Variation and taxonomy of *Biscutella valentina* in Spain

J. DELE OLOWOKUDEJO[1]
Department of Botany, Plant Science Laboratories, University of Reading, Reading RG6 2AS, England

Received July 3, 1985

OLOWOKUDEJO, J. D. 1986. Variation and taxonomy of *Biscutella valentina* in Spain. Can. J. Bot. **64**: 2965–2972.

Morphological studies have been made on herbarium specimens and 25 population samples of *Biscutella valentina* (Cruciferae) in Spain. The discontinuities in morphological characters warrant the recognition of three varieties, var. *leptophylla*, var. *pinnata*, and var. *valentina*, from the mass collections, and a fourth taxon, var. *tenuicaulis*, based on herbarium material. Experimental cultivation revealed that the combination of distinguishing characters for each taxon is genetically fixed while the observed phenotypic plastic range of the vegetative features is not wide enough to affect their taxonomic importance. Artificial crosses performed reciprocally in various combinations on seven of the populations representing three of the varieties resulted in the production of fertile hybrids. A key for identifying the varieties is presented.

OLOWOKUDEJO, J. D. 1986. Variation and taxonomy of *Biscutella valentina* in Spain. Can. J. Bot. **64** : 2965–2972.

Des études morphologiques ont été faites sur des spécimens d'herbier et 25 échantillons de populations du *Biscutella valentina* (Cruciferae) en Espagne. Les discontinuités dans les caractères morphologiques réclament qu'on reconnaisse trois variétés des collections en masse: var. *leptophylla*, var. *pinnata* et var. *valentina*, et un quatrième taxon, var. *tenuicaulis*, basé sur le matériel d'herbier. La culture expérimentale a révélé que la combinaison des caractères distinctifs pour chaque taxon est fixée génétiquement tandis que l'étendue observée de la plasticité phénotypique des caractères végétatifs n'est pas assez grande pour affecter leur importance taxonomique. Des croisements artificiels effectués réciproquement dans diverses combinaisons sur sept des populations représentant trois des variétés ont produit des hybrides fertiles. Une clé d'identification des variétés est présentée.

[Traduit par la revue]

Introduction

Biscutella valentina (L.) Heywood (Cruciferae) is a widespread species occurring throughout much of central and southeast Spain. This species encompasses substantial morphological variation and several variants have been recognized either as distinct species (Jordan 1864; Pau 1907; Sennen and Pau 1908) or varieties (Malinowski 1910; Machatschki-Laurich 1926). However, in relatively more recent treatments of the genus (Guinea 1963; Guinea and Heywood 1964), *B. valentina* has been regarded as a single species without reference to either the various taxa recognized within it or its morphological variability. Adopting a rather different approach, Bolòs and Vigo (1974) treated *B. valentina* (syn. *B. stenophylla* Dufour) as a subspecies of *B. laevigata* L. and then recognized two varieties within the subspecies.

In the course of a systematic revision of the genus throughout its entire range (Olowokudejo 1980), I have studied all available herbarium specimens of *B. valentina* s.l. in an attempt to understand more fully the nature and significance of the morphological variation in this species. The specimens were inadequate for a detailed analysis of the variation patterns and this necessitated a field investigation of several populations of *B. valentina* in Spain. "Population" has become a key word in taxonomy since the inherent variability of species has been accepted as a phenomenon requiring study and appropriate treatment.

The present study involves a detailed morphological analysis of 25 populations collected from locations representative of the range of the species. Samples of 14 of these populations have been cultivated to assess the phenotypic plasticity or stability of the characters while artificial crosses have been performed to determine the genetical relationships of the populations.

[1]Present address: Department of Biological Sciences, University of Lagos, Akoka, Lagos, Nigeria.

Printed in Canada / Imprimé au Canada

Materials and methods

Preliminary observations were made on herbarium specimens borrowed from or studied at the following institutions: B, BC, BM, GJO, K, MA, MAF, RNG, SEV. Abbreviations follow Holmgren and Keuken (1974).

Mass collection

Eight to 30 specimens were sampled from each of 25 populations in Spain (Fig. 1) in June and July 1978, using mass collection techniques (Anderson 1941, 1943). Entire plants were usually collected and the size of each sample depended on the size of the population. The complete list of localities, collectors, and numbers is given in Table 1. Voucher specimens have been deposited in these herbaria: ATH, B, BC, BM, BUH, HUJ, KRA, M, RNG, SEV, WU.

Morphological data

The patterns of morphological variation within and among populations were determined by assessing 25 characters. All assessments were made on parts at similar developmental stages and in comparable positions on all plants of each population. The quantitative characters are plant height; length and width of basal leaf; petiole length; length and width of sepal, petal, and fruit; length of pedicel and style; and number of serrations on leaf margin. From these characters four derived character ratios were obtained. Descriptive statistics of means, standard deviations, standard errors, and coefficients of variation were calculated for all variables. Also assessed were these qualitative features: pubescence of stem and leaf surfaces; shape, apex, base, and margin of basal leaf; nature of inflorescence and cauline leaf.

On the basis of eight quantitative characters, polygonal graphs were plotted to characterize each population. Each axis of the polygraph represents one character along which the mean is plotted (Fig. 1).

Experimental cultivation

Mature seeds obtained from many plants of each of populations 1–4, 6, 7, 11, 13, and 20–25 were sown and raised to maturity under uniform conditions in the greenhouse. At the fruiting stage, representative plants of each population were harvested, pressed, dried and labelled accordingly. The morphological features were then

TABLE 1. Sources of population samples

Population designation	Sample size	Localities (including altitude), collectors, and collectors' numbers
1	18	Cuenca: Madrid-Valencia N111 road, 20 km from Alarcon, 750 m (J. D. Olowokudejo, 6)
2	11	Cuenca: Madrid-Valencia N111 road, 3 km from Motilla del Palancar, 800 m (J. D. Olowokudejo, 8)
3	20	Cuenca: South of Motilla del Palancar, near El Peral, 750 m (J. D. Olowokudejo, 10)
4	24	Valencia: NW of Requéna, south of Utiél, 700 m (J. D. Olowokudejo, 11)
5	16	Valencia: S of Requéna, N322 road from Albacete, roadside, 700 m (J. D. Olowokudejo, 111)
6	24	Valencia: Requéna-Valencia road, 18 km from Chiva (J. D. Olowokudejo, 12)
7	11	Valencia: N111 road junction to Bunol, 500 m (J. D. Olowokudejo, 13)
8	28	Valencia: between Jalance and Jarafuel, N330 road, steep slopes (J. D. Olowokudejo, 112)
9	8	Albacete: Sierra de Alcaraz, Chorros del Rio Mundo, entre siles y Riopar (J. M. Mesa, 203)
10	18	Jaén: Sierra de la Cabrilla, Barranco del Rio Guadalentin, 1800 m (J. D. Olowokudejo, 79)
11	15	Jaén: Sierra de Segura, near Pontones, 1900 m (J. D. Olowokudejo, 80)
12	8	Jaén: Sierra del Cazorla, 10 km E of Santo Tome, 1850 m (J. D. Olowokudejo, 85)
13	20	Jaén: Santo Tome-Cazorla road, 5 km S of Santo-Tomé, 1600 m (J. D. Olowokudejo, 173)
14	30	Jaén: Sierra del Pozo, Pico Cabañas, 2000 m (J. D. Olowokudejo, 84)
15	24	Jaén: Sierra de la Cabrilla, Loma de Chiclana, 1900 m (J. D. Olowokudejo, 82)
16	24	Jaén: Sierra de la Cabrilla, Loma de Chiclana, 1900 m (J. D. Olowokudejo, 83)
17	23	Jaén: Sierra Cazorla, Loma de Cagasebo, 1650 m (J. D. Olowokudejo, 74)
18	15	Granada: Sierra de la Sagra, N of Doma Ana, 2000 m (O. Socorro, 201)
19	16	Murcia: Sierra de Espuña, NW of Totana, 1200 m (J. D. Olowokudejo, 16)
20	16	Jaén: Sierra del Pozo, Pico Cabañas, 2000 m (J. D. Olowokudejo, 72)
21	27	Jaén: Sierra Cazorla, near Nava de San Pedro, 1400 m (J. D. Olowokudejo, 73)
22	27	Jaén: Sierra del Pozo, W of Tiscar, 1500 m (J. D. Olowokudejo, 171)
23	20	Jaén: Pozo Alcon, Embalse de la Bolera, 1300 m (J. D. Olowokudejo, 70)
24	22	Jaén: Pozo Alcon, near Rio Arroyo de la Venta, 1300 m (J. D. Olowokudejo, 71)
25	24	Jaén: Sierra de Castril, between Cebas and Castril, 1350 m (J. D. Olowokudejo, 77)

assessed and compared with those of the field samples to determine the phenotypic plastic range of the characters. Voucher specimens are at RNG.

Artificial hybridization

Artificial crosses were performed reciprocally in various combinations on populations 1, 3, 6, 11, 21, 23, and 25 (Table 2), representing the three morphological forms recognized within the 25 populations. About 40–60 fully formed buds on two to three inflorescence branches of each population were selected and emasculated before anther dehiscence at the late bud stage. At anthesis, pollen from ripe anthers of other populations was tapped onto glass slides and artificial pollination was effected either by direct contact with a stigma or by using a fine brush. The inflorescences were bagged before and after pollination.

Pollen fertility

Pollen from each of the hybrid plants was mixed with a 0.3% solution of cotton blue in lactophenol on a clean glass slide and left covered for about 30 min. The fertile grains stained dark blue while sterile grains stained only weakly or not at all. The percentage fertility was estimated from two separate counts of 200 grains.

TABLE 2. Percent seed germination of hybrid seed and pollen stainability (in parentheses) of F_1 in artificial crosses among populations of *B. valentina*

Populations (pistillate)	Populations (staminate)						
	1	3	6	11	21	23	25
1	—	84.6 (88.9)	100 (95.8)	0	0	NA*	78.2 (94.0)
3	92.1 (95.7)	—	NA	88.0 (90.0)	94.4 (80.0)	82.2 (78.0)	78.0 (85.6)
6	83.4 (90.0)	NA	—	92.0 (78.2)	NA	89.0 (86.7)	NA
11	0	74.0 (88.7)	92.1 (84.9)	—	NA	97.8 (77.0)	82.0 (90.2)
21	0	88.2 (78.0)	NA	NA	—	NA	66.0 (97.8)
23	NA	75.1 (91.4)	68.0 (93.4)	100 (89.0)	NA	—	NA
25	92.8 (80.0)	100 (73.6)	NA	85.8 (87.9)	100 (98.0)	NA	—

*NA, not attempted.

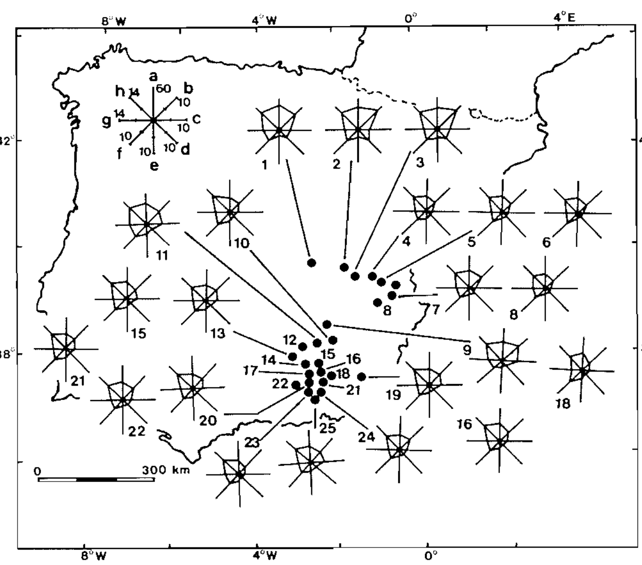

FIG. 1. Polygonal graphs depicting the variation in population means of eight characters for 22 populations of *B. valentina*. The solid circles represent the geographic locations of populations and the numbers refer to populations studied (Table 1). Key to polygraphs: *a*, plant height (cm); *b*, leaf length (cm); *c*, leaf width (cm); *d*, petiole length (cm); *e*, sepal length (mm); *f*, petal length (mm); *g*, fruit length (mm); *h*, fruit width (mm).

Results

Plant height

There is considerable variation in the height of the plants both within and among the populations. The mean values vary from 24.08 cm in population 12 to 52.07 cm in population 1. Populations 1, 2, and 3, located in the northernmost part of the distribution range (Fig. 1), and population 11, one of the central populations, have the highest mean values.

Basal leaves

The basal leaves have always provided most of the taxonomic characters used in the delimitation of species within *Biscutella*. All features of the leaves were therefore carefully assessed and quantified. Figure 2 shows the silhouettes of representative leaf forms illustrating the range of variation in the populations. The leaves revealed the existence of three morphological units within the species. Populations 1, 2, and 3 have oblanceolate leaves with long petioles. The size of the leaves range from 7.52 × 0.33 to 8.66 × 0.35 cm; they are entire or dentate with one to three teeth on each margin, and are sparsely hispid or subglabrous.

The second group consists of populations 4–8, in which the leaves are narrowly linear, subpinnatifid or pinnatifid, with one to two (or three) lobes on each side. The leaves are always smaller than those of the first group, measuring about 3.6 × 0.14 to 5.03 × 0.17 cm. All of the leaves are sparsely setose or glabrous with a characteristic xeromorphic appearance.

The third group consists of populations 9–25. The plants in this group are usually more robust and luxuriant in appearance than those of the previous two groups. The leaves may be lanceolate or oblanceolate with 1–3 teeth on each margin. The size varies from 2.24 × 0.21 to 6.3 × 0.55 cm. Population 12 has unusually small and subsessile leaves.

The scatter diagram in Fig. 3 with axes of leaf length and width characters provides a sharp discontinuity between populations 1, 2, 3, and the remaining 22 populations. Figure 4, which is based on the leaf length/width ratio and petiole length, reveals the existence of the three groups within the populations. The variation in the length of the petiole both within and among the 25 populations is shown in Fig. 5. The populations are arranged in geographic sequence from north to south. Populations 1, 2, and 3 differ from the rest by their longer petioles; they are also the most variable for this character. The other populations show considerable intergradation. The variation pattern is not correlated with the geographical locations of the various populations.

Cauline leaves

These are always sessile and smaller than the basal leaves. They vary from three to seven in number and the size decreases gradually from bottom to top in all the populations.

Floral features

The sepals and petals do not vary much in size either within or among the 25 populations. In groups 1 and 2 the inflores-

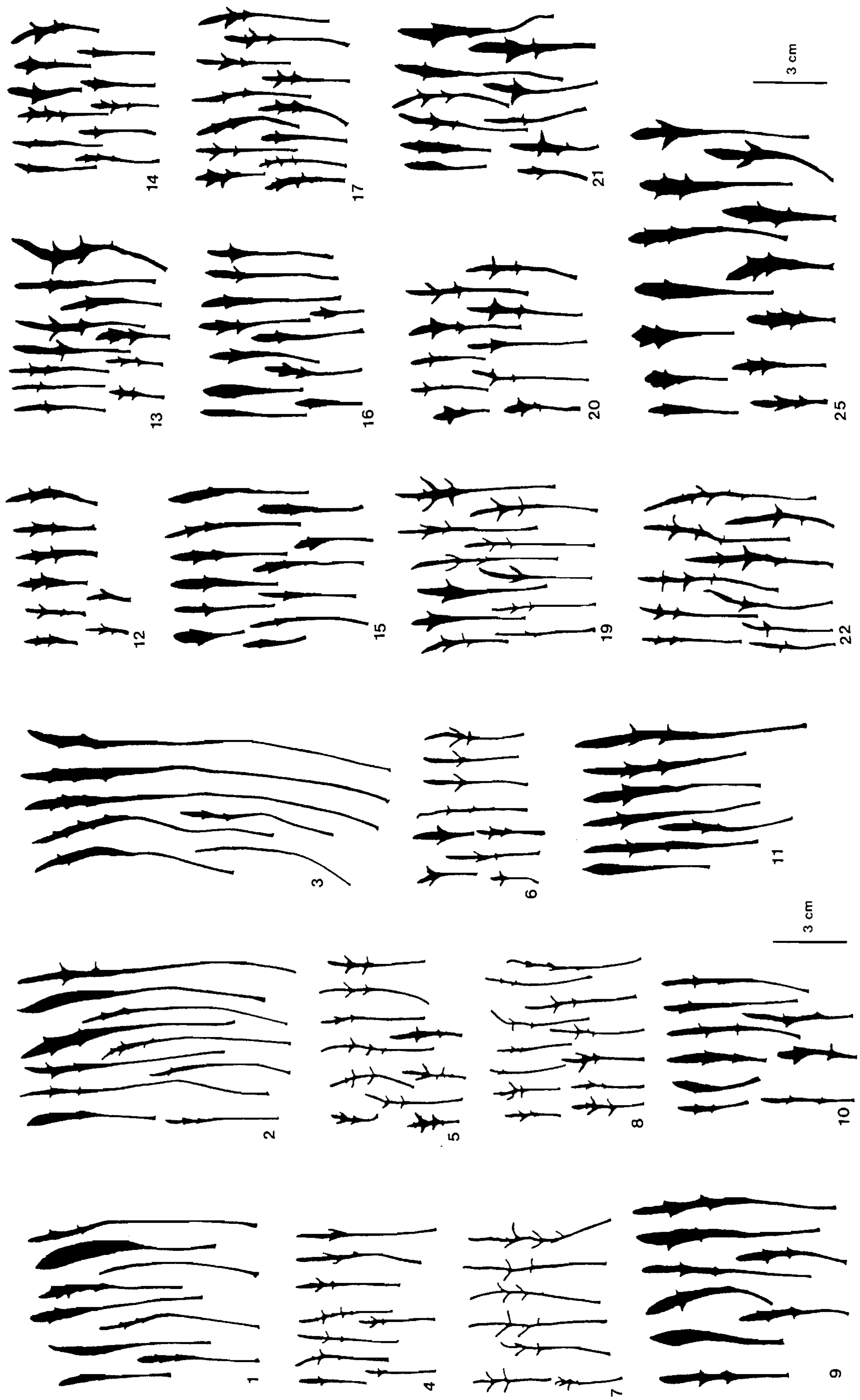

FIG. 2. Silhouettes of representative leaf forms illustrating the range of variation within and among the populations. Numbers designate populations studied (Table 1).

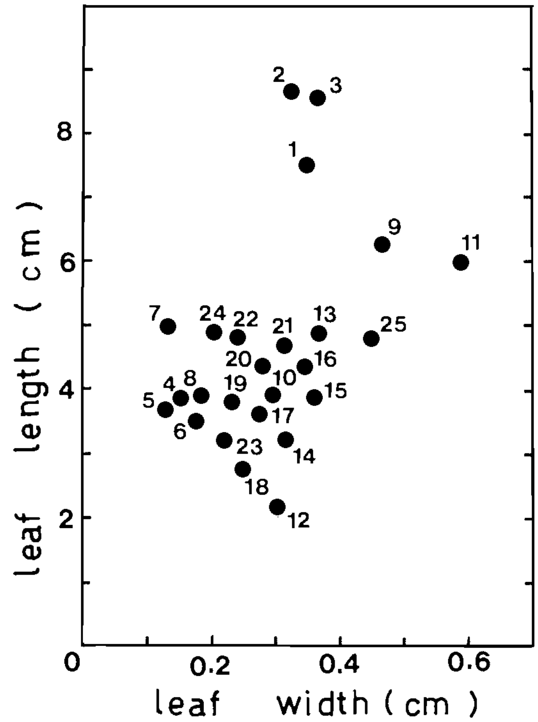

FIG. 3. Scatter diagram of leaf width against leaf length. Numbers designate populations studied (Table 1).

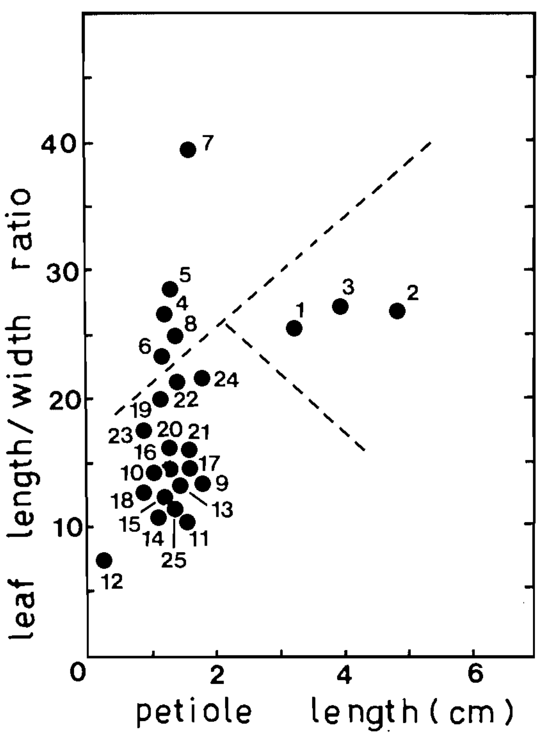

FIG. 4. Scatter diagram of petiole length against leaf length/width ratio. Numbers designate populations studied (Table 1). The three varieties are demarcated by the broken lines.

cence is either a simple raceme or a panicle or both, and the pedicels are usually glabrous or sparsely hairy. In the third group, the flowers are usually arranged in the form of a corymb or in some cases may resemble a capitulum. The pedicels and sepals are usually densely whitish tomentose.

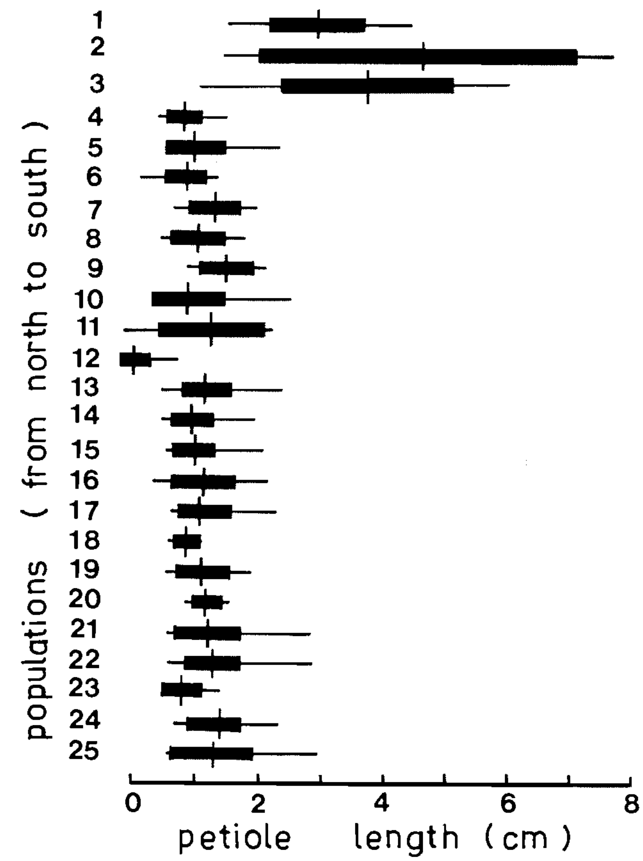

FIG. 5. Variation in petiole length within and among 25 populations of *B. valentina* arranged in geographic sequence from north (1) to south (25). The diagrams illustrate the range (thin horizontal line), the mean (vertical bar), and one standard deviation (thick horizontal line). Numbers designate populations studied (Table 1).

Fruiting characters

The genus is easily recognizable by its highly distinctive didymous fruits, resembling a pair of spectacles. The mean length varies from 4.13 to 6.46 mm while the width ranges from 7.57 to 10.55 mm. The variation among the 22 fruiting populations is continuous, as revealed in Fig. 6, which also shows the strong correlation between the length and width characters.

Populational variation is represented visually in the polygonal graphs shown in Fig. 1. The variation among the populations shows no obvious geographic pattern but the populations constituting each of the three groups recognized above are more similar to each other than to the populations of other groups. For example, there is remarkable uniformity in the morphology of populations 1, 2, and 3. The polygraphs also reveal that there is considerable variation among populations 9–25, which constitute group 3. The vegetative characters such as plant height, leaf length and width, and petiole length are the most variable in all the samples.

Experimental cultivation

The vegetative features showed the highest capacity for response; for example, the mean plant height and leaf size were bigger in the cultivated samples. However, the phenotypic plastic range was not wide enough to affect the taxonomic value of the characters. The cultivated samples retained their characteristic appearances and the various distinguish-

TABLE 3. Summary of differences between the varieties

	var. *leptophylla*	var. *pinnata*	var. *valentina*
Stem height	35–60 cm	20–40 cm	20–60 cm
Basal leaf	5–16 × 0.3–0.6 cm	2–7 × 0.1–0.2 cm	2–7 × 0.1–1.0 cm
	Oblanceolate	Pinnatifid or subpinnatifid	Lanceolate or oblanceolate
	Hispid or subglabrous	Setose or subglabrous	Hispid
Petiole length	2.0–7.5 cm	0.4–2.0 cm	0.1–2.2 cm
Inflorescence	Lax	Crowded	Crowded
	Raceme or panicle	Raceme or panicle	Shaped like a corymb or capitulum
Sepal and pedicel	Sparsely hairy	Sparsely hairy	Densely whitish tomentose

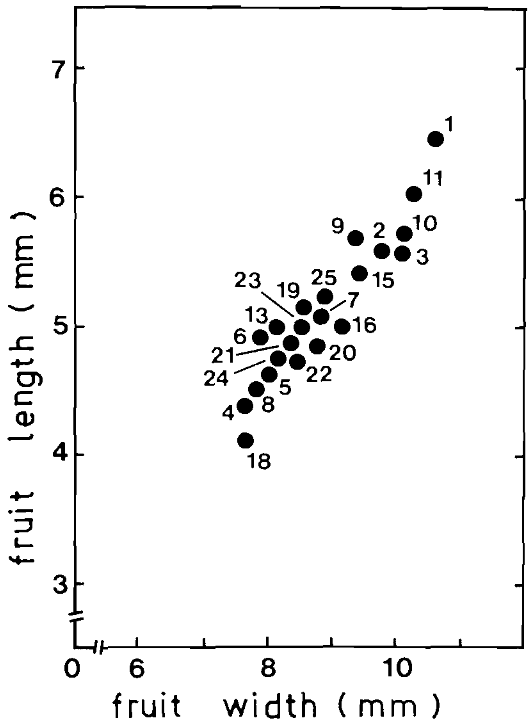

FIG. 6. Scatter diagram showing the correlation between the length and width of fruits among 22 populations of *B. valentina*. Numbers designate populations studied (Table 1).

ing features for each of the three morphological forms remained intact.

Crossability among populations

All but four of the attempted crosses produced seed. The failures involved the reciprocal crosses between populations 1 and 11, and 1 and 21. In the former, four seeds that failed to germinate were produced while in the latter the hand-pollinated flowers all withered and dropped off. The remaining crosses resulted in many viable hybrid seeds with percent germination ranging from 66 to 100% (Table 2). A high proportion of the F_1 hybrids reached maturity and showed high vigour. In most cases the hybrids were morphologically intermediate between the parents while in others they resembled the maternal parent more closely. The percent fertility of the hybrids was equally high, ranging from 74 to 98% (Table 2). The failure of 4 of the 28 attempted crosses may be attributed to experimental errors rather than to any incompatibility mechanisms between the populations. However, these are subjects for further enquiry.

Discussion

This investigation shows that *B. valentina* is widely distributed in central and southeastern Spain where it occupies a wide variety of habitats with an altitudinal range of 600 m in Valencia province to about 3000 m in Pico Cabañas. The latter is one of the highest peaks in the Sierra Cazorla and snow may remain there at least to the end of May. This contrasts sharply with the drier habitats in Cuenca and Valencia provinces.

The observed discontinuities in morphological characters showed that the 25 populations under study consist of three distinctive groups worthy of taxonomic recognition. The first group consists of populations 1, 2, and 3 which are usually tall with longer and oblanceolate leaves and lax inflorescences. These populations were found only in the Cuena province (Table 1). Group 2 is made up of populations 4–8, which occur in Valencia province. The leaves are much smaller and usually pinnatifid, and the inflorescences are crowded. The remaining 17 populations constitute the third group which is the most widely distributed, ranging from Albacete province through Jaen to Granada and Murcia provinces (Fig. 1). The plants are usually more luxuriant with lanceolate or oblanceolate leaves and their characteristic inflorescence looks like a corymb or sometimes like a capitulum. The sepals and pedicels are also usually densely whitish tomentose. The differences between the three groups are summarized in Table 3.

It is now evident that the populations of *B. valentina* are differentiating into rather distinct units, and the process is strongly favoured by the contrasting environments in which the populations grow. The Iberian peninsula shows extreme variation both in the amount of rain and in its seasonal occurrence (Polunin and Smythies 1973). Populations in groups 1 and 2 grow in the dry regions of Cuenca and Valencia provinces where the mean annual rainfall is only about 300–500 mm, whereas the remaining populations (group 3) occur in the high mountain range of southwest Spain with higher mean annual rainfall of about 800–1600 mm (Polunin and Smythies 1973). Therefore, apart from historical considerations, the pattern of variation seen in *B. valentina* may largely be due to the climatic and topographic diversity in the regions. Many of the earlier studies of morphological variation between plant populations have been reviewed by Heslop-Harrison (1964). The observed morphological differences between populations have often been attributed to differences in climatic factors (Clausen et al. 1940, 1948; Björkman and Holmgren 1963), to differences in edaphic factors (Turesson 1922; Gregor 1938), or to biotic factors (Stapledon 1928; Gregor and Watson 1954), but, as Snaydon and Davies (1972) have pointed out, these factors vary simultaneously in the field, and it is therefore difficult to determine with certainty which factors are involved in population differentiation.

The work of Olowokudejo and Heywood (1984) has shown that the three morphological forms under study are diploid with a chromosome number of $2n = 18$. Thus there is no evidence yet that chromosomal differences are associated with morphological variability. The results of artificial crosses also indicate that the three groups are not separated by sterility barriers and are thus genetically closely related. Experimental cultivation revealed that the vegetative parts of the three groups possess the greatest capacity for response, usually in the development of bigger organs. This is not surprising bearing in mind that phenotypic plasticity is an aspect of the adaptive armoury of plants (Bradshaw 1974). However, the observed plastic range of the vegetative characters is not wide enough to affect their taxonomic value. Moreover, each of the three morphological units maintained its characteristic appearance under uniform greenhouse conditions.

Taxonomic conclusions

The morphological evidence regarding the taxonomic recognition of three varieties of *B. valentina* from the population samples seems unequivocal. The partially separate geographic range of the three units appears to reflect ecological differences that are genetically based. In deciding upon the recognition of these taxa I have taken the definition of varieties to be sets of potentially interbeeding populations which differ in minor morphological characters as compared with the species to which they belong. They usually occupy relatively small areas which may or may not be geographically or ecologically isolated.

Populations 1, 2, and 3 are referrable to variety *leptophylla* which Machatschki-Laurich (1926) described as *B. stenophylla* var. *leptophylla*, while populations 4–8 are recognized as a new variety, *pinnata*. The remaining 17 populations represent the typical form of the species, that is, var. *valentina*. The fourth variety, which was not covered by the fieldwork but which is quite easily recognizable in the herbarium, is var. *tenuicaulis*. The full taxonomic treatment of the four varieties will be given in a forthcoming revision of the genus. The key below allows separation of all four taxa.

Key to varieties of *B. valentina*

1. Basal leaves $5-16 \times 0.3-0.6$ cm, oblanceolate, hispid or subglabrous, inflorescence lax . . . . var. *leptophylla*
1. Basal leaves $2-7 \times 0.1-1$ cm; linear; lanceolate, oblanceolate, or pinnatifid; setose, hispid, or subglabrous; inflorescence crowded 2

2. Inflorescence shaped like a corymb or capitulum, sepals and pedicels whitish tomentose; basal leaves lanceolate or oblanceolate, more than 0.3 cm wide, hispid . . . . var. *valentina*
2. Inflorescence a simple or compound raceme, sepals and pedicels sparsely hairy or glabrous, basal leaves narrowly linear or pinnatifid, less than 0.3 cm wide, setose or subglabrous 3

3. Basal leaves entire or dentate with 1 or 2 acute teeth on each side, setose . . . . var. *tenuicaulis*
3. Basal leaves pinnatifid with 1 or 2 (or 3) lobes or teeth on each side, sparsely hispid or glabrous . . . . var. *pinnata*

Acknowledgements

The paper formed part of a thesis submitted for the degree of Ph.D. in the Department of Botany, University of Reading, Reading, U.K. I wish to thank Prof. V. H. Heywood for his suggestions and useful discussions. Prof. C. Gómez-Campo (Madrid) and Dr. J. Varo Alcala and staff of Botany Department, University of Granada, assisted me in various ways during my field studies in Spain; their kindness is gratefully acknowledged. Thanks are also due to the curators for providing their collections and the trustees of the Godman Exploration Fund, British Museum (Natural History), London, for providing a travel grant towards the cost of the field trip.

ANDERSON, E. 1941. The technique and use of mass collections in plant taxonomy. Ann. Mo. Bot. Gard. **28**: 287–292.

——— 1943. Mass collections. Chron. Bot. **7**: 378–380.

BJÖRKMAN, O., and P. HOLMGREN. 1963. Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. Physiol. Plant. **16**: 889–914.

BOLÒS, A., and J. VIGO. 1974. Notes sobre Taxonomia i nomenclatura de plantes. Butll. Inst. Catalana Hist. Nat. **38**: 61–89.

BRADSHAW, A. D. 1974. Environment and phenotypic plasticity. Brookhaven Symp. Biol. **25**: 75–94.

CLAUSEN, J., D. D. KECK, and W. M. HIESEY. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Inst. Washington Publ. No. 520.

——— 1948. Experimental studies on the nature of species. III. Environmental responses of climatic races of *Achillea*. Carnegie Inst. Washington Publ. No. 581.

GREGOR, J. W. 1938. Experimental taxonomy. II. Initial population differentiation in *Plantago maritima* L. of Britain. New Phytol. **37**: 15–49.

GREGOR, J. W., and P. J. WATSON. 1954. Some observations and reflections concerning the patterns of intraspecific differentiation. New Phytol. **53**: 291–300.

GUINEA, E. 1963. El genero *Biscutella*. An. Inst. Bot. A. J. Cavanilles, **21**: 387–405.

GUINEA, E., and V. H. HEYWOOD. 1964. *Biscutella* L. *In* Flora Europaea. Vol. 1. *Edited by* T. G. Tutin, V. H. Heywood, N. A. Burgess, D. H. Valentine, S. M. Walters, and D. A. Webb. Cambridge University Press, Cambridge. pp. 325–330.

HESLOP-HARRISON, J. 1964. Forty years of genecology. Adv. Ecol. Res. **2**: 159–247.

HOLMGREN, P. K., and W. KEUKEN. 1974. Index herbariorum. Part 1. The herbaria of the world. International Association for Plant Taxonomy, Utrecht.

JORDAN, A. 1864. Diagnoses d'espèces nouvelles ou méconnues pour servir de Matériaux à une Flore réformée de la France et des Contrées Voisines. Vol. 1. Paris and Leipzig. pp. 292–329.

MACHATSCHKI-LAURICH, B. 1926. Die Arten der Gattung *Biscutella* L. sect. *Thlaspidium* (Med.) DC. Bot. Arch. **13**: 1–115.

MALINOWSKI, E. 1910. Monographie du genre *Biscutella* L. I. Classification et distribution géographie. Bull. Int. Acad. Sci. Cracovie Ser. B, **1910**: 111–139.

OLOWOKUDEJO, J. D. 1980. Systematic studies in the genus *Biscutella* L. Ph.D. thesis, University of Reading, Reading, England.

OLOWOKUDEJO, J. D., and V. H. HEYWOOD. 1984. Cytotaxonomy and breeding system of the genus *Biscutella* (Cruciferae). Plant Syst. Evol. **145**: 291–309.

PAU, C. 1907. *Biscutella leptophylla*. Butll. Inst. Catalana Hist. Nat. **1907**: 88.

POLUNIN, O., and B. E. SMYTHIES. 1973. Flowers of southwest Europe—a field guide. Oxford University Press, Oxford.

SENNEN, P., and C. PAU. 1908. *Biscutella asperifolia*. Bull. Acad. Int. Geogr. Bot. **18**: 453.

SNAYDON, R. W., and M. S. DAVIES. 1972. Rapid population differentiation in a mosaic environment. II. Morphological variation in *Anthoxanthum odoratum* L. Evolution (Lawrence, Kans.), **26**: 390–405.

STAPLEDON, R. G. 1928. Cocksfoot grass (*Dactylis glomerata* L.) ecotypes in relation to the biotic factor. J. Ecol. **16**: 71–104.

TURESSON, G. 1922. The genotypical response of the plant species to the habitat. Hereditas, **3**: 211–350.