-old seedlings (OLOWOKUDEJO 1986f). Notable examples of such species include *B. glacialis*, *B. scaposa*, *B. valentina* and *B. frutescens*. This character may indicate genetic differences which have found expression at the early stage in the life-cycle of these taxa and, according to DAVIS and HEYWOOD (1963), may be of vital selective value. Moreover, indumentum density may be affected by age; for example, *B. variegata*, *B. foliosa*, *B. megacarpaea*, *B. pinnatifida*, *B. polyclada*, *B. didyma* and *B. sclerocarpa* have densely hairy juvenile leaves which all become sparsely hairy or even subglabrous at maturity.

Among the functions usually ascribed to indumentum are: adaptation to factors of the physical environment, adaptation in relation to biotic interaction and functions related to internal physiological controls. Despite the different indumenta types observed in *Biscutella* no obvious correlation could be established between them and any of these factors. JOHNSON (1975) has suggested that the ecological and evolutionary significance of plant pubescence be queried from a multifaceted stance. Pubescence can no longer be regarded as a simple adaptation to arid environments. Recent studies suggest that leaf indumentum may play a role in reducing herbivory by serving as physical barrier to animal penetration or by emitting toxic or repellent compounds (LEVIN 1973, JOHNSON 1975). Trichomes are also known to produce natural chemicals useful to the plant. For example, glandular trichomes synthesize, metabolise or accumulate and secrete terpenoids, phenolics, mucoproteins and resins (RODRIGUEZ et al. 1984). In general no simple adaptive role can be hypothesized for the

various indumenta types which have almost certainly evolved in response to a whole host of ecological, physiological and developmental factors.

ACKNOWLEDGEMENT

I would like to thank the Head of Botany Department, University of Reading, for permission to use laboratory facilities and the Directors and Curators of the herbaria that have loaned or allowed me to consult their material.

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Received 21 September 1991, accepted 25 February 1992

Plate 22-24

Appendix 1

B. laevigata L. subsp. *laevigata*: Austria: Tirol, Virgin ad colles, vi.1865, GANDER s.n. (BM); Stiria superior, ca 2000m, vii.1909, FEST s.n. (BM); Tyrol, Alpes de Stubai, Vallée de Gschnitz, 1230m, 17.vi.1974, PODLECH 7423, 7424 (BC, MAF, RNG, SEV); Alpes de Tende, 18.v.1959, GAVELLE s.n. (BC, MA); France: Pyrénées Orientales, Le Vernet, 2.vii.1872, GADEGEAU 133 (BM); Hautes Alpes, Lautaret, viii.1866, VERLOT s.n. (BM); Haute Savoie, Mt. Lachat above Col de Voza, 10.vii.1929, HEARD s.n. (BM); Haute Garonne, 13.vii.1899, MURRAY s.n. (BM); Basses-Alpes, 25.vii.1895, VIDAL 3874 (BC); Dauphine, Vallée du Torrent de Roche Noir near the Col du Lautaret, c. 2500m, 13.viii.1922, LACAITA s.n. (BM). Germany: North side of Zugspitze, Habitual 1640m, 20.viii.1972, PLUMLEY s.n. (RNG). Switzerland: Valais, Zermatt, 20.vii.1881, LINTON s.n. (BM); Albula Pass, 2100m, viii.1890, GROVES 22 (BM); Silva-plana, Grisous, 15.vii.1886, MURRAY s.n. (BM); Rocky pasture, La Follaleric, Valais, 26.iv.1923, YOUNG s.n. (BM); Walliser Alpen, Zermatt, W-Hang, 1650m, vii.1968, POLATSCHKE 1313G (W). Spain: Burgos, Montes de la Hoz, vers 600m, 20.v.1920, ELIAS 4124 (BC, BM, MA); Catalogne, Berga a Cagastel, 18.vii.1911, SENEN s.n. (BC), Aragon, 2000m, vii.1862, PARQUET s.n. (BM); Sierra del Pinar, Grazelema, 1200m, 11.vii.1929, FONT QUER s.n. (BC). Italy: Alpes Maritimes, prov. di Cuneo, 1560m, 14.vi.1911, BICKNELL s.n. (BM); Pierrailles au Col de Tende, 11.vii.1861, BOURGEAU 27 (BM). Yugoslavia: Slovenia, Julijske Alpe, 1780m, 6.viii.1971, TPIN 79320 (GZU). Rumania: Transsilvania, 1600m, 27.v.1911, CLUI s.n. (K); Moldova, distr. Neamt; 1650, 26.v.1924, NYARADY s.n. (K).

B. laevigata L. subsp. *austriaca* (JORD.) MACH.-LAUR.: Austria: Tyrol, Zwieselstein, Oetzal, 1490m, 12.vi.1937, BRICKER s.n. (K); Styria, ALEXANDER s.n. (K); Steiermark, vii.1902, CONRATH s.n. (K); Maaberg bei Mödling, 19.iv.1859, FRITSCH 756 (GZU); Austria superior STEININGER 3665 (GZU); Steiermark, 900m, 8.vi.1880, PREISSMANN s.n. (W); Niederösterreich, Perbutz-ntiván, 3.v.1912, FILARSZKY & KÜMMERLE 197 (BC, GZU, K); Budapest, v.1920, SZÉPLIGETI s.n. (W). Yugoslavia: Triften am N.O. - Abhang der Crnoprst, 1750m, 3.viii.1889, DOLENZ 838 (GZU).

B. laevigata L. subsp. *kernerii* MACH.-LAUR.: Austria: Steiermark, Schlofsberge von Graz, 420m, 19.v.1883, PREISSMAN s.n. (W). Czechoslovakia: Mähren, Blansko Punkwatal, 8.vi.1930, RONNIGER 21368 (W); Mähren, Znaim, 13.v.1878, OBORNY s.n. (K). Hungary: Rochers de dolomite du mont Aldersberg, pres ofen, v.1873, RICHTER s.n. (K).

B. laevigata L. subsp. *gracilis* MACH.-LAUR.: Germany: Auf sändigen Ebenen und Anhöhen an Ufer Elbe jenseits Dresden, 1831, REICHENBACH 85 (K).

B. laevigata L. subsp. *tenuifolia* (BLUFF et FINGERH.) MACH.-LAUR.: Germany: Harz, Gypselsens des Kohnsteines bei Nordhausen und des Mülberges bei Niedersachswerfen, 4.vi.1879, EVERS s.n. (GZU).

B. laevigata L. subsp. *guestphalica* MACH.-LAUR.: Germany: Süntel, an den Kalkfelsen de Hohnstein bei Hess-Oldendorf, 26.vi.1879, EVERS 833 (GZU); Harz, Kohnstein bei Nordhausen, Gypselsens, v.1875, EVERS 4663 (GZU). Austria: Ostalpen, Österreichische Alpen, Hochschwabgruppe, 25.vi.1959, HACHTMAN s.n. (GZU).

B. laevigata L. subsp. *varia* (DUMORT.) ROUY et FOUC.: France: Glacis de Strasbourg, 17.vi.1897, PETRY s.n. (GZU); Terrain graveleux du Polygone a Strasbourg, BILLOT s.n. (BM). Germany: Oldenburg, Allemagne, SCHULTZ s.n. (BM). Auf Felsen und in Weinbergen auf beiden Rheinseiten bei St. Goar v.1869, HERPEL s.n. (BM).

B. laevigata L. subsp. *subaphylla* MACH.-LAUR.: France: Paturages et prairies seches, terrain graveleux, a Strasbourg, 4.vi.1838, LERAS 17 (K). Germany: Nahe, Tranfsen, 11.v.1863, BOCHKOLTZ s.n. (K). Switzerland: Engadin Valley, Canton Grisons, 1862, HOOKER s.n. (K).

B. laevigata L. subsp. *tirolensis* (MACH.-LAUR.) HEYWOOD: Austria: Tirol, Oberinntal, am Wege (Strasse) von Serfaus gegen die Kölnerhütte (Furglerspitze), 16.v.1974, MECENOVIC s.n. (GJO); Ungam, Tirol, Finsterstern bei Sterzing, 1894, WETTSTEIN s.n. (WU). Italy: Bolzano, Ostufer des Reschensees 2 km südlich Graun (Curon), 1500m, 1.vii.1972, PODLECH 23385 (G); Trento, racailles au dessus du Passo di Rolle, 2200m, 27.viii.1968, CHARPIN s.n. (G).

B. laevigata L. subsp. *angustifolia* (MACH.-LAUR.) HEYWOOD: Austria: Fend in Tyrol, 21.vi.1860, NEURANTNER s.n. (GZU); Niederösterreich, Glaneck, 21.v.1899, FRITSCH s.n. (GZU); Tirol, 22.vii.1911, DOLENZ s.n. (GZU); Tirol, Matreier Gruke, 1900m, 4.viii.1886, HORA s.n. (GZU); Stiria superior ca 2000m, vii.1909, FEST s.n. (BC); Salzburg, Bad Fusch, 24.vi.1896, FRITSCH s.n. (GZU). Italy: Trentino-Tiroler Etschland, 1800m, 8.vii.1975, WOSCHL & PITTONI s.n. (GZU). Yugoslavia: Vigaun, v.1882, DOLENZ s.n. (GZU); Hercegovinae, in graminosis alpinis montani, 1400m, vii.1887, VANDAS s.n. (K). Switzerland: Cal de Chéville (Valais) pastures, 19.viii.1879, Herb, LACAITA (BM).

B. laevigata L. subsp. *illyrica* MACH.-LAUR.: Yugoslavia: Kroatien, Fiume, Grobnik Feld, 14.v.1882, UNTCH s.n. (GZU); Slovenia, near Orozkovi Koza, vii.1938, MARTINDALE 20A(K). Hungary: Budapest, Leopoldifeld, 19.v.1882, SZÉPLIGETI s.n. (K). Austria: Austria Superior, STEININGER s.n. (BM).

B. laevigata L. subsp. *lucida* (DC) MACH.-LAUR.: Austria: Tirol, Kalkgeröll am Haller Salzberg, 12.vii.1876, EVERS 2397 (BC); Kärnten, Karawanken, 550m, 27.v.1964, HÖPFLINGER s.n. (K); Dachstein, Austriahütte, ca 1700m, 1947, HESKE s.n. (GZU); Kärnten, Karawanken, 30.vi.1932, RONNIGER 5087 (W); Styria, Haindlkar, Guustaler Alps, on limestone scree, 1400m, 23.viii.1932, WYATT 186 (K). Italy: Venetia, in rupestribus elatis mt. Malera, prov. Veronae, 1600-1800m, 21.vii.1884, RIGO s.n. (K). Yugoslavia: Within 6 miles of Bled (Beldes) which includes the lower slopes of Mt. Triglav, 1000-4000ft., 1923, LEATHES s.n. (BM); Switzerland: Saint Gothard, 1893, THOMAS 970 (SEV).

B. scaposa SENNEN ex MACH.-LAUR.: Spain: Madrid, between El Escorial and Valle de les Caides, 1100m, 5.vii.1978, OLOWOKUDEJO 94 (BM); Sierra de Malagon, Las Herreras, 1300m, 5.vii.1978, OLOWOKUDEJO 99 (RNG); Soria, Lubia territory, v.1927, WILMOTT s.n. (BM); Lagos de Ruidera, 2.v.1975, HEYWOOD et al. s.n. (RNG); Cerdagne, Caldegas, 1200m, viii-ix.1917, SENNEN 2967 (BC, BM, MA). France: Pyrénées Orientales, Vernet, 1000m, 30.vi.1934, WYATT 4 (K); Pyrénées Orientales, dry slopes, 18.vi.1925, ELLMAN & SANDWICH 231 (K).

B. flexuosa JORDAN: France: Hautes-Pyrénées, L'hieris, 1838, JORDAN s.n. (LY); Haute-Garonne, Bagnères-de-Bigorre, 2.vi.1842, PHILIP s.n. (K); Basses-Pyrénées, 30.iv.1928, LACAITA 32144, 32145 (BM); Pyrénées-Orientales, Mont Louis, 1500m, 17.vii.1934, WYATT 181 (K). Spain: Catalaunia, Monerat, vi.1871, COSTA s.n. (BM); Sierra de Cadi (Pyr. Catal.), vii.1906, PAU s.n. (MA); Montserat, 16.vii.1917, FONT QUER s.n. (BC); Cerdagne, Vallée de Llo, rochers schisteux, 2200m, 7.viii.1916, SENNEN 2538 (BM, MA); Lerida, Fuente de les Bagasses, road between Ager and remps, 410m, 16.v.1971, HEYWOOD 25 (RNG); Huesca, Pyrénées, between Benasque and Carler, 20.vii.1978, HARROLD & MCBETH 442 (RNG).

B. variegata BOISS. et REUTER: Spain: Almeria, Sierra Nevada, Beires de Minas, 3.vi.1924, LOFTHOUSE s.n. (BM); Albacete, Sierra de Alcaraz en la Molata, 24.v.1928, CUATRECASAS 246 (BM, RNG, WU); Jaen, Sierra de Jaén, carchelejo, 20.v.1941, GUINEA s.n. (RNG); Sierra de Segura, 8 km S of Orcera, Yelmo, 1700m, 8.vii.1979, CANNON et al. 953 (RNG); Sierra del Pozo, 30 km N of Pozo Alcon, 1800m, 20.vi.1978, OLOWOKUDEJO 78 (B, BM, M, SEV, WU); Granada, Sierra Nevada, vii.1809, REUTER s.n. (G); Sierra Nevada, Barranco de Benaleazar, vii.1853, ALIOTH s.n. (G); Malaga, road to El Torcal-Antequera, 1000m, 28.vi.1978, OLOWOKUDEJO 90 (BM, M, RNG, WU).

B. megacarpa BOISS. et REUTER: Spain: In montibus Ronda, v.1837, BOISSIER s.n. (K); Cádiz, Bois de pins pres de Chiclana, 30.iv.1849, BOURGEAU s.n. (G); Chiclana, 27.v.1925, FONT QUER s.n. (BC); Albacete, Sierra de Alcaraz, Barranco de la Molata, in dumetis, 24.v.1928, LACAITA 32132 32133 (BM); Ronda, 660m, 8.v.1924, ELLMAN & HUBBARD 298 (K); Sierra Prieta, 700m, 19.v.1978, SMYTHIES 1315 (RNG); El-Burgo to Ronda N344 road, km 22, 1200m, 28.vi.1978, OLOWOKUDEJO (BM, RNG, WU); Granada, Sierra de Cazulas, 5.vi.1969, GODAY & CARBONELL s.n. (MAF). Morocco: Noyen Atlas, Bekrit, 2000m, 2.vi.1924, JOHANDIEZ 515 (G); Gomara, in rupestribus calc., 2050m, 22.vii.1930 FONT QUER s.n. (BC).

B. foliosa MACH.-LAUR.: Malaga: Hispania Baetica de Ronda per viam ad El Burgo, 900-1100m, 18.vi.1972, BERNARDI 13714, 13615 (G); Serrania de Ronda, between Ronda & Gaucin, near Algotocin, 28.vi.1978, OLOWOKUDEJO 93 (BM, RNG, WU).

B. gredensis GUINEA: Spain: Avila, Sierra de Gredos, 2500m, 2.viii.1924, GROS s.n. (BC); Canchales y roquedo alto de Sierra de Bejar En el Trampal c.d. El Calvitero, 2300m, 25.vii.1967, MARTÍNEZ & SEVILLANO s.n. (MAF); Canchales de Penalara, 2000m, 11.viii.1974, VALDÉS s.n. (MAF); Sierra de Gredos, rocky sides of Circo, NE of the Laguna, 2.vii.1927, WILMOTT s.n. (BM); Sierra de Gredos, Penascos de las faldas del Morécon, 15.viii.1974, ANTONION et al. s.n. (MAF).

B. neustriaca BONNET: France: Eure, Les Andelys, rochers Saint-Jacques, sur la craie, 23.vi.1878, BONNET et al. s.n. (G); Eure, aux Andelys, 14.v.1882, BONNET 189 (G); Andelys, 7.vi.1890, TOUSSAINT s.n.; Les Andelys, rochers Saint-Jacques, 10.vii.1927, SENAY 2023 (BC); Les Andelys, sur la route de Tosny, 19.vii.1927, CHEVALIER 1958 (BC).

B. frutescens COSSON: Spain: Malaga, Sierra de Ronda, 26.vi.1849, BOURGEAU s.n. (BM, K); Serrania de Ronda, 1849, BOISSIER & REUTER s.n. (BM, K); Sierra de Alfarnate, 26.vi.1919, GROS 259 (BC); Serrania de Ronda, 400-1000m, 9.vi.1895, PORTA & RIGO 45 (HBG); Grazalema, vertical cliffs of Penon Grande, 21.vii.1948, HEYWOOD & DAVIS 796 (BM); Granada, Sierra de Loja, Cruz de Periquete, 23.vi.1978, OLOWOKUDEJO 187 (B, BM, M, RNG, WU); Sierra de Loja, Santa Cruz de Albama, 1250m, 23.vi.1978, OLOWOKUDEJO 189 (B, M, RNG, SEV WU). Algeria: Oran, 28.v.1856, BOURGEAU s.n. (BM). Morocco: Moyen Atlas, Ras el Ma, 1650m, 27.vi.1923, JOHANDIEZ 624 (BM); Chorfas d'Infrane, 1200m, 26.v.1924, JOHANDIEZ 447 (BC, BM).

B. vinctina (SAMP.) ROTHM. ex GUINEA: Portugal: Algarve, Cabo de St. Vincente, 25.v.1938, ROTHMALER s.n. (B, G); Sagres a caminho da Fortaleza, 18.iv.1945, SILVA et al. 19522 (G); Cabo de St. Vincente, 4.v.1951, FERNANDES et al. 3675 (BM); Vila de Bispo pr. Rapoazeira, 110m, 31.iii.1962, RAINHA 5282 (BC); Punta de Sagres, 20.iv.1968, GALIANO et al. 5737 (SEV); Carpentiera, dunes above cliff, 100m, 30.iii.1971, DAVIS 50871 (RNG).

B. sempervirens L.: Spain: Valencia, In montibus Bernia, 21.vi.1923, GROS s.n. (B, BC); Sierra de Benicadell, 29.vi.1946, BORJA s.n. (BC); Alicante, Dénia, rochers du Mongo, 1.vi.1883, ROUY s.n. (G); Dénia, 12.v.1928, ELLMAN & SANDWICH 1134 (K); Almeria, Barranco de los Castanes c. Vacares, 3.vi.1929, GROS s.n. (BC); Sierra de Gata, 15.iv.1968, MERXMÜLLER & LIPPERT 23438 (G); Sierra de Cartana, les rochers, 9.v.1888, REVERCHON s.n. (K); Bois de pins pres de Chiclanam, 30.iv.1849, BOURGEAU 27(K); Granada, Sierra de Lujar, 1300m, 16.iv.1973, LEADLAY et al. 221 (RNG); Sierra de la Yedra, 1200m, 14.vi.1978, OLOWOKUDEJO 120 (B, BC, BM, M, RNG, SEV, WU); Granada-Guadix road, Beas de Granada, 1300m, 14.vi.1978, OLOWOKUDEJO 129 (B, BC, BM, HUIJ, KRA, M, RNG, SEV, WU); Sierra Elvira, 21.vi.1978, OLOWOKUDEJO 87 (RNG); Jaen, Sierra de Almaden, 1400m, 10.v.1978, SMYTHIES 1311 (RNG); Valencia, Gardia, Castillo de S. Juan, 3.iv.1884, LACAITA 5448 5449 (BM); Sierra de Chinchilla, 31.v.1850, BOURGEAU s.n. (G). Gibraltar: in fiss. rup. calc. arides, 17.iv.1926, LINDBERG 612 (B); Ganoín Hacho c. 1000m, 29.iv.1929, HAYNES 17 (BM); Gibraltar, 24.iii.1969, HEYWOOD et al. 24 (RNG); Gibraltar, 15.v.1887, REVERCHON 4946 (G).

B. glacialis (BOISS. et REUTER) JORDAN: Spain: Granada, Sierra Nevada, viii.1837, BOISSIER s.n. (GJO, W); Sierra Nevada, Picacho de Veleta, 27.vi.1851, BALL s.n.; Macizo de la Sagra, 14.vi.1960, ELLALIANO 963 (SEV); Sierra Cazorla, East of Uheda, 2.iv.1970, FRASER-JENKINS 125 (RNG); Sierra Nevada, 3400m, 3.vii.1974, VALDÉS & LOPEZ 92426 (MAF); Sierra Nevada, near the Veleta peak, 3200m, 17.vi.1978, OLOWOKUDEJO 67 (BM, M, RNG, WU); Sierra Nevada near the Mulhacén peak, 3480m, 17.vi.1978, OLOWOKUDEJO 200 (M, RNG, WU); La Sagra, Barranco rio Lanjaron, 2200m, 20.vi.1978, OLOWOKUDEJO 69 (BM, M, WU); Sierra Harana, Gueva del Agua, 2000m, 12.vi.1976, SOCORRO 208 (RNG); Baza, Sierra de Baza, Cerro de Santa Barbara, 2200m, 4.vii.1979, CANNON et al. 776 (RNG); Jaen, Sierra del Pozo, East of Cazorla, 2100m, 19.vi.1978, OLOWOKUDEJO 177 (RNG); Siena Harana, Cortijo del Sotillo, 2000m, vi.1976, SOCORRO 209 (RNG).

B. brevifolia ROUY et FOUC.: France: Hautes Pyrénées, chateau de Ste Maria, v.1872, BORDÉRE s.n. (K); Luz, vi.1872, BORDÉRE s.n. (GJO); Pyrénées, val d'Aspé, vi.1900, BORDÉRE 19097 (BM); Gavarnie vallée d'Ossone, 1800m, 30.vii.1907, COSTE s.n. (BC).

B. cuneata (FONT QUER) FONT QUER ex MACH.-LAUR.: Spain: Tarragona, Punta dels Tres Pins, Ports de Tortosa, 1300m, 30.vi.1917, FONT QUER s.n. (BC, MA); Catalaunia, 1300m, 18.v.1935, FONT QUER & ROTHMALER 219 (B, BC, BCC, BCF, BM, K, MA, MAF); Cardo, 900m, 27.vi.1918, FONT QUER s.n. (BC); Fussa de Caro, Tortosa, 26.vii.1917, FONT QUER s.n. (BC); Sierra de Prades, 700m, 29.vi.1918, FONT QUER s.n. (BC).

B. rotgesii FOUC.: Corse: Rochers schisteux au lieu dit Rotajo, 20.iv.1900, ROTGES s.n. (BC, G); Rochers a l'entré du Dafila du l'Insecca (entré Chisoni et ghisonacinal localité unique), 20.iv.1927, CREVALS s.n. (BC); Env. de Ghisoni, schistes, 9.v.1907, BRIQUET s.n. (G).

B. lamottii JORDAN: France: Randanne, vii.1849, LAMOTTE s.n. (LY); Auvergne, Puy-de-Dome, La Roche-Noire, v.1908, HERIBAUD s.n. (BC); Gravenoire, Puy-de-Dome, 21.vii.1879, HERIBAUD s.n. (G); Puy de Gravenoire, Royat les Bains, 17.viii.1927, BORTT-DAVY s.n. (K); Auvergne, Puy-de-Dome, Env. de Clermont-Ferrand, vi.1934, D'ALLEIZETTE s.n. (BC, HBG).

B. sclerocarpa REVEL: France: Aveyron, Firmy. Puy de Volf 30.v.1879, SALTAL s.n. (G); Puy de Volf 450m, 5.vii.1899, COSTE 1057 (G); Firmy Puy de Volf, 1.vii.1916, CUEDI s.n. (G, MA).

B. arvensis JORDAN: France: Débris de rochers volcaniques en haut de la vallée d'Enfer au Mont-Dore, 13.vii.1885, SCHULTZ 2117 (BM, G, K); Puy-de-Dome, 1700m, 7.vii.1959, CHARPIN 132626 (G); Mont Dore, Le Sancy, viii.1900, PITARD s.n. (G); Cantal, Le Plomb de Cantal, Ravin des Gardes, 25.vii.1915, COST & DESPATY 1557 (BC, G).

B. divionensis JORDAN: France: Cote d'Or, 14.v.1873, BONNET s.n. (K); Rochers d'Gevrey v.1878, GILLOT s.n. (BM); Cote d'Or, Gevrey 14.vi.1882, OZANON s.n. (G); Cote d'Or, 400m, 15.v.1925, DESPLANTES s.n. (G).

B. controversa BOREAU: France: Allier, rochers de Neuvielle, 24.iv.1876, SCHMIDELY s.n. (G); Chinon, 29.vi.1884, TOURLET s.n. (G); Arthez (Tarn) sur le micasciste, 2.v.1896, SUDRE s.n. (GJO); Cher Dun-sur-Auron, 9.vi.1900, GRAND 4684 (BC, G); Puy-de-Dome, Thiers, 6.vi.1895, ARBOST 3736 (BC, G); Thiers. v.1911. CHASSAGNE s.n. (BC); Gorges de la Sioule, le long de la route N715, entre Chouviigny et Pont-de-Ménat, 350m, 2.v.1974, DE RETZ 68952 (BC, G, RNG, SEV); Haute Garonne, Pic de Gard, vii.1872, BORDÉRE s.n. (GJO).

B. brevicaulis JORDAN: France: Basses-Alpes, 1950m, 10.viii.1972, PODLECH 24484 (G); Alpes du Dauphine, 29.v.1871, BOREL s.n. (K); Mont-du-Lure, 26.v.1889, BRUYAS s.n. (BM); Vaucluse, sommet de ventous,

19.viii.1877, REVERCHON s.n. (BM); Hautes Alpes, Mt. Aurouse, 21.vi.1863, BOREL s.n. (K); Gap mont aurouse, 16.viii.1872, REVERCHON s.n. (LY).

B. coronopifolia L.: France: Allier Montluçon, 28.viii.1868, PERARD s.n. (K); Basses-Alpes, Monstiers, 20.iv.1885, WILMOTT s.n. (K); Bouches-de-Rhône, Marseille, iv.1843, MUTE s.n. (MA); Tarn, Arthez, 30.iv.1892, SUDRE s.n. (MA); Ardèche, Cévennes, summit of Mt. Mézenc, 1750m, 2.ix.1948, SANDWITH 3317 (K); Vaucluse, Mont Ventoux, 1900m, 15.vi.1952, SOUSTER 1307 (K); Alpes Maritimes, 900m, 20.v.1972, PODLECH 22821 (G). Italy: Pedemontium - Prov. di Torino, 1450m, 15.viii.1914, MATTIROLLO 2441 (G). Spain: Catalaunia, 800-1000m, 7.iv.1885, PORTA & RIGO s.n. (G, K); Montserrat, 25.iv.1882, LACAITA 5445 (BM); Tarragona, Serra de Balaguer, 1.vi.1918, SENNEN s.n. (BC, BM); Teruel, sierra de Javalambre, 1600m, 13.vii.1979, CANNON et al. 1155 (RNG).

B. intricata JORDAN: France: Balmes de la Loire, 357m, v.1868, BILLOT 3811 (BM, G, LY); Loire, Roanne, 20.v.1919, THIEBAUT 2960 (G); Ardèche, Tournon, 29.iii.1902, CHATENIER s.n. (BC, MA); Ardèche, Tournon, naturalise a Villeurbanne pres Lyon, 25.iv.1866, JORDAN s.n. (LY).

B. apricorum JORDAN: France, Var, Draguignan, v.1910, GIROD s.n. (G); Rebouillon pres Draguignan, v.1911, GIROD s.n. (G); Collobrières, 7.iv.1856, JORDAN s.n. (LY); Collobrières, v-vi.1858, JORDAN s.n. (LY).

B. granitica BOREAU ex PERARD: France: Allier, Neris, 22.v.1869, BOREAU s.n. (K); Allier, Coteaux granitiques de Nérès-les-Bains, 24.v.1865, BILLOT 3516 (BM, G); Montluçon, vallée de L'Amoron, au Roc-du-Saint, 10.vi.1882, PERARD 190 (G). Spain: Catalogne, Vallirana, fourrés, 2.vii.1917, SENNEN s.n. (BM), Cerdagne, Estavar, 1200m, 12.vii.1923, SENNEN s.n. (MA); Barcelone, 400m, 4.vi.1929, SENNEN 7232 (BM, MA); Barcelona, La Panadella, 800m, 16.v.1971, HEYWOOD 2 (RNG).

B. pinnatifida JORDAN: France: Aude, du Mas Cabardes, 20.v-vi.1862, JORDAN s.n. (LY); Plantes du versant meridional de la Montagne-noire, Cabardes, vi.1860, DÉSÉGLISE 312 (BM).

B. polyclada JORDAN: France: Drome, Nyons, 1864, JORDAN 5236 (LY); Gard, Coteaux calcaires au Vigan, 22.iv.1867, TUEZKIEWICZ 3812 (BM, MA); Drome, Bourg-de-Peage, 20.iv.1897, CHATENIER s.n. (G); Pateurs au de Crest, rocailles calc., 250-400m, 16.v.1925, BRIQUET 17 (G).

B. lusitanica JORDAN: Portugal: Estremadura, 600m, 25.iv.1939, ROTHMALER & SILVA 15116 (B); Sierra de Arrabida, Mata do Vidal, 350m, 14.v.1952, LIBA & FOUTES 5079 (BCF); Sierra de Arrabida, Mata do Solitario, 17.iv.1968, GALLIANA et al. 5475 (SEW). Spain: Burgos, Arranda de Duero, v.1842, LOPEZ s.n. (MA).

B. mediterranea JORDAN: France: Montpellier, 1835, MAIRE s.n. (G); Environs de Toulon, 26.iv.1862, MERCIER s.n. (G); Hérault, Castelneude-Guers, 24.vi.1908, DEHNAS s.n. (GJO); Colonibiere pres de Gracia, v.1847, BOURGEOU 426 (K); Catalogne, Vallirana, fourrés, 2.vii.1917, SENNEN s.n. (BC); Turi de Montcada, 10.vi.1946, BOLÓS & BOLÓS 109458 (BC); Valencia, East of Jativa, 550m, 10.vi.1978, OLOWOKUDEJO 14 (B, BM, M, RNG, WU); Alicante, Sierra de Carrascal, 450m, 10.vi.1978, OLOWOKUDEJO 15 (B, BM, M, RNG, WU).

B. nicaeensis JORDAN: France: Alpes Maritimes, 25.iv.1861, BOURGEOU s.n. (G); Gourdon, 760m, 20.v.1972, PODLECH 22859(G); Alpes Maritimes, 1841, RISSO s.n. (LY). Italy: Liguria occid. prope Bordighera, 150m, 2.v.1911, BRICKNELL & POLLINI 1682 (BM).

B. intermedia GOUAN: Spain: Sierra de Guadarrama, vii.1858, BOISSIER & REUTER s.n. (G); Monte Guadarrama, 23.vii.1879, LERESCHE s.n. (BC); South of La Granja, on slopes of Pico de Penelara, 1850-2100m, 6.vi.1924, ELLMAN & HUBBARD 1087 (K); Soria, Sierra de Toranzo, 9.vi.1934, VISIOSO s.n. (MAF); Guadalajara, 14.vi.1944, GODAY & BELLOT 71678 (MAF), Girona, Pyrénées, 2.vi.1960, SANDWITH 5866 (K); Pyrénées a Nuria,

paturages, 2300 a 2500m, 2.viii.1914, SENNEN 1916 (BC, BM, K, MA). France: Haute-Pyrénées, Port de Gavarnic, vii.1878, BORDERE 110 (K); Port de Gavarnic, vii.1880, BORDERE s.n. (K); Pyrénées Orient., 2400m, 10.vii.1934, WYATT 150 (K).

B. guillonii JORDAN: France: Deux-Sevres, Paizay le chapt., 26.v.1851, GUILLON s.n.; Charente-Inférieure, Aulnay, v.1886, GIRAUDIAS s.n. (BC, GJO); Terrains calcaires a Aulnay v.1887, GIRAUDIAS s.n. (G, MA); Saint-Andre-de-Cubzac, vi.1876, JARRIS 1965 (K); Dordogne, rochers d'Argentine, pres la Roche-Beaucourt, 20.vi.1902, HOSCHEDE 77 (G); Vendée, Benet, 7.v.1926, CHARRIER 303 (BM).

B. valentina (L.) HEYWOOD: Spain: Alicante. Sierra Aitana, prés d'Alcoy 18.vi.1862, LERESCHE s.n. (K); Almeria, Sierra Cabrera, 200-300m, v.1890, PORTA & RIGO 280(BM); Valez-Rubro, 5-6.v.1926, ELLMAN & SANDWITH 529 (K); Requena, 2 km S. of Villa de Ves, 21.vi.1979, CANNON et al. 116 (RNG); Sierra de Segura, 1050m, 27.vi.1955, HEYWOOD 2962 (MA, RNG); Sierra de Espuna, 1000m, 20.v.1929, JERÓNIMO 7102 (BC, MA); Sierra de Espuna, N.W. of Totana, 1200m, 11.vi.1978, OLOWOKUDEJO 16 (B, BC, BM, M, RNG, SEV, WU); Ciudad Real, El Cascajal, 24.v.1933, ALBO s.n. (MA); Teruel, Alcala de la Selva, 1600m, 2.vii.1946, FONT QUER & SIERRA 428 (BC, MA, MAF); Serrania de Cuenca, 9.vi.1976, PRENTICE 53 (RNG); Sierra de Cazorla, Cuerda de Los Moras, 1300m, 21.vii.1951, HEYWOOD 1456 (BM); Pozo Alcon, Embalse de la Bloera, 1300m, 19.vi.1978, OLOWOKUDEJO 70 (B, BC, BM, M, RNG, SEV, WU); Sierra Cazorla, near Nava de San Pedro, 1400m, 19.vi.1978, OLOWOKUDEJO 73 (B, BC, BM, HUI, KRA, M, RNG, SEV); Pedro, 1400m, 19.vi.1978, OLOWOKUDEJO 73 (B, BC, BM, HUI, KRA, M, RNG, SEV WU); Castille, Valverde de Mirande de Ebro, 15.v.1907, ELIAS 17773 (BM); Montagnes de Valverde de Miranda, 13.vi.1906, SENNEN & ELIAS 29 (BC, GJO, MA); Valencia, N.W. of Requena, 700m, 9.vi.1978, OLOWOKUDEJO 11 (B, BC, BM, HUI, KRA, M, RNG, SEV, WU); Albacete, 800-900m, 3.vi.1891, PORTA & RIGO 166 (K); Cuenca, Madrid-Valencia N111 road, near Alarcon, 750m, 8.vi.1978, OLOWOKUDEJO 6 (B, BM, M, RNG, WU).

B. microcarpa DC.: Spain: Cádiz, Chiclana, 3.iv.1873, FRITZE 10 (BC); Baetica, in arenosis prope San Roque, 3.v.1922, GROS 217 (BC, BCF); Puerto Real, Pinar de Villanueva, 1.iv.1925, GROS s.n. (BC); Barranco de Ojeu (Sierra de Algeciras), 7.iv.1950, BORJA et al. 4603 (BCF); El Colorado, near Chiclana de la Frontera, 13.iv.1972, HEYWOOD et al. 138 (RNG).

B. baetica BOISS. et REUTER: Spain: Malaga, Estepona, 7.iv.1943, GUINEA 9602 (RNG); N.W. of Marbella, Sierra Blanca, 300, 18.iv.1973, LEADLAY et al. 243 (RNG); Punta Umbria, 28.iii.1956, GODAY s.n. (MAF); Sevilla, Merida road, 24.iv.1973, HEYWOOD et al. 121 (RNG); Baetica, pr. Ubrique, 500m, 18.vi.1925, FONT QUER & GROS 218 (BCF); El Ronquillo, 150-160m, 16.iii.1968, SILVESTRE & VALDES 1027 (BC). Morocco: El Ksar-el-Quebir, 27.iii.1930, FONT QUER s.n. (BC). Tunisia: Souk el Arba, N. Jen douba to Ain Draham, 350m, 11.v.1975, DAVIS & LAMOND 57684 (BM).

B. eriocarpa DC.: Corsica: Saint-Florent, 13.iv.1971, LAMBINON 5947 (MAF, SEV).

B. lyrata L.: Sicilia: Syracuse, 2.iv.1898, RIGO 1386 (BC); Palermo, 300m, 30.iii.1953, HOPFLINGER s.n. (W). Tunisia: El Kef, 12.iv.1938, SIMPSON 38215 (BM). Algeria: Al, Dj. Chrea above Blida, 850m, 4.v.1971, DAVIS 57925 (RNG); West of Tiaret, 4.v.1937, ALSTON & SIMPSON 37780 (BM). Morocco: Mazuza, 16.v.1932, SENNEN & MAURICIO 7775 (BC, BM, BCF); Cap Beddouza, 25.iii.1972, BRANWELL et al. 150 (RNG); El Hoccina, 16.iv.1971, DAVIS 51325 (RNG); Asni to Ichoukak, 31.v.1936, BALLS 2502 (BM); Moyen Atlas, Laza, 1200m, 31.v.1929, JOHANDIEZ 333 (BM).

B. didyma L.: Spain: Malaga, Ronda, 19.v.1890, REVERCHON s.n. (BC); Laguna de Janda, 8.iv.1950, RIVAS et al. 52 (BCF). Morocco: Casablanca, ii.1934, JALLU 7116 (BC, BCF BM); Rabat plain, 100m, 26.xii.1966, HOLLIDAY 7 (BM). Algeria: Djebel Adar Amellal, 24.iv.1937, ALSTON & SIMPSON 37482 (BM); Constantine 3 km

W. Bou-Nouara, 650m, 25.iv.1976, SUTTON & SUTTON 681 (RNG). Tunisia: Gafsa, iv.1909, PITARD s.n. (BM); Dejebel-Djeloud, in arvis, iv.1907, PITARD 27 (BM). Libya: Jefren, 23.ii.1954, GUICHARD 574 (BM); Leptis Magna ruins, 11.iii.1952, GUICHARD 148 (BM). Egypt: Alexandria, 25.v.1907, AUGUSTO s.n. (BC). Greece: Argolis, Tolon, near Nafplion, iii.1978, BOWEN 991 (RNG); Rhodes, 5.iv.1969, MILLWARD 97 (BM). Cyprus: Nicosia, iii.1955, BAKER 152 (BM); Herogarkar Gorge, iii.1930, NORMAN 424 (BM). Turkey: Mersin, 25.iv.1972, SPITZENBERGER 47 (W); Mugla, Marmaris-Emecik, 350m, 25.iii.1956, DAVIS & POLUNIN 25367 (BM). Iraq: Kurdistan, 1.v.1951, THESIGER 659 (BM).

B. radicata COSSON: Algeria: Djebel Magris, 1600m, vi.1893, REVERCHON 275 (BC, BM, MA); Col de Telmet, Batna, 21.iv.1937, SIMPSON 37382 (BM); Entre l'Alma et la Reghaia, 23.iv.1930, MAIRE 2449 (BC, MA); East of Tetuan, Monte Cajo, 680m, iv.1931, GOURLAY et al. 717 (BM). Tunisia: Gafsa, iv.1908, PITARD s.n. (BC).

B. auriculata L.: Spain: Almeria, Finana, champs, 30.iii.1933, JERÓNIMO 9003 (BC); Albacete, Sierra de Alcaraz, 25.vi.1979, CANNON et al. 383 (RNG); Cuenca - Valencia road junction, 8.vi.1978, OLOWOKUDEJO 5 (B, BC, BM, M, RNG, SEV, WU); Ciudad Real, Cabeza de Buey 600m, 29.vi.1974, LEADLAY & PETTY 152 (RNG); Murcia, Sierra de Espuna, 800m, 21.iv.1930, JERÓNIMO 7313 (BC, BCF); Sevilla, El Coronil Olive grove, 31.iii.1969, HEYWOOD et al. 396 (RNG). Balcares: Pont d'Inca, route de Sineu, 20.ii.1919, BIANOR 3692 (BC, BCF). Portugal: Algarve, Vila de Bispo nas Searas, 110m, 27.iii.1962, RAINHA 5251 (BC). Morocco: Beni-Snassen, Berkane, 14.iv.1934, SENNET & MAURICIO 9242 (BC, BCF, BM). Algeria: Oran, Entre Qued-Imbert, 2.iv.1915, FAURE s.n. (BC); 10km N. of Batna, Kasrou, 1750m, 25.iv.1976, SUTTON & SUTTON 653 (RNG); Champs a Batna, 16.v.1866, BILLOT 3517 (BM). Tunisia: N. of Sbeitla, 16 km from Siba, 730m, 4.v.1975, DAVIS & LAMOND 57186 (RNG). Canary Islands: Teneriffe, 1846, BOURGEAR 374 (BM); Rio Palmas, 28.v.1895, LOWE s.n. (BM).

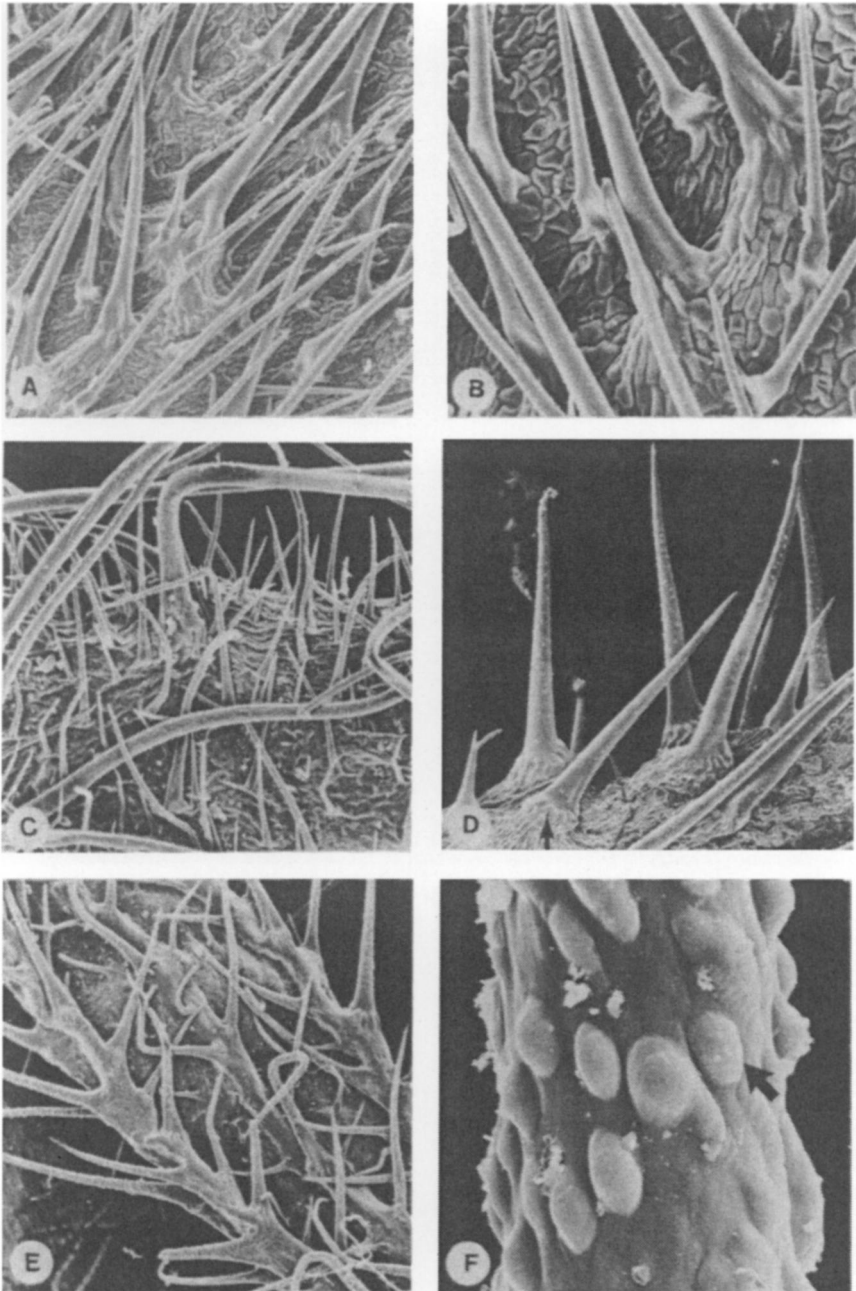
B. cichoriifolia LOISEL.: France: Haute-Alpes, Col de Theus, 1100m, 10.vi.1901, FAURE 4683 (BC, BM); Haute-Garonne, Bogrères de Luchon, 21.vi.1973, LOUSLEY s.n. (RNG); Bormes, Ravin de Pramoussquier 4.v.1913, CORAZE & REYNIER 755 (RC); Luchon, montagne de Cazarilh, 850m, 24.vi.1889, FAGES s.n. (BM); Alpes Maritimes, Environs de Fontan, 4.viii.1875, LERESCHE s.n. (BC); Fontan, Vallée de Caïros, 7.vii.1886, REVERCHON s.n. (BM); Rochers de Irandaïse, pres Culoz, 300-400m, 15.vii.1927, BRIQUET 5170 (BM); Haut-Bugey, 240-300m, 7.vi.1920, BRIQUET 518 (BM). Spain: La Molina, Campes, vi.1958, CASAS s.n. (BCF); Arragon, La Maladetta, 2500m, 1862, PARQUET s.n. (BM); Cerdagne, Alp au val de la Molina, 1400m, 30.vii.1920, SENNEN 3894 (BC, BM). Yugoslavia: Dalmatia, Montes prope Clisor v.1879, PICHLER s.n. (BC).

Appendix 2

Sources of Seed Samples

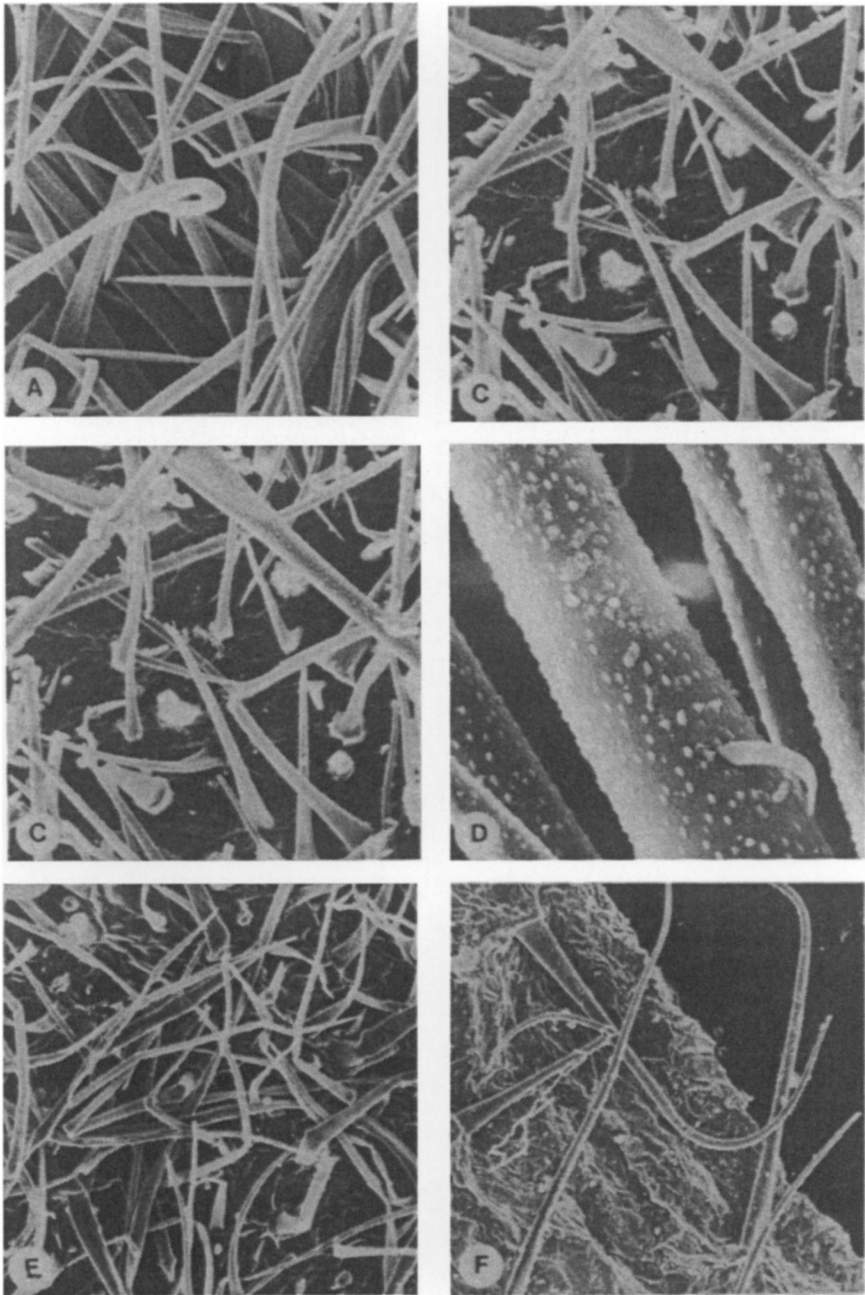
Taxa	Source & Ref. No.	Locality (Country: Province/County/Town)
<i>B. laevigata</i>		
subsp. <i>laevigata</i>	BG 780348	Switzerland: Valais, 1550m
	BG 780349	Switzerland: Valais, Lac de Salanfe
	BG 780416	Austria: Kärnten, Hohe Tauern
	BG 780423	Switzerland: Saint Gall, Walensee
	BG 187	France: Dépt. Nord, Valenciennes
subsp. <i>lucida</i>	BG 780420	Switzerland: Alpes Valaisannes
subsp. <i>kernerii</i>	BG 780544	Czechoslovakia: locality unknown
subsp. <i>gracilis</i>	BG 780311	Switzerland: Unterwald, Tribsee
subsp. <i>guestphalica</i>	BG 780419	Germany: Frankfurt

Taxa	Source & Ref. No.	Locality (Country: Province/County/Town)
<i>B. scaposa</i>	Olowokudejo 94	Spain: Madrid, El Escorial, Valle de los Caidos
	Olowokudejo 96	Spain: Madrid, El Escorial, Valle de los Caidos
	Olowokudejo 98	Spain: Madrid, Peguerimos
	Olowokudejo 99	Spain: Madrid, Sierra de Malagón
	Olowokudejo 100	Spain: Madrid, North of Las Herreras
<i>B. variegata</i>	Olowokudejo 60	Spain: Granada, Barranco de San Juan
	Olowokudejo 62	Spain: Granada, Sierra Nevada/Guejar Sierra
	Olowokudejo 88	Spain: Granada, Sierra Loja
	Olowokudejo 90	Spain: Malaga, Antequerra-El Torcal
<i>B. megacarpaea</i>	Olowokudejo 91	Spain: Malaga, El Burgo-Ronda
	Olowokudejo 92	Spain: Malaga, El Burgo-Ronda
<i>B. foliosa</i>	Olowokudejo 93	Spain: Malaga, Serrania de Ronda
<i>B. gredensis</i>	Gómez-Campo 2295	Spain: Avila, Circo de Gredos
<i>B. frutescens</i>	Olowokudejo 187	Spain: Granada, Sierra de Loja, Cruz de Periqueta
	Olowokudejo 188	Spain: Granada, Sierra de Loja, Santa Cruz de Alhama
<i>B. sempervirens</i>	Leadlay et al. 314	Spain: Malaga, Marbella-Ojen road
	Olowokudejo 120	Spain: Granada, Sierra de la Yedra
	Olowokudejo 122	Spain: Granada, S. of Huerto Santillán
	Olowokudejo 129	Spain: Granada, Guadix
	Olowokudejo 232	Spain: Almeria, Sierra de Gador
	Olowokudejo 234	Spain: Almeria, Almeria-Enix
<i>B. glacialis</i>	Gómez-Campo 53-2161-72	Spain: Granada, Sierra Nevada
	Olowokudejo 200	Spain: Granada, Sierra Nevada, Mulhacén
	Socorro 209	Spain: Granada, Sierra Harana, Cortijo del Sotillo
<i>B. sclerocarpa</i>	BG 180	France: Aveyron, Firmy, Puy de Wolf
<i>B. coronopifolia</i>	BG 780336	France: Vaucluse, Mont Ventoux
<i>B. polyclada</i>	BG 780429	France: Drome, Bourg-de-Péage
<i>B. mediterranea</i>	Olowokudejo 15	Spain: Alicante, Sierra de Carrascal
<i>B. intermedia</i>	Gómez-Campo 54-1199-68	Spain: Madrid, Sierra de Guadarrama
<i>B. valentina</i>	Olowokudejo 72	Spain: Jaén, Sierra del Pozo, Pico de Cabanas
	Olowokudejo 73	Spain: Jaén, Sierra de Cazorla
	Olowokudejo 82	Spain: Jaén, Sierra de Cabrilla
	Olowokudejo 8	Spain: Cuenca, Motilla del Palancar
<i>B. microcarpa</i>	Heywood et al. 138	Spain: Cadiz, El Colorado, near Chiclana de la Frontera
<i>B. lyrata</i>	BG 771147	Italy: Sicilia, Siracusa
	BG 780185	Morocco: Melilla, Sidi Musa
	BG 780356	Algeria: Bouchata Mahmoua
<i>B. didyma</i>	BG 7711425	Spain: Malaga, Ronda
	BG 7800337	Egypt: Alexandria
	BG 7800339	Greece: Attica, Athens
<i>B. auriculata</i>	Olowokudejo 5	Spain: Cuenca, Alarcón
	Olowokudejo 7	Spain: Cuenca, Alarcón
	Olowokudejo 9	Spain: Cuenca, Motilla del Palancar
	Gómez-Campo 1164-67	Spain: Ciudad Real, Alhambra
	BG 781184	Portugal: Algarve, Castro-Marim
<i>B. cichoriifolia</i>	BG 780335	France: Hautes Pyrenées Bagnères de Luchon



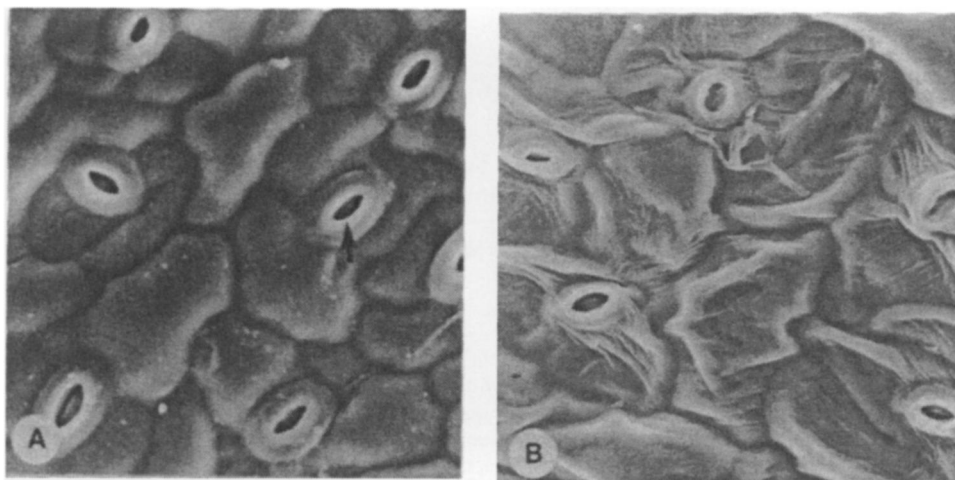
Leaf trichomes and indumenta of *Biscutella*

A - *B. coronopifolia* with attenuated hair (x 50). B - *B. coronopifolia* with enlarged hairs bases and epidermal walls (x 200). C - *B. vincentina* showing a mixture of long and short hairs (x 50). D - *B. mediterranea* showing stiff trichomes with enlarged bases (arrowed) (x 50). E - *B. valentina* showing stiff trichomes found mainly on the margins and midrib, note the presence of numerous tubercles or bosses on each trichome (x 30). F - *B. valentina* showing tubercles on a portion of the trichome (x 900).



Leaf trichomes and indumenta of *Biscutella*

A - *B. sempervirens*, dense soft hairs (x 50). B - *B. sempervirens*, curly, contorted trichomes with tubercles and striae (x 900). C - *B. sempervirens* showing long and short trichomes with swollen bases (x 50). D - *B. sempervirens*, trichomes with tubercles (x 600). E - *B. frutescens* with tomentose indumentum (x 50) F - *B. laevigata* subsp. *austriaca* sparsely distributed attenuate trichomes (x 50).



Leaf surfaces of *Biscutella*

A - *B. laevigata* subsp. *lucida* with glabrous leaf showing smooth epidermal walls and stomata (x 300). B - *B. valentina* showing a glabrous surface with irregular cuticular folds and stomata (x 300).