EDINB. J. BOT. 50(1): 1–31 (1993)

TAXONOMY AND NOMENCLATURE OF *BROMUS* SECT. *GENEA*

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A modern re-assessment is given of the taxonomy and nomenclature of the 8(-9) annual taxa within the mainly Mediterranean/SW Asiatic *Bromus* L. sect. *Genea* Dum. (Poaceae): *B. diandrus* Roth var. *diandrus*, *B. diandrus* var. *rigidus* Roth, *B. fasciculatus* Presl, *B. madritensis* L., *B. rubens* L., *B. sterilis* L., *B. tectorum* L. subsp. *tectorum* and *B. tectorum* subsp. *lucidus* Sales; less emphasis is given to *B. madritensis* and *B. rubens*. None of these taxa has previously been investigated throughout their total areas and the taxonomic conclusions expressed here are a result of a multidisciplinary approach. For reasons of convenience the species are considered in three informal groups based on overall similarities: i, *B. sterilis*, *B. diandrus* and *B. rigidus*, so often recognized as independent species in recent Floras but here regarded as varieties of one species; ii, *B. madritensis*, *B. rubens* and *B. fasciculatus*, with particular attention given to *B. fasciculatus*; and iii, *B. tectorum* subsp. *tectorum* and subsp. *lucidus*, previously regarded as independent species.

TAXONOMIC HISTORY

Bromus L. includes annual and perennial species, typically of the temperate areas of Eurasia and America. Its highest diversity occurs in Eurasia, especially in SW Asia where it is believed to have originated (Stebbins, 1981). Occasionally, it grows above the arctic circle; it is also in tropical areas at mountain-subalpine altitudes. It is wholly introduced and naturalized in other temperate areas, such as Australasia.

Influenced by the wide range of morphological variation, many taxonomists divided *Bromus* into smaller groups which were given the rank of genus, subgenus or section. For a long time, the species that are investigated here were variously given generic, subgeneric and sectional status for which the correct names are respectively: *Anisantha* K. Koch, subgen. *Stenobromus* (Griseb.) Hackel, and sect. *Genea* Dum. With the exception of some 'Soviet' taxonomists the generic name *Zerna* Panzer has been correctly rejected or neglected because, apart from the sect. *Genea* elements in it (*madritensis*, *sterilis* and *tectorum*), it originally included many foreign taxa from sect. *Pnigma* Dum. and the genus *Festuca* L. Although *B. sterilis* was the type species proposed for *Zerna* (Hitchcock, *U. S. Dept. Agric. Bull.* 772: 24, 1920), the only illustration in the original publication is probably not a species which could be referred to sect. *Genea*. Contrasting with the earlier lack of agreement concerning the taxonomic rank given to sect. *Genea* (or indeed other groups within *Bromus* s.l.), for the last 10–20 years almost all taxonomists have restricted themselves to using sectional status, e.g. Bor (1970), Smith (1981, 1985a) and Clayton & Renvoize (1986).

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It was Dumortier (1823) who, for the first time, divided *Bromus* s.l. into sections: sect. *Genea*, sect. *Bromopsis*, sect. *Pnigma* and sect. *Bromium*. A criticism must be made of Dumortier's descriptions of his sections: apart from *Bromus* and *Pnigma* he does not use the same characters throughout to define these sections. It is, therefore, very difficult, or impossible, to compare and contrast them. However, because of the way he presents and describes these sections it is my belief that each sectional description excludes the following ones. If my interpretation is correct, Dumortier could have keyed out the four sections as follows:

1. Paleola exterior in setam canaliculatam desinens, apice bilaciniata ______ sect. *Genea*
1b. Species that do not present the above characters ______ 2

2. Seta fere terminalis, basi per apicem paleolae biaurita ______ sect. *Bromopsis*
2b. Species that do not present the above characters ______ 3

3. Axis basi circumsutus, seta dorsalis ______ sect. *Pnigma*
3b. Seta dorsalis, axis dorso continuus ______ sect. *Bromium*

In the descriptions of the sections, Dumortier used two rather ambiguous expressions: 'axis basi circumsutus' and 'axis dorso continuus'. To interpret them it is necessary to understand what Dumortier meant by 'axis' in his work on grasses. I agree with Tournay (1961) in that these two expressions should be interpreted respectively as: 'dorsal surface of glumes separated from the pedicel of the spikelet by an annular strangulation' and 'dorsal surface of glumes joining the pedicel without strangulation'. However, this character does not seem very significant because I have observed a strangulation not only on specimens of sect. *Pnigma* but also on those of other sections. Apart from these negative aspects, Dumortier's descriptions of the sections are based on very few characters. Nonetheless, these are the earliest valid, legitimate sectional names. More characters have been added to better define these subgeneric groups as botanists, still convinced of the reality of the subgeneric divisions of *Bromus*, widened their knowledge of its range of variation. The most recent description of sect. *Genea* was given by Smith (1985) and in this paper I adopt a modified version of it.

Section **Genea** Dum., Obs. Gram. Fl. Belg. 116 (1823).
Annuals, sometimes biennials, with lateral growth when growing in wet places (not their native habitat). Spikelets lanceolate when young, soon becoming cuneiform, broader at top, lower glume 1–3(–5)-veined, upper 3–5(–7)-veined. Leaves emarginate, rounded on back. Awn single, usually longer than lemma, canaliculate in section, rough, straight or weakly, sometimes strongly, out-curved, usually twisted once.
Lectotype species: *B. sterilis* L.; cf. Tournay, *Bull. Jard. Bot. État*, 31: 294 (1961).

The section is widely distributed in Mediterranean countries, SW Asia and also in northern Europe; some taxa are important introduced weeds in other regions of the world, mainly within a Mediterranean-type of climate.

I have accepted in this paper the lowest taxonomic rank given so far to this group of species (section) because I do not think there are enough multidisciplinary data on the infrageneric groups in *Bromus* to give them all a higher rank. For reasons of convenience, I consider here *Genea* as a discrete group in the genus, but I doubt its reality as an independent taxonomic unit. There seems to be a continuous range of variation between sect. *Bromus* and sect. *Genea* via the *B. pectinatus* complex of sect. *Bromus*. This complex seems to link with sect. *Bromus* through the diploid *B. japonicus* Thunb. How the *B. pectinatus* complex relates to sect. *Genea* is not yet fully understood, but the link seems to be via *B. tectorum* s.l. Both subspecies and this other complex form a misty boundary between sect. *Bromus* and sect. *Genea* thus questioning the taxonomic reality of these two sections.

KEY TO THE SPECIES OF SECT. *GENEA*

I found it impossible to construct a normal dichotomizing key to the species of *Genea* because of the great morphological variability and overlapping of character states. Different species have several characters in common. As a result of my studies I concluded that the nine characters used below provide, in combination, the best tool for identification.

The characters used in the key are indicated by capital letters (A, B) and the character states by numbers (A1 & A2; B1 & B2). The character states are:

A1 Long glumes and lemmas - upper glume 1–47mm long.
A2 Shorter glumes and lemmas - upper glume 7.5–10(–21)mm long. [*B. sterilis* occasionally has upper glumes up to 21mm].

B1 Rachilla of top sterile florets twisted.
B2 Rachilla of top sterile florets not twisted.

C1 Panicle branches longer than spikelets.
C2 Panicle branches shorter than spikelets.

D1 Panicle branches with few ramifications - up to 2–3.
D2 Panicle branches with more ramifications - more than 3.

E1 Panicle erect.
E2 Panicle nodding.

F1 Glumes and lemmas very narrow - lemma 1.3–1.8mm wide.
F2 Glumes and lemmas wider.

G1 Caryopsides twisted.
G2 Caryopsides not twisted.

H1 Caryopsides straight.
H2 Caryopsides outcurved.

I1 Awns straight.
I2 Awns curved.

Thus, the six species are defined by the following list of characters states:

B. diandrus – **A1**, B2, C1 & C2, D1, E1 & E2, F2, G2, H1, I1

B. tectorum – A2, **B1**, C1 & C2, D1 & D2, **E1**, F2, G2, H1 & H2, I1.

B. sterilis – A2, B2, **C1**, **D1**, E2, F2, G2, H1 & H2, I1

B. madritensis – A2, **B2**, C1 & C2, **D2**, E1 & E2, F2, G2, H1 & H2, I1

B. rubens – A2, B1, C1, **D2**, E1, F2, G2, **H1**, I1

B. fasciculatus – A2, B2, C2, D1, E1, F1, **G1** & G2, **H2**, I2

Character states that are of greater taxonomic significance in identification are indicated in bold.

TAXONOMY

1. *B. STERILIS* AND THE *B. DIANDRUS-RIGIDUS* COMPLEX

These three species are closely related morphologically. There is an almost continuous range of variation in some characters, from '*B. rigidus*' to *B. diandrus* to *B. sterilis*, the latter being better differentiated. *B. sterilis* also has some similarities to *B. madritensis* but it has been regarded as one of the parents of *B. diandrus* (*B. diandrus* = *B. rigidus* x *sterilis*; Cugnac, 1931, 1932, 1934).

B. diandrus and *B. rigidus* are, in general, robust plants with bigger glumes, lemmas, paleas and awns than *B. sterilis*, which has a quite stable morphology throughout its geographical range and does not pose any complicated taxonomic problems. *B. sterilis* is the most common Genea species in Europe, often a ruderal. It is not common in N Africa nor in SW Asia. It was introduced into N and S America. In contrast, the enormous morphological variation of *B. diandrus* and '*B. rigidus*' has been much discussed and different taxonomic treatments proposed.

B. sterilis L., Sp.Pl. 77 (1753).

Syn.: *Zerna sterilis* Panz. in Denkschr. Akad. Muench. 1813: 297 (1814) [formal combination not made here but clearly based on *Bromus sterilis* L.]; *Anisantha sterilis* (L.) Nevski in Acta Univ. Asia Med. ser. 8b (Bot.) 17: 20, 22 (1934). Type: see comments below at lectotype.

Icon.: Bor, N.L.in Fl. Iraq, ed. Townsend et al. 9: 158, pl. 54 (1968). Hubbard, C.E., Grasses, ed. 3, 42 (1985).

Annual, 4–c.100cm tall, with solitary or loosely tufted, ascending to erect, slender glabrous culms. *Leaf* sheath softly villous to pilose with retrorse-patent hairs, apically glabrous or occasionally throughout; ligule fringed, acute or round at the base. Leaf blade acuminate, 1.5–23 x 0.1–0.7cm, very often with longer hairs along the margin continuing along the margin of the sheath near the ligule. *Panicle* condensed and ascending when young, very soon becoming open, lax, deltoid in outline, up to 17cm long from the lowest to the uppermost node. In very small plants, the panicle is reduced to 1 spikelet (var. *oligostachyus* Ascherson & Graebner, *Syn. Mittleleur. Fl.* 2: 592, 1901). Panicle axis usually glabrous, sometimes with short hairs apically. Panicle branches slender, spreading, sometimes with short hairs. Branches longer than spikelets, shorter only when panicle is reduced to 1 or very few (2, 3) spikelets, simple, rarely 1 branch of the lowermost node with 1 ramification, up to 12cm long. *Spikelets* 1(–2) per branch, cuneate, broadening at maturity when the florets diverge from the axis. *Florets* 4–12 per spikelet of which 2–4 are sterile. Rachilla segments of very uniform length along the spikelet. *Glumes* and lemma usually tinged with dark red-purple at maturity, with a narrow hyaline margin, glabrous or with short or long hairs. Lower glume narrowly lanceolate, 1(–3)-veined, 5.5–14.7 x 0.4–1.2mm; upper glume lanceolate, 3(–5)-veined, 7.5–21 x 1.6–3mm. *Lemmas* of fertile florets 7-veined, 10.5–30mm long, with 2 acute teeth at apex; lemmas of sterile florets smaller. *Awn* straight, slender, often with a single twist, inserted 1-5mm below the lemma apex; awn length quite uniform in a spikelet, but the awns of sterile florets always shorter and more slender. Awn of second floret 9.5–29mm long. *Palea* 9.5–17mm long, much shorter than lemma, 2-veined, glabrous on adaxial surface; abaxial surface glabrous or hairy between the veins; veins with long spreading hairs or short and erect, longer near the apex. *Stamens* 3; anthers 0.5–2mm long. *Caryopsides* usually straight, sometimes curved slightly outwards, shorter than palea, 10–15mm long. Callus of rachilla segments well differentiated and therefore disarticulating below each fertile floret, obtuse. Scar of rachilla segments round.

Lectotype: While investigating the typification of *B. sterilis*, I came across a major problem in that the proposed lectotype (Smith, 1985) is not *B. sterilis* but *B. diandrus*, and there are no other original elements for the name which can be unequivocally identified as belonging to *B. sterilis* of current usage. To avoid a major nomenclatural disruption if the name *B. sterilis* were to disappear I have proposed conserving it with a new type (Sales,1992).

Diagnostic features of the lectotype [93.19 LINN] proposed by Smith (1985b) compared with my own observations of a wide range of *B. sterilis* specimens:

	[93.19 LINN]	*B. sterilis*
Panicle branches length	5 (robust)	Up to 12 (slender)
(cm)	17	5.5–14.7
Lower glume length (mm)	25	7.5–21
Upper glume length (mm)	29	10.5–30
Lemma length (mm)	robust	slender
Awn	a little pointed/ round/circular	almost circular
Callus/scar shape		

Habitats. Europe/Mediterranean: Maquis, in thickets, granite slopes, with *Cercis*, *Pinus brutia*, *Cistus ladanifera*, *Quercus pyrenaica*, *Paliurus*, vineyards. N Africa: with *Cedrus atlantica*, *Argania*; SW Asia: rocky limestone slopes, scree, in *Quercus* woodland (*Q. persica*, *Q. aegilops*), with *Cercis*. Throughout its range: grassy slopes, waste places, roadsides, in orchards, hay fields, 20–1500(–2400)m.
Selection of material examined:

EUROPE. AUSTRIA: Wien, near Matzleinsdorf, 22 vi 1898, *Krebs* s.n. (E); Styria, 1842, *Alexander* s.n. (E); Graz, Gosting, 360m, Fritsch in *Hayek* 406 (E). BULGARIA: Sofia, near the airport, 5 vi 1977, *Vihodcevsky* s.n. (SOM); Struma, near Kocerinovo, *Stoeva* 1000 (E); N Bulgaria, Lovec, 1894, *Krumoff* s.n. (SOM); CZECHOSLOVAKIA: Brno to Vinohradska, 220m, 7 vi 1962, *Grull* s.n. (E); Kauden, Atschau, *Steltzhamer* 808 (BG). DENMARK: Kristrup, Randers, *Lojtnant* 726 (BG); Zealand, Hojby station, *N. Jacobsen* 264 (O). FRANCE: Rhône, Arnas, *Gandoger* 389 (O); Ile Vilaine, St Michael, 18 vi 1954, *Stromer* s.n. (O); Pyrénées, *Luchon-Zetterstedt* 389 (O). GERMANY: Thuringia, Haustadt, vi 1908, *Reineck* s.n. (O); Bavaria, SE Wurzburg, *L. Gross* 473 (BG); Baden, Karlsrühe, *Kneucker* 287 (E). GREECE: E Aegean, Psara island, 'Ahladhokambos', *Greuter* 10822 (E). HUNGARY: Budapest, 100m, *Degen* 229 (E). IRELAND: Dublin, Portmarnock, vii 1857, *J. Ball* s.n. (E). ITALY: Pisa, 1846, *Flora Etrusca Exsiccata* s.n. (E); Insula Caprearum, iv 1842, *J. Ball* s.n. (E); Naples, v 1842, *J. Ball* s.n. (E); Sicily, 10Km NE Nicolosi, 1000m, *Davis & Sutton* D.64447 (E). NETHERLANDS: Den Haag, *Leenhouts* 3380 (O). NORWAY: Rennesoy, Dale, 10 vi 1929, *Holmboe & Lid* s.n. (BG); Rog. Stav. Pedersgaten to Hannesiloen, 18 vii 1983, *Halvorsen* s.n. (BG). PORTUGAL: Coimbra, Choupal, v 1880, *Moller* (COI); Alto-Alentejo: Castelo de Vide, 401m, *Beliz* 1530 (ELVE); Torre de Moncorvo, v 1887, *Mariz* s.n. (COI); Madeira, Santo da Serra, *Davis & Macpherson* D.70993 (E). SPAIN: Sierra de Gredos, El Arenal, 900m, *Deverall & Flannigan* 267 (E); Rio Tiradero, *B. M. Allen* 7529 (E); Malaga, Gobantes to Antequera, *Galiano et al.* 1480.69 (E). SWEDEN: Lund, *Sandin* s.n. (BG); Skåne, Helsingborg, 10 vii 1907, *Stensson* s.n. (BG); Paroecia Kavlinge, Kavlinge, *H. Tedin* 258 (O). SWITZERLAND: Basel, 1912, *Jermstad* 152 (O); Geneva, 1820, *Blytt* 389 (O). TURKEY: Istanbul, Yildiz bahcesi, *A. Baytop* 7635 (E). UNITED KINGDOM: England: Surrey, Tothill near Headley, *Hubbard* 9045 (E); Leatherhead, *H. Burkill* 1531 (E); Sussex, East Grinstead, *Davis* 16930 (E). Scotland: Midlothian, Edinburgh, *Dunnett* 9 (E); Moray, Mains of Craigmell Dallas, *McCallum Webster* 16417 (E); Fife, Burntisland, 22 vii 1848, *Lauder Lindsay* s.n. (E). UKRAINE: Crimea: Sokoll, Sudak, *Callier* 232 (O). YUGOSLAVIA: Hercegovnia: Trebinje, Golobrdo, 12 v 1898, *Baenitz* s.n. (E); Trieste, 3 v 1896, *O. Krebs* s.n. (E); Sarajevo, v 1885, *Beck* s.n. (E).

N AFRICA. MOROCCO:. Middle Atlas, between Azrou and Timhadite, *Paunero et al.* 1986: 69 (E); High Atlas, Demnate, *Whiting & Richmond* 224 (K); Immouzer valley, N of Agadir, *Bramwell* 292 (K). TUNISIA: Gafsa, iii 1909, *Pitard* s.n. (E).

ASIA. AFGHANISTAN: Kataghan: 25km S Pul i Khumri, 800m, *Rechinger* 33775 (E); Kabul: Kabul, Tang-i Gharu, 1500m, *Hedge & Wendelbo*, W.2807 (E); Bamian: near Panjao, *Hedge & Wendelbo*, W.4927 (BG). AZERBAIDJAN: Chatschmas, Chudat to Schollar, *Zakarjan & Schevljai* 32909 (E). CYPRUS: Paphos forest, Stavros, *Foggie* 219 (E). GEORGIA: Tiflis, *Grossheim* 4728 (E). IRAN: Lorestan: Ilan, c.1800m, *Jacobs* 6828 (E); 60km W Khorramabad, 1160m, *Archibald* 1642 (E); Kerman: Djamal Bariz, Bam to Djiroft, 2400m, *Rechinger* 3878 (E). IRAQ: Baghdad, Jadriyah, *Wheeler Haines* 1615 (E); Kirkuk: Jarmo, 760m, *Wheeler Haines* 269 (E); Rowanduz: Shaqlawa, 900m, *Wheeler Haines* 683 (E). ISRAEL: Edom, Har Nevo, *Gabrielith* s.n. (HUJ); Mt Carmel, 200m, *Dinsmore* 2734 (E); Shomron, Jebel Eteri near Bat Shelomo, 10 iv 1946, *D. Zohary* s.n. (HUJ). LEBANON: Mt Lebanon, 1600m, 13 v 1877, *J. Ball* (E). TURKEY: Hatay: Kirikhan to Hamam, 100m, *Coode & Jones* 578 (E); Izmir: Camlibel, Germencik to Selcuk, 200M, *Davis* 41763 (E); Mardin: Mardin, 1100m, *Davis & Hedge* D.28365 (E).

AMERICA: USA, Washington: Washington, 23 v 1897, *Steele* s.n. (E). CANADA: Vancouver Island, Victoria, 27 v 1893, *Macoun* (E).

AUSTRALIA: W Australia: Midland Junction, x 1905, *Staer* (E); S Australia: northern Yorke peninsula, *Copely* 768 (E).

COMMENTS ON INFRA-SPECIFIC VARIATION

All the infra-specific taxa of *B. sterilis* that have been recognized were at the ranks of varietas and forma. Many were based on varying pubescence (e.g. f. *glaberrimus* Soo , var. *glabrescens* Zapal, f. *hirsutior* Waisbecker, var. *pilosus* Rohl, var. *pubescens* (Ascherson) Kuntze, var. *velutinus* Volk ex Hegi); others were based on lemma colour (e.g. var. *purpurens* Schur. var. *viridis* Schur.) and some were recognized for plants with reduced panicles, sometimes to one single spikelet (var. *oligostachyus* Ascherson & Graebner). From my own experience in the field and herbarium, these infra-specific taxa are not worth recognition. Pubescence is very variable in the genus *Bromus* s.l. and within individual species. The dark red colour of the lemmas towards maturity occurs in differing degrees in most members of sect. *Genea.*

B. DIANDRUS-RIGIDUS COMPLEX

B. diandrus Roth, Bot. Abh. Beobacht. 44 (1787).
Annual, 15–120cm tall, with solitary or loosely tufted, ascending to erect, ± robust culms, glabrous, except for the upper part just below the panicle. *Leaf* sheath softly villous to pilose with retrorse-patent hairs, wholly glabrous, or only apically or at the base, occasionally glabrous with 2 rows of long hairs along the margins; ligule fringed, acute or round at the base. Leaf blade acuminate, 4.5 x 0.18cm to 22 x 0.85cm with sparse usually long hairs, especially so at margins, somewhat denser on abaxial surface. *Panicle* condensed and ascending when very young; shape varying from contracted, stiffly erect, narrowly ovate in outline, to lax spreading and broadly ovate; at maturity ± 1-sided, nodding, up to 19cm long from lowest to uppermost node; in very small plants the panicle sometimes reduced to 1–2 spikelets. Panicle axis ± densely hairy. Panicle branches robust (more rarely slender), straight, erect when young, ± curved downwards at maturity, shorter than spikelets (sometimes as short as 0.7cm) or longer (up to 14cm), usually single, sometimes the longest lower one with a ramification. *Spikelets* narrowly-ovate, cuneate, tapering when young, usually ± truncate and broad at maturity but sometimes without change of shape at maturity (in clearly cleistogamous plants), 1.7–5.1cm long. *Florets* (5–)6–11, of which (1–)2–4 are sterile. Rachilla segments very uniform in length along the spikelet. *Glumes* and lemma very often dark red-purple at maturity with a narrow hyaline margin, with very short or longer hairs at least towards the apex. Lower glume narrowly lanceolate or lanceolate 1(–3)-veined, 12 x 1.6mm to 36 x 2.6mm; upper glume more broadly lanceolate, 3(–5)-veined, 18 x 1.4mm to 47 x 3mm. *Lemmas* or fertile florets 7-veined, 13–53mm long with 2 acute teeth at apex; teeth 0.18–9.5mm long; lemmas of sterile florets smaller. *Awn* straight, robust, often with a single twist; awn length quite uniform in a spikelet, but awns of sterile florets always shorter and more slender. Awn of second floret 3.5–10.5cm long, often purple sometimes even before maturity and when glumes and lemmas are still green. *Palea* 10–20.5mm long, much shorter than lemma, glabrous on adaxial surface; abaxial surface glabrous or hairy with short, erect, clearly spaced hairs along the 2 veins, longer near the apex. *Stamens* 2 or 3; anthers usually 0.45–1.3mm long but up to 5.9mm. *Caryopsides* straight, c.0.15mm shorter than palea. Callus of rachilla segments differentiated below each fertile floret, pointed or ± obtuse. Scar of rachilla segments narrowly elliptic to ± round.

The description above combines the two morphological extremes that have previously been given independent specific status: *B. diandrus* Roth and *B. rigidus* Roth. Although there are no geographical differences between these two extremes, I have noticed some correlation between ecology and some particular morphological features. Plants with the callus/scar pointed/elliptic, short branches, narrow erect panicles (*rigidus*) occur more often on sandy soils, usually maritime sand dunes and sandy river banks; whereas plants with the callus/scar round/circular, long branches, broad, lax panicles, bigger anthers (*diandrus*) are more often found on heavier, less freely draining limestone kind of soils with more humus. This correlation is apparently still weak because in many cases it fails to occur, but it may show an evolutionary tendency in embryo.

A multidisciplinary study of a very large number of specimens, mainly in the herbarium but also in the field, has led me to believe that these two taxa are not distinct enough to be given a taxonomic rank higher than variety.

KEY TO THE TWO VARIETIES

1a. Panicle contracted, stiffly erect, narrowly ovate; panicle branches mainly shorter than spikelets; florets and rachilla segments imbricate, less exposed; lemma involute with margins touching at maturity; base of lemma in side-view straight (Fig. 1A), scar of rachilla segments elliptic (Fig. 2A); anthers up to 0.7mm, long included; caryopsides usually inrolled __ *B. diandrus* Roth var. *rigidus* (Roth) Sales

1b. Panicle lax, spreading, broadly-ovate, branches mainly longer than spikelets, sometimes contracted, panicle sometimes with shorter branches especially in specimens growing in conditions of water stress; florets and rachilla segments at flowering time spreading exposed ; lemma involute with margins nor touching at maturity; base of lemma in side-view with a constriction at the callus/scar area (Fig. 1B) scar of rachilla segments oval (Fig.2E); anthers 0.7–5.9mm long, included and exserted; caryopsides quite often flat __ *B. diandrus* Roth var. *diandrus*

B. diandrus Roth var. **diandrus**

Syn.: *A. diandra* (Roth) Tutin in Clapham et al., Fl. British Isles ed. 2: 1149 (1962); Tzvelev in Not. Syst. (Leningrad) 22: 4 (1963). Type: Neotype (selected here): *Gr. Bromoides, locustis maximus, lanuginosum, Italicum. Hist. Nat.*: 261. no. 444 (Scheuchzer Herb., OXF!).

B. gussonii Parl., Rar. Pl. Sic. 2:8 (1840). *Anisantha gussonii* (Parl.) Nevski in Act. Univ. Asia Med. VIIIb. Bot. 17:20 (1934). *Zerna gussonii* (Parl.) Grossh., Trudy Bot. Inst. Azerbaidzh. Fil. Akad. Nauk S.S.S.R. 8: 305 (1939). Type: see notes below.

Icon.: Bor, N. L.in Fl. Iraq, ed. Townsend et al. 9:143, pl. 48 (1968). Hubbard, C.E., Grasses, ed. 3, 48 (1985).

Roth's specimens were destroyed at Berlin (B) in 1943 during the war, but there are two references in the protologue that provide some guidance in the choice of a neotype for *B. diandrus*. One is the sentence '*Semina inter passulas majores lecta Majo mense terra comissa plantas nunc (Octobri mense) florentes producerunt*' [seeds collected among big raisins, planted in May and now (October) producing flowers]; this is a reference to Roth's interest in the 'impurities' (seeds), found among raisins, grown in his own garden. Possibly, the *Bromus* 'seeds' were brought with raisins from south Germany or Italy by merchants. The other relevant reference is to a very good description of the species by Scheuchzer: 'Scheuchz., *Agrost.* pag. m. 261 (descriptio optima)'. Scheuchzer in page

261 refers to a grass that grows in Italy, near Rome and Florence. Scheuchzer's specimens are at Oxford (OXF) and the more complete of the two relevant specimens is chosen here as the neotype.
Habitats. Open woodland, wet shady ground, shingle banks, edge of stream, maquis, in pasture land, roadside, waste ground, fallow fields, cultivated fields; on calcareous, serpentine, clay and sandy soils. From sea level to 1550m (to 2400m in western N America).
Selection of material examined:

EUROPE. FRANCE: Paris, Côté de Dreux, 9 v 1897, *Jeanpert* s.n. (E); Loire, Nantes, 28 vi 1954, *Stormer* s.n. (O). GREECE: Crete: Ep. Kydonia, Agia, 50m, *Gradstein & Smittenberg* 236 (E); Kos: Kos, s.l., *Davis* 40555 (E). ITALY: Liguria, *Kneucker exsicc.* 653 (E); Trieste, Pola, 21 v 1902, *O. Dahl* (O); Sicily, Palermo, *Todaro* 518 (E). MAJORCA: Palma, 5 v 1903, *White* (E). MADEIRA: above Pousada dos Vinháticos, 660m, *Davis* 70741 (E). MALTA: *Somerville* 191 (E). NORWAY: Oslo, Gronlien, *Fridtz* 7011 (O); Sogn og Fjordane, Jolster hd., 5 ix 1955, *Befring* (BG). PORTUGAL: Trás-os-Montes & Alto Douro: Bragança, 720m, *P. Silva et al.* 7592 (LISE); Beira Litoral, c.6.5km from Vagos to Ilhavo, *A. Marques* 51 (COI); Estremadura, Loures near Ponte de Frielas 50m, *A. Teles & M. Silva* 1234 (LISE); Algarve, praia da Rocha, s.l., *Davis* 50970 (E). SPAIN: Guipuzcoa, San Sabastian, *Gandoger* 118 (E). SWEDEN: Malmo, 18 vi 1920, *Holmberg* (O). UNITED KINGDOM: England: Bournemouth, v 1922, *Sherrin* (BG). Scotland: Midlothian, Currie to Colinton, vi 1874, *Sadler* (E); Midlothian, Leith Docks, 1922, *Grierson* (E); Galashiels, Gala water, *O. Stewart* 136/74 (E). YUGOSLAVIA: Croatia: Susak to Martinscicam, 60m, *Degen* ('Gram. Hung.') 232 (O); Jiume (Rijeka), 20m, *Smoquina* ('Gram. Hung.') 233 (E).
N. AFRICA (+ Canary Islands). ALGERIA: Kerrata, 800m, *Reverchon* 274 (E); 03: above Tlemcen, Col des Zarifète, 1200m, *Davis* 58843 (E). CANARY ISLANDS: Tenerife, 11km E Puerto de la Cruz, 20m, *D. Long* 5567 (E). LIBYA: Tripolitania: Marcella, Gargaresh, 15m, *Keith* 872 (K); Tripoli, nr University of Tripoli, 100m, *Davis* 49453 (E). TUNISIA: NE Cap Bon, La Haouaria to Kelibia, *Davis* 56873 (E).
ASIA (+ Cyprus).AZERBAIDJAN: Apzheronskiy peninsula, E of Baku, 13 v 1952, *Tzvelev* s.n. (K). CYPRUS: Kyrenia range, Yaila, 800m, *Davis* 2842 (E). IRAQ: Erbil: greater Zab near Eski Kellek, 300m, *Gillett* 8206 (K); Kirkuk: 30km S Durbendikhan, Diyala river, *F. Barkley* 7376 (K). ISRAEL: Acre Plain, Qiryat Bialik, *Koppel* 11218 (HUJ); Hula valley, Wadi Dardara, 24 iv 1925, *Smolly* s.n. (HUJ). TURKEY: Adana: Tuzla, s.l., *Coode & Jones* 316 (E); Izmir: Çesme to Sifne, 30m, *Davis* 41783 (E).
N. AMERICA: U.S.A. Arizona: Chiricahua mts, Barfoot Park, 2440m, *Blumer* 1585 (E); Washington DC, 6 vi 1901, *Steele* s.n. (E); California: Monterey Co., below Big Sur, s.l., *Davis* 66798 (E); California, Sonoma Co., Santa Rosa, *Heller* 5322 (E).
AUSTRALIA: S Australia: E slopes Mt Lofty range, Monarto South, *Symon* 3120 (K). New South Wales: 18km Goulburn to Yass, Wologorong Creek, *de Nardi* 476 (K). Tasmania: Blackman's Bay near Kingston, *Rodway* 2061 (K).
JAPAN: Honshu, Ishikawa, Taki, Hakui-shi, *Pl. Jap. Exsicc.* 977 (E).
NEW ZEALAND: Clutha railway station, 1 xii 1974, *Hubbard* 9 (K); Kiaora, N Otago, 7 x 1974, *Hubbard* 16 (K).
SOUTH AFRICA: Cape Province, George, xi 1947, *Wilman* s.n. (K); near Muizenberg, 30m, *Crook* 1098 (K).

B. diandrus Roth var. **rigidus** (Roth) Sales, **stat. nov.**

Syn.: *B. rigidus* Roth in Bot. Mag. (Römer & Usteri) 10 (33): 21–23 (1790). *Anisantha rigida* (Roth) Hyl., Uppsala Univ. Årsskr. 7: 32 (1945). *Anisantha diandra* Roth subsp. *rigida* (Roth) Tzvel., Grasses of the Soviet Union, Part I: 324 (1984). Type: Neotype (here selected): '*Triandria Digynia. Bromus rigidus spiculis* *multifloris lato-lanceolatis rigidis, floribus diandris, panicula contracta*. Roth, Catal. Bot. 1. p. 17. Habitat in Europa australi' (Willdenow Herb., B!).

B. maximus Desf., Fl. Atl. 1: 95 (1798). Type: see notes below.

Icon.: Hitchcock et al., Vascular Plants of the Pacific Northwest. 1, p. 512: *B. rigidus* var. *rigidus* (1969). Pignatti, Flora d'Italia 3: 526 (1982).

Habitats. Sand dunes, often by the sea, fixed dunes in maquis, riverside, terrace walls (wheat fields in S Africa). From sea level to 950m.

Selection of material examined:

EUROPE. AÇORES: Terceira, Praia da Vitória, 5m , *Dansereau et al.* 89 (LISE). FRANCE: Vaucluse, v 1844, *J. Ball* s.n. (E). GREECE: Attica, Phaleri, *Orphanides* 1198 (E); Insula Syro, *Orphanides* 1102 (E). ITALY: Sicily, Caltanissetta, 10km W Gela, Manfria, s.l., *Davis* 63222 (E); Sallipoli, ann. 1883, *Groves* s.n. (E). PORTUGAL: Douro Litoral: Leça da Palmeira, Boa Nova, *Malato-Beliz & Guerra* 13266 (ELVE). Beira Litoral: Ovar, beach of Furadouro, 10m, *Silva et al.* 4566 (LISE). Estremadura: Serra da Arrábida, beach of Creiro, 30m, *Pedro et al.* 177 (LISE). Alto Alentejo: Elvas, beside river Guadiana, 158m, *Beliz et al.* 351 (LISE). Algarve: Cape St Vicente, 50m, *Silva et al.* 661 (LISE). SPAIN: Sierra de Gredos, N El Arenal, 950m, *Deverall & Flannigan* 0102 (E). Cadiz: Barbate to Cabo Trafalgar, c. 20m, *Davis* 61624 (E).

ASIA. ISRAEL: Coastal Galilee, Akhziv, sea shore, 19 iii 1955, *Feinbrun* s.n. (HUJ); Jaffa, near s.l., *Dinsmore* 1484 (E). SYRIA: Caiffa, 1863-64, *Lowne* s.n. (E).

N. AFRICA (+ Canary Islands). ALGERIA: La Macta, near Mostagenem, 3 v 1936, *Faure* s.n. (E). LIBYA: Tripolitania, E Tagiura, *Sandwith* 2062 (K). MOROCCO: WS, El Jadida to Azemmour, *Davis* 9407 (E); SW, Essaouira (Mogador), 2m, *Davis* 48353 (E). TUNISIA: N: Ain Sebaa to Jebbara beach, *Davis* 57752 (E); Hammamet, s.l., *Davis* 70171 (E). CANARY ISLANDS; Tenerife, Barranco at Los Arulejos, *Dickson* 105 (E).

AUSTRALIA: New South Wales, Norwood, s.l., viii 1906, *Black* 3 (K); South Australia, Meningie, 1 vii 1953, *Robertson* 1 (K).

SOUTH AFRICA: S Cape: Riversdale, 60m, *Bohnen* 4531 (K); Cape Town, Malmesbury to Hopefield, *Fourie* 3318 (K).

COMMENTS ON SYNONYMS OF VAR. *DIANDRUS* AND VAR. *RIGIDUS*

B. gussonii Parl., Rar. Pl. Sic. 2: 8 (1840). Type : [Sicily] '*In collibus, ad sepes et in sylvaticis frequens occurrit*' (FIAF, photograph seen).

The general facies of the three Parlatore specimens from Sicily is certainly that of *B. diandrus*, but I have no information about the shape of the callus/scar.

B. hispanicus Rivas Ponce in Lagascalia 3: 53 (1973). Type: Spain, arenales del rio Tajo en Alconetar (Caceres), Rivas Goday 3335 (holo-MAF!) = *B. diandrus* s.l.

The description of *B. hispanicus* is based on a single specimen. According to its author it differs from B. rigidus by its slender awns, oval lodicules, glabrous sheaths and blades; and from *B. diandrus* by its acute callus and longer awns. However, the specimen described by Rivas Ponce comes well within the range of variation I have observed in these two taxa and should not be considered a separate species. As with many other specimens I have observed, the type of *B. hispanicus* is so much intermediate between *B. diandrus* and *B. rigidus* that I cannot assign it to either of these varieties.

Characteristic features/measurements of the type specimen:

Longest panicle branch of the first node of the panicle: 5.7cm

Shortest panicle branch of the first node of the panicle: 3.5cm
Callus/scar shape: strongly acute/elliptic
Lower glume length: 19mm
Upper glume length: 39mm
Lemma length: 28mm
Palea length: 14mm
Awn length: 9cm
Caryopsis length: 9mm (but immature)
Anther length: 4mm

B. maximus Desf., Fl. Atl. 1:95 (1798). Type: Gramen avenaceum paniculatum, locustis spadiceo-albidis. T. Cor. 39 - Vaill. Herb. (holo-P!) = *B. diandrus* var. *rigidus*.

Desfontaine's herbarium is at Paris (P). The label of the type specimen of *B. maximus* refers to '*ex Cretâ*' which is quite surprising because the species was published in Desfontaine's *Flora Atlantica*.

Characteristic features/measurements of the type specimen are:
Longest panicle branches of the 1st node of the panicle: 20mm
Shortest panicle branches of the 1st node of the panicle: 3mm
Callus/scar shape: strongly acute/elliptic
Lower glume length: 25–28mm
Upper glume length: 32–35mm
Lemma length: 26–29mm
Palea length: much shorter than lemma
Awn length: 64mm
Caryopsis length: 11–11.5mm
Anther length: 0.7mm

B. rigens L., Mant. Pl. 1: 33 (1767). Type: LINN 93/34 = *B. scoparius* L.

Although *B. rigens* has often been regarded as a synonym of *B. rigidus*, it is, in fact, a synonym of *B. scoparius* L. (sect. *Bromus*). Probably due to the similarity between the two epithets and their meaning, '*rigens*' was used, wrongly, to designate *rigidus*-like plants. As far as I could trace, this mistake was first made by Dumortier (1823) when he included both *B. rigidus* and *B. rigens* in sect. *Genea*.

B. villosus Forssk., Fl. Aegypt.-Arab. 23 (1775). Lectotype (selected here): Herb. Forsskalii no. 69 (C!) = *B. madritensis*.

B. villosus was first related to *B. rigidus* by Ascherson & Graebner (1901) who considered *B. rigidus* a variety of *B. villosus*. However, the four specimens of *villosus* from Forsskal's herbarium (C !) are, in fact, *B. madritensis*. The lectotype, here selected, is the most complete specimen and the only one that has a label by Ascherson identifying it as *B. villosus* Forssk. and *B. rigidus* is given as a synonym.

Characteristic features/measurements of the lectotype here selected are:
Longest panicle branch of the 1st node of the panicle: 18mm
Lower glume length: 6.5–7mm

Upper glume length: 10mm
Lemma length: 14mm
Palea length: shorter than lemma
Awn length: 20mm
Caryopsis length: 8–10mm
Callus/scar shape: rounded/rounded

MORPHOLOGY OF *B. STERILIS* AND *B. DIANDRUS*

The taxonomy of *B. sterilis* has been very straightforward. Its morphology is relatively clear-cut and its most distinctive characteristics are the broadly lax panicle and the long panicle branches bearing usually one single spikelet.

There is far more to say about the multiple morphologies associated with the names *B. diandrus* and *B. rigidus*. Botanists overlooked or neglected Roth's descriptions of both species and for a long time these names were not used. The same plants were later described by other botanists with different names; e.g. *B. maximus* Desf. (1798) [= *B. rigidus* Roth] and *B. gussonii* Parl. (1840) [= *B. diandrus* Roth]. These names, *maximus* and *gussonii*, were used at species level and lower ranks, but only rarely in recent times (e.g. *B. gussonei* in Pignatti, 1982). The name *B. villosus* (= *B. madritensis*) was used by Ascherson & Graebner (1901) to embrace all the variants between *B. diandrus* and *B. rigidus*. The same procedure was followed much later by Maire & Weiller (1955). Contemporary botanists usually recognize two separate species in this group, *B. diandrus* and *B. rigidus*. Ovadiahu-Yavin (1969) recognized them as two subspecies of *B. rigidus*, and Hitchcock et al. (1969) as two varieties of *B. rigidus*.

The characters most often included in recent keys to separate *B. diandrus* from *B. rigidus* are: 1) the panicle structure (lax and spreading or nodding in *diandrus*; dense and stiffy erect in *rigidus*); 2) the callus shape (rounded in *diandrus* ± as in the other species of the section; pointed in *rigidus*, a unique feature in the whole section) and 3) the scar shape (almost circular in *diandrus* ± as in the other species of the section; elliptic in *rigidus*, also a unique feature in the whole section). However, I have observed all variations from dense and stiffly erect panicles to lax and spreading ones. In both species the panicle nods at maturity because of the weight of the caryopsides although in *B. diandrus* the panicle branches droop much more obviously but probably just because they are much longer (this last character is often difficult to assess in herbarium specimens and accurate observations are only possible on living material); the callus/scar shape is also very variable. Although most plants with other *rigidus*-like features have a very pointed callus and a very elliptic scar, the *diandrus*-like morphology can have less typical rounded and circular callus/scar and may even have pointed and elliptic ones (e.g. the type specimen of *B. hispanicus*).

Cugnac (1931, 1932, 1934) favoured the theory that *B. diandrus* was a hybrid between *B. rigidus* and *B. sterilis*. In contrast, Fouillade (1933) believed that the polymorphism of *B. diandrus* is due to phenotypic plasticity, *B. diandrus* being more *rigidus*-like in difficult, arid conditions and more like *B. sterilis* in better ones. The question of hybrid origin has been kept open because the only way to conclusively prove it is to produce an artificial hybrid that is *diandrus*-like, but this has not yet been done. Recently, electrophoretic studies of some enzymes and the study of meiosis failed to prove hybrid origin of *B. diandrus*. Common isoforms of malato, alcohol, isocitrato, glutamate and glucose 6-phosphate dehydrogenase and leucine aminopeptidase were rarely found between *B. diandrus* and *B. sterilis* and *B. rigidus* (Esnault-Blanchard, 1981); and all the meiosis studies in *B. diandrus* were very regular (Esnault & Huon, 1985).

THE PRESENT ANALYSIS

The characters usually used to distinguish *B. rigidus*, *B. diandrus* (panicle branch length and callus/scar shape) and *B. sterilis* (size of spikelet parts) were re-assessed and other characters, such as the base of lemma including the callus/scar area, were analysed. Special attention was given to the probable methods of dispersal, and to related structures. Morphological variation was analysed in relation to geography and ecology and extensive herbarium material covering the whole range of native and introduced distribution was studied.

Detailed field observations on dispersal biology of *B. diandrus* and *B. rigidus* were carried out in Portugal.

Pairs of characters were analysed in 75 herbarium specimens to determine any possible correlation. These pairs were: scar length/lemma length; scar length/panicle branches length; scar length/anther length; anthers length/lemma length. This study revealed that for the pairs of characters analysed, any combination is possible and often character states of typical *B. diandrus* were combined with typical character states of *B. rigidus*.

The differences between vars *diandrus* and *rigidus* are so subtle that the identification of many specimens often cannot go any further than a mere *B. diandrus* s.l.

Notes on Particular Features

PANICLE SHAPE THROUGH THE PROCESS OF MATURATION

Two populations of *B. rigidus* and occasional plants of *B. diandrus* were measured for the angle that individual spikelets make with the ground. In the early stages of panicle development of var. *rigidus*, the spikelets are erect making an angle of 0° or nearly so with the vertical. Towards maturity, the whole plant bends and the panicle axis droops. Individual spikelets of the lower node of the panicle pass through an angle of 180°, being at the end of the life cycle almost vertically upside down, facing the ground at an angle of more than 45° with it. In cases where the panicle is very condensed and with very few nodes, as I have seen in herbarium specimens of *B. rigidus*, the panicles seem to remain erect. This could be due to the process of pressing but I believe that it can be genuinely so when the panicle is rather reduced. In *B. diandrus*, from the very beginning, the panicles are looser than in *B. rigidus* and eventually the spikelets face the ground vertically.

PANICLE BRANCH LENGTH

The length of panicle branches is a plastic character in *B. sterilis*. In poor water conditions, the length and number of branches, and as a consequence the number of spikelets, is much reduced.(I have observed during a phenotypic plasticity experiment, unpublished, that *B. sterilis* growing in dry conditions often has only a single spikelet).

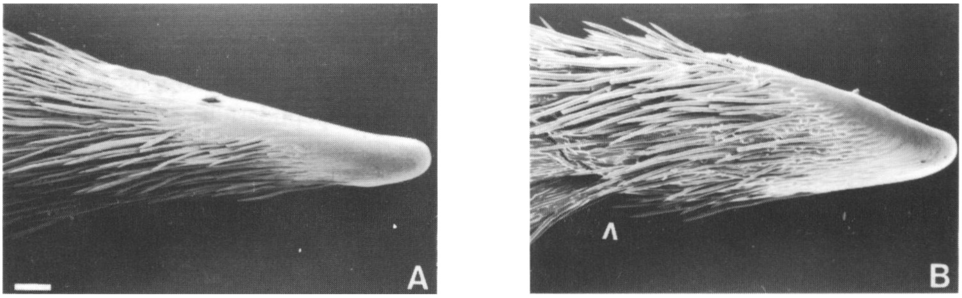


FIG. 1. Base of second floret in side view. A, *B. diandrus* var. *rigidus* where the articulation is absent; B, *B. diandrus* var. *diandrus* showing a constrictoin. Scale bar = 100µm.

However, short branches cannot be a mere reduction induced by the environment in *B. diandrus* s.l. In fact, the increased branch length in var. *rigidus* growing in non-restricted water conditions was not significant. Furthermore, in the survey of the herbarium specimens, I found that long panicle branches are more strongly associated with features of var. *diandrus* (more rounded callus/scar, longer anthers and base of lemma with a constriction at the callus/scar area - see following heading); but short panicle branches are linked both with the typical var. *rigidus* morphology and to a greater extent with var. *diandrus*. Because it is often difficult to judge whether reduction is induced by the environment or not the relevance of this character on its own is very limited.

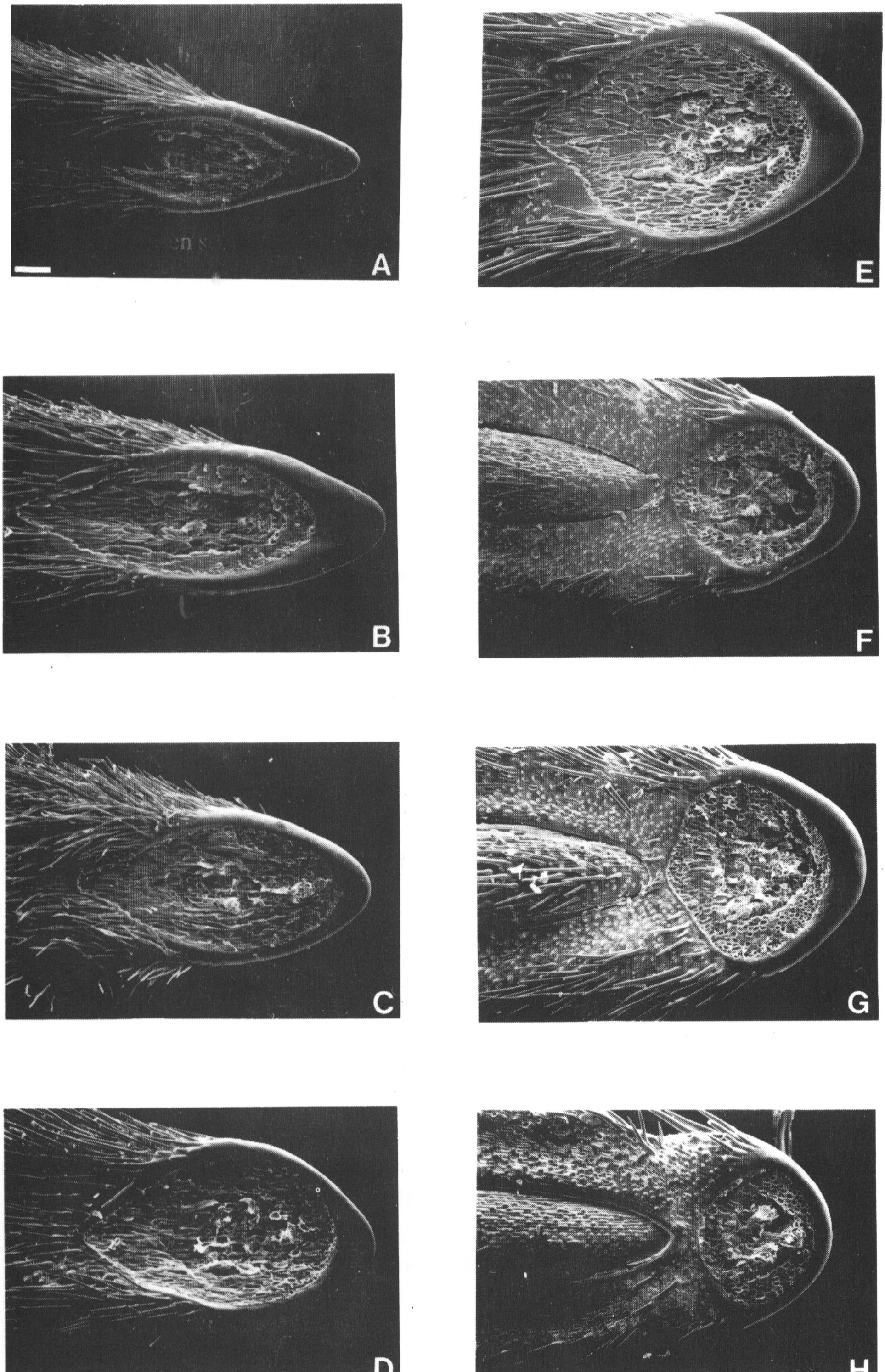
CALLUS AND SCAR SHAPE

There is a great variability of callus and scar shape in this group and there is no clear delimitation between the so-called elliptic morphology usually associated with *B. rigidus* and the ovate one associated with *B. diandrus*. I also found that there is no clear distinction between the ovate shape in *B. diandrus* and the round shape of the callus/scar in *B. sterilis*. The intermediate morphologies between *B. rigidus*, *B. diandrus* and *B. sterilis* are strikingly illustrated in Fig. 2. In spite of this continuous variation, it is still possible to a degree, to relate the elliptic/pointed, the ovate/round and the circular/round callus/scar to respectively *B. rigidus*, *B. diandrus* and *B. sterilis*. However, this character, as well as branch length, cannot be used alone to distinguish the three taxa.

FLORET BASE SHAPE

In sect. *Genea* (as in many other *Bromus* species) the florets ± diverge from the rachilla axis towards maturity due to movements centred on a point of articulation at the base of the lemma, as shown as a constriction in *B. diandrus* var. *diandrus* (Fig. 1B). Towards maturity the angle between the scar (rachilla axis) and the lemma at this articulation region widens so that the whole lemma is separated from the rachilla axis. Apart from this, in some cases the curving of the rachilla segments themselves results in an extra

Opposite. FIG. 2. Scanning electron micrographs of the base of the second floret (callus/scar area) illustrating the continuous range of callus shape from pointed to rounded and scar from narrowly ovate to transversely obovate. A & B, *B. diandrus* var. *rigidus*, callus/scar very pointed /narrowly ovate; C & D, *B. diandrus* s.l.; E, *B. diandrus* var. *diandrus*, callus/scar pointed/angulate obovate; F, G & H, *B. sterilis*, callus/scar round/transversely obovate. Scale bars = 100µm. Shape terminology according to the Systematics Association Committee for descriptive biological terminology in *Taxon* 11: 145–156, 245–247 (1962).


A
E
B
F
C
G
D
H

widening of the whole structure. In contrast, a callus/scar elliptic/pointed as in var. *rigidus* is always associated with lemmas without the previously mentioned articulation area (Fig. 1A). For this reason, the florets remain condensed, which is further emphasized by the rachilla segments remaining straight.

The existence of numerous intermediates and an incomplete, unclear ecological or geographical separation, have accounted for the varietal rank I have given to *diandrus* and *rigidus*. I consider that the differences between both varieties are significant, but not yet distinct enough for a higher taxonomic rank. In the fulness of time and with unchanged selection pressures, these minor taxa may further diverge, eventually meriting higher status.

The most distinctive *rigidus* morphology is comparable to nothing else in the section, but the most typical *diandrus* resembles *B. sterilis* in panicle structure. As a consequence, *diandrus* has been regarded as intermediate between the other two, sometimes more *rigidus*-like, other times more *sterilis*-like.

There has to be some speculation on how to explain *diandrus* origin. Phenotypic plasticity (Fouillade, 1933) might explain some aspects of the variability of the panicle structure, e.g. number of panicle branches. However, as I have observed, callus/scar shape is not affected by the environment, nor is spikelet structure. The chromosome number fits well with Cugnac's theory of hybrid origin: *B. sterilis* (2n=28) x *B. rigidus* (2n=42) = *B. diandrus* (2n=56)! Alternatively, the chromosome numbers could have a different explanation: *rigidus* could have evolved from *diandrus* at a time that this was a tetraploid and since then *diandrus* ploidy has increased. The lack of evidence so far that *B. diandrus* var. *diandrus* has a hybrid origin strengthens my belief that the intermediate position of this taxon is due instead to: 1) real closeness to *B. sterilis*; 2) recent evolution and incomplete separation of *B. diandrus* var. *rigidus* which is evolving from var. *diandrus*.

2. *BROMUS MADRITENSIS*, *B. RUBENS*, *B. HAUSSKNECHTII* AND *B. FASCICULATUS*

These taxa have small lemmas and erect, contracted panicles, but the existing great morphological variation makes it difficult to define precisely the boundaries of the constituent members. *B. madritensis* occupies a rather intermediate position between this group and that of *B. sterilis* especially because its panicle contraction and branch length is very variable. The number of taxa thus far recognized in this group is very considerable.

The species of this group are mainly Mediterranean, with some extensions into SW Asia. The most lax-panicled forms of *B. madritensis* colonize some areas in central and atlantic Europe, but only *B. rubens* is naturalized in large areas of the New World. *B. fasciculatus* and *B. hausskneehtii* have the most restricted distribution, being mainly confined to the E Mediterranean and more western parts of SW Asia.

It is worth mentioning that there are relatively few collections of *B. fasciculatus*, although there are references to well-established and numerous populations.

B. MADRITENSIS, B. HAUSSKNECHTII AND B. RUBENS

B. madritensis is a highly polymorphic species, sometimes with longer panicle branches and looser panicles, but quite often with more *rubens*-like condensed panicles. The great number of imprecise subspecific taxa that have been or are recognized within *B. madritensis* and *B. rubens* mirrors the difficulties that botanists have had in understanding both their morphological variability and their similarities.

B. madritensis and *B. rubens* have traditionally been separated as independent species on the basis of panicle shape, branch length and division, spikelet length, and lemma length and width. However, the character states of these characters often overlap and some are plastic (Esnault, 1984; and personal observations during a phenotypic plasticity experiment). They are, therefore, not precise enough to clearly separate the taxa.

An intensive overall taxonomic revision is much needed to assess the value of: 1) the traditional characters and the recent assessment of them (*B. madritensis*; Esnault, 1984); 2) newly proposed characters, such as panicle structure (Rivas Ponce, 1988); 3) weighting of certain morphological aspects (such as the structure of sterile florets, Scholz, 1981) that are related to the dispersal biology.

More detailed investigations of these very problematic taxa is required before more conclusive taxonomic decisions can be reached, but my provisional conclusions are that all the material is of one species. If *B. madritensis* and *B. rubens* have to be combined, it appears that the epithet to be adopted is *B. madritensis*. It should be noted that both species were described by Linnaeus in *Cent. Pl.* I (1755) and were first combined as *B. madritensis* subsp. *rubens* (L.) Husnot (1899).

At the boundary between *B. madritensis* and *B. rubens* there are taxa that have been named *B. madritensis* subsp. *kunkelii* H. Scholz (*Willdenowia* 11: 249-258, 1981) and *B. haussknechtii* Boiss. (*Fl. Orient.* 5: 648, 1884). I have studied the type specimens of these four taxa and my observations are summarized in Table 1. *B. flabellatus* Boiss. is another taxon within this group; I have not studied its type specimen ('prope Hierosolymam', Jerusalem), but from its description it also seems to be intermediate between *B. madritensis* and *rubens*.

B. fasciculatus C. Presl, Cyper. Gramin. Sicul. 38 (1820).

Syn: *Anisantha fasciculata* (C. Presl) Nevski in Acta Univ. Asia Med. Ser. 8b (Bot.) 17: 21 (1934); *B. rubens* L. subsp. *fasciculatus* (C. Presl) Trabut in Batt. & Trab., Fl. Alger. Mon. 226 (1895). Type: Sicily; 'in arvis arenosis, Panormi in planitie della Cunzulazione' (PRC). Lectotype selected here - see below.

B. madritensis L. var. *delilei* Boiss., Fl. Orient. 5: 649 (1884). *B. fasciculatus* C. Presl subsp. *delilei* (Boiss.) H. Scholz in Willdenowia 6: 291 (1971).). Type: see note below.

B. fasciculatus C. Presl var. *alexandrinus* Thell. in Repert. Spec. Nov. Regni Veg. 5: 161 (1908).

B. fasciculatus C. Presl var. *fallax* Maire in Bull. Soc. Hist. Nat. Afr. Nord. 33: 97 (1942).

TABLE 1. Diagnostic features of the type specimens of *B. madritensis*, *B. madritensis* subsp. *kunkelii*, *B. haussknechtii* and *B. rubens*, based on observations in this study.

			B. madritensis	*B. madritensis* subsp. *kunkelii*	*B. haussknechtii*	*B. rubens*
Culm pubescence			glabrous	hairy below panicle	–	hairy below panicle
Panicle length including awns (cm)			13	6.5–8.5	7.5	7.5
First panicle internode (cm)			1.7	–	1.4	1.3
Panicle branches (longest of lower node)	Posture		loosely erect	erect	erect	erect
	Length	Longer	19	8	2.2	0.9
		Shorter	–	2	0.35	–
	Division		1	2	2	2(1)
	Pubescence		glabrous	hairy	–	many short hairs
Spikelet size (mm)			5–5.4 (including awns)	2.3–2.9	–	3.7–3.9 (including awns)
No. florets	Fertile		–	5	–	–
	Sterile		–	6	–	–
Lower glume (mm)			9	9	5.3	8
Upper glume (mm)			14	11.2	8.5	11
Lemma (mm)			17	18	10.3	15
Awn (mm)			2–2.1	13.5	10.4	19–20
Palea (mm)				14	8.2	
Anthers (mm)				0.7	0.6	
Caryopsides (mm)			–	–	8	10

Icon: Bor, N.L. in Fl. Iraq, ed. Townsend et al. 9: 145, pl. 49 (1968). Täckholm, V., Students' Fl. Egypt, ed. 2, pl. 251A (1974). Plitman, U. et al., Pictorial Fl. Israel, p. 345 (1983).

Annual, 7–30cm tall, with tufted, sometimes solitary, slender culms, usually geniculate at base, glabrous, puberulous below the panicle or with very short hairs. Basal leaf sheath with short, retrorse or retrorse-patent hairs or longer woolly hairs, occasionally glabrous throughout; ligule fringed, acute or round at base. *Leaf* blade acuminate, 2–8 x 1–1.8cm with short or longer hairs ± equally dense on both surfaces. *Panicle* flabellate, at least at maturity, markedly cuneate at the base, stiffly erect, usually condensed (in very dwarf plants reduced to (1–)2 spikelets), 3–7.5cm long including the awns, up to 3.5cm from the lower to the top node. Panicle branches simple or with ramifications, very short. Panicle axis and branches glabrous or hispidulous. *Spikelets* lanceolate at earlier stages when glumes and lemmas are strongly imbricate, soon broadening and becoming flabellate, 20–30mm long excluding awns, up to 8mm wide, cuneate at base, compressed, with florets well-separated at maturity. *Florets* (6–)10–15 per spikelet with 2–3 uppermost ones sterile. *Glumes* and lemmas narrowly lanceolate, dark purple at maturity with a hyaline margin, variously hairy, sometimes ciliate at margins, more rarely glabrous; lower glume 1-veined, 6.7–8 x 0.6–0.9mm, upper glume 3-veined, 10.8–12 x 1.4–1.6mm. *Lemmas* 7-veined, 11–16 x 1.3–1.8mm, 2-toothed, margins usually overlapping at maturity. *Awn* straight only when very young, soon curving both outwards and upwards, twisted, inserted 1.5–3.5mm below lemma apex, as long as or a little longer than lemma; awn of second floret 14–18mm long. *Palea* a little shorter than lemma, 9.5–13mm long, glabrous on adaxial surface; abaxial surface glabrous or hairy. *Stamens* 3; anthers 0.3–0.5mm long. *Caryopsides* needle-like, curved outwards, ± twisted, often inrolled, 7–12.7 x 0.25–0.5mm. The combined twist of caryopsides and awns often gives an overall twist to the whole spikelet. Callus of rachilla segments round or oval.

B. fasciculatus differs from *B. rubens* by the generally flabellate panicle and flabellate mature spikelets, narrow glumes and lemma, recurved awns, out-curved and often twisted grain and the straight rachilla segments of the top sterile florets.

The type material of *B. fasciculatus* is a mixed gathering of several specimens of *B. fasciculatus* and another grass, probably a *Vulpia*. Although the name *Festuca scoparia* occurs on the label, the description on the label is remarkably similar to Presl's later protologue of *B. fasciculatus* (1820).

Diagnostic features of the lectotype based on my own observations are:

Habit: tufted and solitary plants, geniculate at base
Height: 6–16cm
Leaf sheath hairiness: short, retrorse and woolly hairs
Panicle shape: flabellate, strongly cuneate at base, stiffly erect, dense; some panicles with only 2 spikelets
Panicle length: 3–5cm; axis length up to 2cm from the lowest to the top node
Spikelet shape when young: lanceolate, glumes and lemmas imbricated
Spikelet shape when mature: flabellate, cuneate at base, compressed, florets well-separated at maturity

Lower glume size: 7–7.5 x 0.8mm
Upper glume size: 8.6–10.2 x 1–1.4mm
Lemma size: 13.5–14.5 x 1.2mm
Lemma hairiness: glabrous or with very short hairs
Awn posture: curved outwards and upwards, twisted
Awn insertion: 3–3.5mm below lemma apex
Anther length: 0.4mm
Caryopsides shape: needle-like, curved outwards and twisted, inrolled
Caryopsides size: 10 x 0.4mm
Callus shape: ovate

Habitats. Europe-Mediterranean area: dry places in general; maritime sands, calcareous soil and grassy areas, sometimes along roads. N Africa and SW Asia: along the coast, in wadis, dry steppe and desert; in maritime and desert sands, rocky places, sandy loam, limestone, calcareous, gravelly clay soil, granite, basalt and andesite (in Saudi Arabia), in limestone maquis with *Juniperus phoenicea* and *Pistacia lentiscus* in Libya; sometimes in classical ruins; very common in some localities in Cyprus, Israel, Saudi Arabia (Taif Mountains) and Iraq. From 5–1220m, up to 2133m in Saudi Arabia and to 380m in the Dead Sea area.
Selection of material studied:

EUROPE. GREECE: Crete, Akrotiri, Korakies hills, 200m, *Rechinger* 13293 (BM); Kos, Kos town, *Brenan* 11175 (K); Rhodos, *Rechinger* 8373 (K). ITALY: Erauria: Isle of Pianosa, 5–30m, *Sommier* 1220 (K); Sicily: Syraceuse, *Bucknall & White* 506 (E). MALTA: sine loc., *Wright* 681 (K). SARDINIA: Antioco, iv 1828-9, *Muler* s.n. (K); Torre delle Stelle, 30 vi 1981, *Hygur* s.n. (O).

N AFRICA. ALGERIA: Oran, Djebel-Santo, *Balansa* 298 (E). EGYPT: Gebel Atagga, 600–800m, *Davis* 6592B (E); Wadi el Arish, *Simpson* 2565 (K); Mariut: Abu Sir, *Davis* 6498B (K). LIBYA: Benghasi prov., 30km S Agedabia, *Simpson* 39079 (K); 5km W Baiadas, 300–350m, *Davis* 49954 (K).

ASIA (+ CYPRUS). CYPRUS: Lacovounera forest, 183m, *Chapman* 358 (K). IRAQ: DWD: Jabal Ana, 100–150m, *Khayat & Hamal* 51745 (K); DSD: 12km ESE of Salman, 240m, *Guest et al.* 18848 (K); FUJ: Jebel Makkul near Ajn dibbs, 250m, *Gillett & Rawi* 7208 (K). ISRAEL: 54km N Eilat, Arava Valley, 13 iii 1951, *Orshan & Zohary* s.n. (HUJ); near Ballut: 35°E 32°N, 26 iv 1919, *Ogilvie* s.n. (K). JORDAN: Transjordan: Wadi Ram, 914m, *Davis* 9007 (K); Azraq Druze, *Townsend* 65/318 (K). LEBANON: Beirut, *Herb. Post.* 163 (K). OMAN: 45km SW Muscat: Jebel Aswad, 1371m, *Munton* 16 (K). SAUDIA ARABIA: Jiddah-Taif road, 1066m, *Collenette* 3983 (K); 85km SW Tabuk: Jabal Dabbagh, 1371m, *Collenette* 4396 (K); 80km SW Madinah: Jabal Warjan, 2133m, *Collenette* 5225 (K); Taif Highlands, 21°10'N 40°20'E, 2133m, *Fitzgerald* 17060/4 (K). SYRIA: Damascus, *Pastuchov* 730 (LE); Palmyra, 435m, *Samuelsson* 3514 (K). TURKEY: C3, Antalya Konya Alti, 10m, *Tengwall* 436 (K).

MORPHOLOGY OF *B. FASCICULATUS*

The name *B. fasciculatus* was published in 1820 by Presl based on a specimen from Sicily. It is of historical interest in that it seems there was an earlier recognition of this taxon by Delile, but a description of it was not published. The herbarium at Edinburgh (E) holds several presumed Delile specimens collected by himself or else gathered by his co-collectors in 1801 (when he was with Napoleon's army in Egypt) . These specimens can be easily recognized because of the characteristic handwriting on the labels. One of these specimens at Edinburgh is clearly *B. fasciculatus*, but its label is: '*Bromus hexastachyos* Del. Catal. [possibly a manuscript catalogue housed at Paris (P) or Montpellier (MPU), - pers. inf. I.C. Hedge] n[ou]velle Éspèce, Egypte'. The name *B. hexastachyos* was never validly published, nor does it occur as a nomen in Delile's Flora of Egypt, where the only relevant *Bromus* listed and illustrated is *B. fasciculatus* (*Fl. Aegypt. Illustr.* pl. 11, fig. 2, 1813), but named as *B. rubens*. Later, Boissier (*Fl. Orient.* 5: 650, 1884) cites *B. rubens* sensu Delile as a synonym of *B. fasciculatus*. It seems that initially Delile thought that the dwarf grass, with geniculate and tufted culms, flabellate panicles and curved awns he found in Egypt was a new species but later, recognizing some similarities between this plant and *B. rubens*, gave up his first idea and determined '*B. hexastachyos*' as *B. rubens*.

The similarities between *B. fasciculatus* and *B. rubens* have been taxonomically recognized as, for example, in the combination *B. rubens* L. subsp. *fasciculatus* (Presl) Trabut. Because of its dwarf appearance *B. fasciculatus* has also been placed with depauperate forms of *B. madritensis/haussknechtii* (*B. madritensis* L. var. *delilei* Boiss.). But most often *B. fasciculatus* has been recognized as a separate species.

Two taxa are often recognized within *B. fasciculatus*. They are *B. fasciculatus* var. *alexandrinus* Thell. (1908), based on a well-developed indumentum; and *B. fasciculatus* subsp. *delilei* (Boiss.) H. Scholz, a name whose application is decidedly confusing.

The type locality of *B. madritensis* var. *delilei* Boiss. is '*Egypto circa Alexandrian*, Delile' and Boissier cites as second localities - '*in deserto Aegyptiaco-Arabico variis locis*, Schweinfurth 28! 130! 253! et 456!' plus a reference to '*B. rubens* Desf., Ill. p.164, t.11, fig.2'. There is, however, no illustration of *B. rubens* in any of Desfontaine's publications and Boissier was almost certainly referring to Delile's *Fl. Aegypt. Illustr.* pl. 11, fig. 2, 1813. There are only the Schweinfurth specimens in Boissier's herbarium (G-BOISS!)and the Delile specimen is apparently not in the Delile's herbarium at Paris (P) nor at Geneva. Recently, Scholz (1971) designated as the lectotype of *B. madritensis* var. *delilei*, unwisely in my opinion, one of the Schweinfurth specimens cited as secondary collections by Boissier (*Schweinf.* 456). In fact, apart from being cited as second place, the Schweinfurth specimens cited by Boissier are mixed gatherings: *Schweinf.* 456, the lectotype chosen by Scholz, is *B. fasciculatus*; *Schweinf.* 28 is *B. haussknechtii* also described by Boissier (*Fl. Orient.* 5: 648, 1884) as a new species from Baghdad, related to *B. madritensis*; *Schweinf.* 130 and 253 are mixtures of both *fasciculatus* and *haussknechtii*. Furthermore, the description of *B. madritensis* var. *delilei* is not precise and fits both *B. fasciculatus* and *B. haussknechtii* specimens. In the absence of Delile's Egypt-Alexandria specimen (maybe at Montpellier, MPU) that might clarify Boissier's concept of var. *delilei*, it is unwise to lectotypify it with a *B. fasciculatus* specimen. The type of *B. haussknechtii* at Geneva (G!) is a taller, more robust plant than the *B. haussknechtii* specimens included in var. *delilei* and this may be the reason why the two plants were placed separately.

I suspect that since Boissier's time nobody has studied the Montpellier type specimen of *B. madritensis* var. *delilei*. Nevertheless, this taxon has been included in *B. madriten-*

sis at subspecific level (Maire, 1955; Ovadiahu-Yavin, 1969) and more recently considered as a synonym of, or a taxon within, *B. fasciculatus* (e.g. Bor, 1968; Scholz, 1987).

Lately, Scholz (1971, 1987) recognized two subspecies in *B. fasciculatus* and drew attention to a new character: the shape of the callus/scar and pointed out its connection with geographical distribution and hairiness.

THE PRESENT ANALYSIS

The present analysis is based on the macro-morphological observations of 100 specimens covering the whole range of distribution.

B. fasciculatus has a quite uniform morphology and its variation is mainly that of the number and length of culms per tuft and number of spikelets per panicle. These variations are most probably related to environmental conditions. There is also great variation in the degree of pubescence and some variation in the shape of the callus/scar on the rachilla segments.

Notes on Particular Features

PUBESCENCE

The infraspecific classification of *B. fasciculatus* has been almost entirely based on the different degrees of pubescence. Pubescence on glumes and lemmas has been most often used (Maire, 1955; Bor, 1968; Ovadiahu-Yavin, 1969; Feinbrun-Dothan, 1986): glabrous versus pubescent; pubescent with or without cilia on margins. However, I have found great variation both in the type and degree of pubescence on the whole plant making it quite impossible to establish a clear distinction between the different types described. Other combinations are:

glabrous, but with cilia at margins;
different degrees of density of hair coverage including cilia;
different degrees of the length of hairs including cilia.

Scholz (1987), using the characters of the pubescence of the lower leaf sheaths together with the shape of the callus/scar on rachilla segments and geography, divided *B. fasciculatus* into two subspecies: the type subspecies with leaf sheaths densely villous and callus/scar pointed/ovate, from the Mediterranean area; and subsp. *delilei* with dense to sparse, short hairs and callus/scar round, from the W Irano-Turanian region. However, I found different degrees of pubescence in both geographical areas and even in different plants of the type specimen of *B. fasciculatus*. The variation is continuous throughout the total range, from totally glabrous to an indumentum of numerous long hairs giving a woolly cover. There is, therefore, strong evidence to consider the pubescence of leaf sheaths of no taxonomic importance.

CALLUS/SCAR SHAPE

My observations have confirmed the existence of two different forms of the callus/scar and also some geographic connection with them. However, these differences are not as distinct as Scholz's illustrations imply (1987), neither is the geographical separation between them as clear-cut as he describes. It is true that the more eastern plants have a round callus/scar (Figs 3 & 4A) and the western ones have an oval one (Figs 3 & 4C). But in the E Mediterranean both forms co-exist (Fig. 3) with dominance of the oval type.

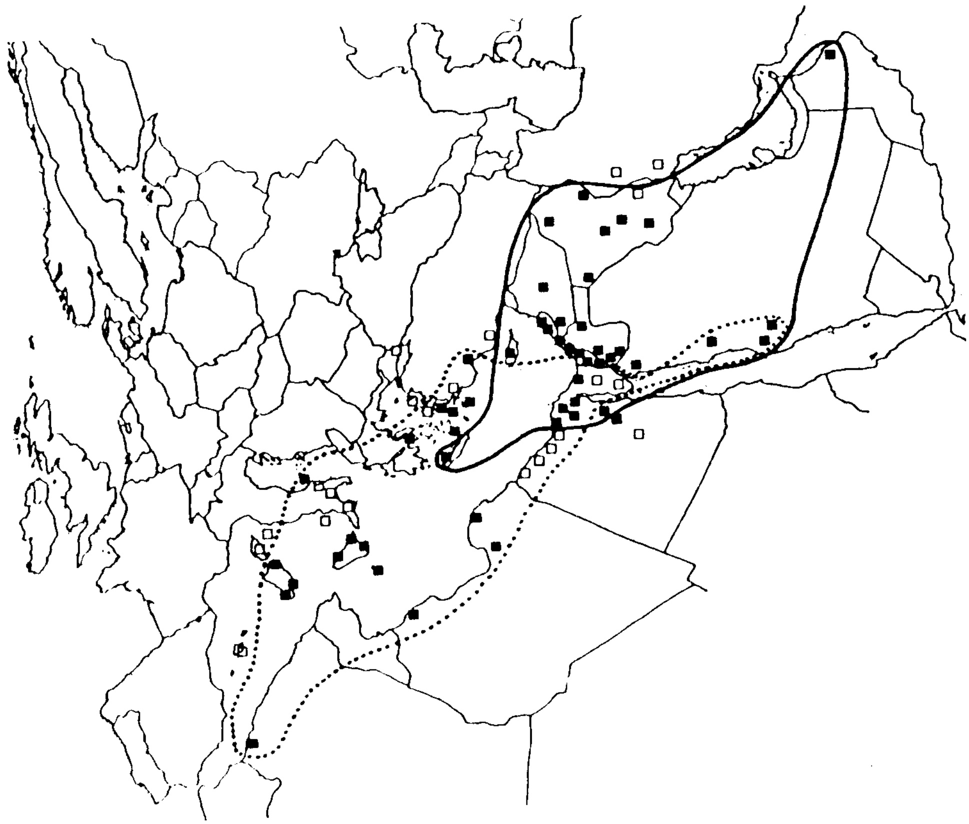


FIG. 3. Distribution of *B. fasciculatus*. Often each square represents more than one gathering. E Mediterranean is the area where both callus/scar forms exist and where populations are particularly abundant. ■ specimens studied by the author; □ reliable literature records; ? doubtful records; ..... general distribution of specimens with callus/scar ovate; — general distribution of specimens with callus/scar round.

Further, the type specimen of *B. fasciculatus* and some specimens from Cyprus, Libya and the southwest of the Arabian Peninsula are of intermediate morphology (Fig. 4B) [Greece: Kos, Kos town, *Brenan* 11175 (K); Cyprus: Lakkovaunera forest, *Meiton* 962 (K); Libya: 5km W Baiadas, *Davis* 49954 (K); Jordan, Jebel el'Uweinid, W Azraq, *Townsend* 65/177 (K); Saudi Arabia: Jabal Warjan, 80km SW Madinah, *Collenette* 5225 (K)]. Very rarely the callus is also elliptic (Fig. 4D) [Libya: 30km S Agedabia, *Simpson* 39079 (K); Egypt: Sinai, iii 1929, *Meinertzhagen* s.n. (K); Israel: Shehumat-Borochov, 14 iii 1933, *Naftolsky* s.n. (K)].

Despite the geographical connection, the taxonomic significance of the callus/scar shape in *B. fasciculatus* is in no way comparable to the significance of the same character in *B. diandrus/rigidus*. In *diandrus/rigidus* the extreme forms, pointed and oval, are indeed very distinct and easily recognizable.

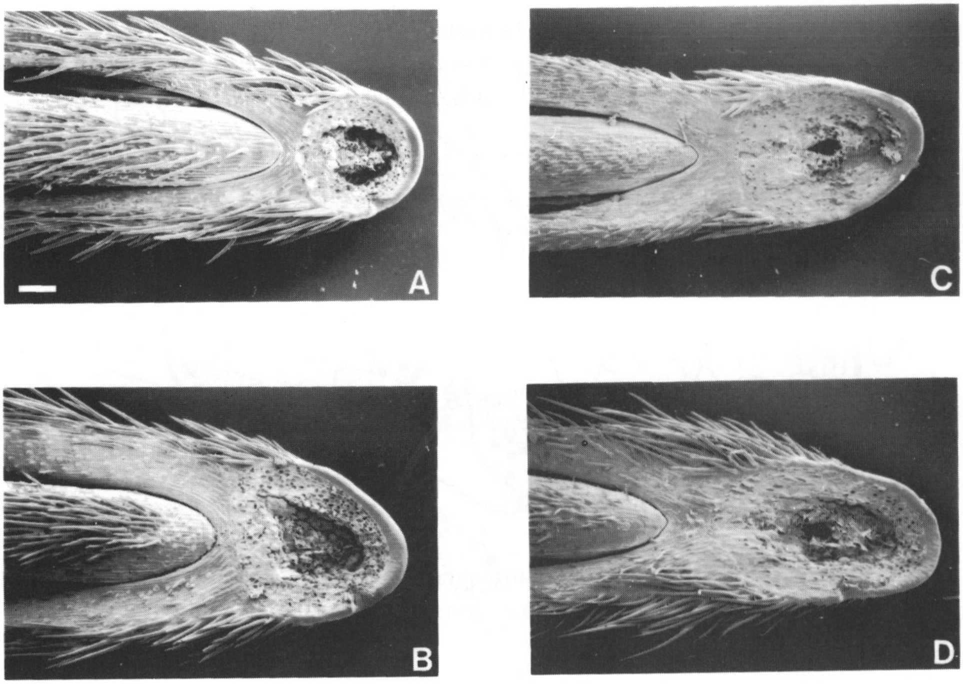


FIG. 4. Scanning electron micrographs of the base of the second floret (callus/scar area) in *B. fasciculatus*. A, E Mediterranean specimen, callus/scar transversely broadly obovate; B, E Mediterranean specimen, callus/scar less transversely broadly obovate; C, W Mediterranean (type specimen from Sicily) callus/scar broadly obovate; D, E Meditteraneanspecimen, callus/scar narrowly obovate. Shape terminology according to the Systematic Association Committee for descriptive biological terminology(see Fig. 2).

3. *B. TECTORUM / LUCIDUS* COMPLEX

The two species, *B. tectorum* L. described from Europe, and *B.'sericeus'* Drobov described from C Asia, were previously discussed in some detail and combined at subspecific level (Sales, 1991b): *B. tectorum* L. subsp. *tectorum* and subsp. *lucidus* Sales. Here only their formal taxonomy is presented.

B. tectorum L., Sp. Pl. 77 (1753).

Annual, 6–90cm tall, with solitary or loosely tufted, ascending to erect, slender culms, often minutely pubescent below the nodes and always so just below the panicle. Leaf sheath softly villous to pilose with retrorse patent hairs, apically glabrous or minutely pubescent; occasionally glabrous throughout; ligule fringed, acute or rounded at base. *Leaf* blade acuminate, 1.5–15 x 0.2–0.4 (–9.5)cm with short or long hairs, denser on the adaxial surface, very often with longer hairs along the margin continuing along the margin of the sheath near the ligule. *Panicle* condensed and ascending when young, soon becoming lax, nodding and clearly unilateral, deltoid or oblong in outline, 1–15cm long from the lowest to the uppermost node. Panicle branches slender, tortuous. Panicle axis and branches slightly to densely pubescent with short or long hairs. Branches longer to shorter than spikelets, with up to 5 ramifications, 0.6–8cm long. *Spikelets* 1–14 per branch, cuneate, broadening and shortening at maturity when the rachilla segments curve. *Florets* 5–17 per spikelet of which only 1–3 are fertile. *Glumes* and lemma pale-green, often tinged with purple, with a broad hyaline margin giving a silvery/shiny appearance to the spikelets, usually with small scattered or dense longer hairs, more rarely glabrous. Lower glume narrowly lanceolate, 1–3-veined, 5.7 x 1mm to 10.6 x 1.8mm; upper glume lanceolate, 3–7-veined, 8 x 1.6mm to 13.5 x 2.2mm. *Lemmas* of fertile florets 7-veined, 6.5–24mm long, 2-toothed at apex; lemma size and vein number decreasing considerably towards the top sterile, narrow-lanceolate, 1-veined florets. *Awn* straight, very rarely slightly curved, slender, often with a single twist, inserted 2.5–6mm below the lemma apex; awn length varying on individual spikelets: their apices either all clearly at the same level or else somewhat irregular with the lowermost always much below the others. Awn of second floret 10–26mm long. *Palea* 6.8–14mm, shorter than lemma, glabrous on adaxial surface; abaxial surface glabrous or hairy with shorter or longer hairs, these sometimes present only between the veins and the margins; long, spreading hairs along the two veins, longer near apex. *Stamens* 3; anthers 0.5–1.3mm long. *Caryopsides* usually straight, sometimes slightly curved outwards, usually c. 0.2mm shorter than palea, sometimes as long, or c. 0.3mm longer. Callus of rachilla segments differentiated only below the upper sterile florets.

This description combines the two morphological extremes that have previously been given independent specific status: *B. tectorum* L. and *B. 'sericeus'* Drobov and the many intermediates between them.

B. tectorum L. subsp. **tectorum**

Syn: *Zerna tectorum* (L.) Panz. in Denkschr. Königl. Akad. Wiss. München 1813: 297 (1814) [formal combination not made but clearly based on *Bromus tectorum* L.]. *Anisantha tectorum* (L.) Nevski in Acta Univ. Asia Med. ser. 8b (Bot.) 17: 20, 22 (1934); *Schedonorus tectorum* (L.) Fries in Bot. Not. 9: 131 (1843). Type: Europe. LINN 93/25! - (Smith, 1985: 500, designated this specimen as lectotype.

B. scabriflorus Opiz, Naturalientausch. 9: 119 (1825). Type: 'Bohemia', loc. illegible, *Opiz* [Herb. Cech. Mus. Nat. Prague, no. 495725c !].

Anisantha pontica K. Koch in Linnaea 21: 394 (1848). Type: Turkey, Çoruh, Ispir, *Koch* (B†).

Icon.: Sibthorp & Smith, Fl. Graeca 1: tab. 82 (1806); Hubbard, Grasses, ed. 3, 62 (1985).

Diagnostic features of the type specimen (LINN 93/25) based on my own observations are:

Leaf blade length: 9-11.5cm
Panicle length: 8.5-9.2cm
Longest panicle branch in the lowermost panicle node: 4.9cm
No. of nodes in the panicle branch above: 1 node with 2 branches
No. of spikelets in the panicle branch above: 3
Panicle branches pubescence: short erect hairs
Spikelet length: 3.5 cm

No. of florets per spikelet: 6
Glume shape: lanceolate
Vein no. on lower glume: 1
Vein no. on upper glume: 3
2nd lemma length: 13mm
Top of spikelet including awns: irregular
Anther length: 0.7mm
Callus on rachilla at the base of each fertile plant: fully developed.

Habitats. From sea level up to 4000m; on chalk, gypsum, limestone, clay igneous, volcanic ash, basalt, sandy or rocky soil; in semi-desert wadis, steppe, open woods or among shrubs in isolated areas or plantations, in very arid conditions but also irrigated fields, hill slopes, grasslands, meadows, roadsides, disturbed areas; in SW Asia often associated with *Juniperus polycarpos*, *Quercus aegilops*, *Q. coccifera*, *Amygdalus* sp., *Astragalus* sp., *Pistacia* sp. and *Populus*.
Selection of material examined:

EUROPE. AUSTRIA: Wien, near Nussdorf, 170m, *Keller* 5372 (E); Burgenland, near Neusiedl am See, *Jacobs* 5986 (BG). BELGIUM: Goé, 18 v 1908, *Mairlot* s.n. (O). BULGARIA: Turnovo, 14 v 1915, *Mruvicka* s.n. (SOM); Varna, 1896, *Javasott* s.n. (SOM); Sofia near Airport, 22 v 1977, *Vibodeevsky* s.n. (SOM). CORSICA: Propriano, *Webster* 14451 (E). CZECHOSLOVAKIA: Praha, 300m, *Rohlena & Domin* 712 (E). Brno, Cerná, c.250m, 23 v 1947, *Jedlicka* 1396 (E). DENMARK: Silkeborg, 9 vii 1883, *Holm* s.n. (O); Skanderborg, 7 vii 1971, *Lojtnant & Pedersen* 696 (O). FRANCE: Auvergne, Puy de Dome, viii 1840, *J. Ball* s.n. (E); Paris, *Jervett* s.n. (E); Nantes, 28 vi 1954, *Stormer* (O). GERMANY: Würzburg, c.180m, *Botanische Vereinigung Würzburg*. 391 (BG); Karlsrühe, c.117m, *Kneucker* 289 (O); Berlin, Potsdam, *J. Ball* s.n. (E); Hamburg, vii 1840, *Maly* s.n. (E-GL). GREECE: Psara Island, 10-100m, 22 iv 1973, *Greuter* 10978 (E); Porto hago, 22 iv 1965, *Coode & Jones* 42 (E). HUNGARY: Budapest, Scti Gerardi Hill, 120m, *Degen* 231 (E). IRELAND: Cork, 19 vi 1891, *Scully* 1837 (E). ITALY: Pedemonte, Val Tournanche near Busserailles, vii 1879, *J. Ball* (E); Verona, Venetia, near Rivoli, 160–190m, 2 vii 1897, *Herb. J. Landmark* s.n. (BG); Calabria, 43km N of Catanzaro, *Davis & Sutton* D.65321 (E). NORWAY: S: West-Agader, Kristiansand, Odderoya, Silokaia, *Tore Ourem* 38098 (O); SE: Oslo, *Hovda* 115 (O); SW: Bergen, 1908, *Holmboe* s.n. (O); N: Tromso, Tromsoya, Rundvannet/ Stakkevollan, 160m, 5 x 1982, *Elven* s.n. (O); N: Nordland, Sør-Trøndelag, Buvik, *Lyche* 32606 (O). PORTUGAL: N: Bragança, Lameiros, *Pereira Coutinho* 188 (LISU); N: Trás-os-Montes & Alto Douro, Mirandela, *Beliz & Ruivo* 800 (ELVE); C: Guarda, Torriäo, 500-1000m, *R. Fernandes & Sousa* 3265 (COI); S: Alto Alentejo, Portel Hills, road to Oriola, Abegoaria, c.400m, *Malato-Beliz et al.* 16607 (ELVE). ROMAINIA: Brasov, near 'Rétyi Nyir', 1911, *sine coll.* 352 (E). ROSSYA: Pskov, 18 v 1913, *Andreev* s.n. (E); Novgorod, 17 vii 1925, *Selivanova* s.n. (LE); Moskva, 30 vi 1967, *coll. illeg.* s.n. (LE). SICILY: Catania, N of Nicolosi, 2500m, *Davis & Sutton* D.64415 (E); Etna, v 1841, *J. Ball* s.n. (E). SPAIN: Sierra de Gredos, 950m, *Deverall & Flannigan* 0151 (E); Granada, Sierra Nevada, 3100m, *Chamberlain et al.* 258 (E); Cuenca: Sierra de Valdeminguete, 1600–1700m, *Brummitt et al.* 595 (E); Logrono/Soria: Sierra de la Urbion, 1700m, *Dresser* 627 (E). SWEDEN: Uppsala, *Hartman* 389 (O); Öland, 22 vi 1974, *Halvorsen* s.n. (O); Gotland, 26 vi 1926, *Asplund* 257 (O); Kristianstad, 10 vii 1912, *Tufvesson* s.n. (O). SWITZERLAND: Grimsel Alps, viii 1858, *Balfour* s.n. (E); Zermatt, viii 1905, *Brown* s.n. (E-GL); Basel, vi 1918, *Jermstad* s.n. (O). TURKEY: A2, Istanbul: Alibey Koyu, *Aveigoil* 5848 (E). UNITED KINGDOM: England, Suffolk, Thetford, 29 vi 1885, *Linton* 2797 (E). Wales, Aberdare, 1902, *Riddelsdell* 1837 (E). Scotland, Selkirk, 10 vi 1966, *Webster* 10571a (E); Edinburgh, Leith Docks, 20 vi 1883, *Christie* s.n. (E). UKRAINE: Kerson, *E. Pobedimova* 5109 (E); Kiev, Tarashcha, 30 vi 1916, *D. Litvinov* s.n. (E). YUGOSLAVIA: Sarajevo, 13 vii 1960, *Webster* 4031 (E).

N AFRICA (+ CANARY ISLANDS). ALGERIA: A1, Chréa, c.1500m, *Davis* 59132 (E); C1, Col de Telmet, W Batna, 1450m, *Davis* 52584 (E); H1, Tiaret to Aflou, 1100m, *Davis* 58588 (E). CANARY ISLANDS: Tenerife: El Portillo, 2030m, *Tore Ourem* 30637 (BG); Llano de Ucanca, 2250m, 11 iii 1960, *Johannes Lid* s.n. (O). Los Azulejos, 2230m, 29 iv 1957, *Johannes Lid* s.n. (O); B'co. Riachuelo, 2050m, 28 iv 1984, *C. Rodriguez* s.n. (E-GL). MOROCCO: MA, between Azrou and Timhadite, 1850m, *E. Paunero et al.* 1928-29 (E).

ASIA (+ CYPRUS). AFGHANISTAN: N: Baghlan: W-exposed slopes in dense *Juniperus polycarpos* stand, 2400m, *Freitag* 2707 (hb. Freitag); SW: Herat: mountain above Chesmeh Obeh, stony slopes, 2400m, *Hedge, Wendelbo & Ekberg, W.* 7853 (E); SE: Zabul: Kalat-i-Ghilzai, 15km SW, intensively grazed, dominated by dwarf *Amygdalus* semidesert, 1550m, *Freitag* 413 (hb. Freitag); E: Kapisa: Panjir-Tal, [2n=14], 2500m, *Podlech* 12811 (E); NE: Badakhshan: Anjuman Pass, 4050m, *Podlech* 12344 (E); C: Banian: Band-i-Amir, c.2800m, *Rechinger* 18400 (W). ARMENIA: Vedibassar Prov., prope Beink-Vedi, mont. Jlanln, *Schelkovnikov* 10128 (E); Erivan, Schugavit-Noragavit, *Araratian* 11627 (E). CHINA: Qinghai: Huang Yan Hsien (W from Xining), in vegetable garden, *Keng* 5477 (K); Gansu: Labrang, Kan-ping-ssu, near Xining, exposed steppe, *Keng* 5750 (K); Sichuan: between Batang and Iachienlu, ix–x 1904, *Hosie* s.n. (K). CYPRUS: Tripilos, 9 iv 1933, *Foggie* 164 (E); 1380m, 9 vi 1961, *Young* 7368 (E). EGYPT: *A. Kaiser* 783 (G); *Schimper* 175 (E-GL). IRAN: N: Azerbaijan: 47°50'E, 38°24'N, 2400m, *D. Walton* 98 (E); E of Arak, 1645m, *Archibald* 1732 (E); E: Shahrud-Bustam: Qaleh Bala, 1120m, *Rechinger* 50356 (W); C: Tehran: Tehran, taller plants from close to rock, shorter from open ground, c.1700m, *Lamond* 2783 (E); S: 42Km Kerman to Bam, 1900m, *Léonard* 6014 (BR). IRAQ: MRO: Shaqlawa, abundant, 1066m, *R. Haines* 727 (E). JORDAN: Gerash, 530m, *Meyer & Dinsmore* G747 (E); Petra, 970m, *J. Dinsmore* 6747 (E). PAKISTAN: W: Baluchistan: Ziarat, 2438m, *R.R. Stewart* 27935 (RAW); near Quetta, common desert annual near Quetta, *R. R. Stewart* 27934 (RAW); NW Himalaya: Chamba, Pangi, Hunan Mullah, c.3352m, 9 vii 1917, *R. R. Stewart* s.n. (RAW); Lahul, Kyelang, *Bor* 9220 (RAW); Kashmir: Astor Distr., Chillam, Gilgit road, 3048m, *R. R. Stewart* 18995 (RAW). SYRIA: Jabal Druze, N of Shahba, Tell Shihan, *Barkoudah* 1263 (E); Nebk, Mar Musa, *Davis* 5542 (E). TURKEY: A5, Yozgat, Cekerek, 1250m, *Dogan* 218 (E); B9, Bitlis, Bitlis, 1550m, *Davis* 43370 (E); C5, Nigde, Hasan Dag, 2300m, *Davis et al.* 18944 (E); C8, Mardin, Savur, 900m, *Davis & Hedge* D.28547 (E). TURKMENSAKA: Krasnowodsk, *Sintenis* 1585 (K); Kopet Dag mountains, 900m, *V. V. Nikitin et al.* s.n. (K). UZBEKSKAYA: c.70km W Buchara, 0m, *C. Townsend* 86/104 (K).

AMERICA. CANADA: Ontario, Niagara Falls, 11 vi 1891, *J. Macoun* s.n. (E); U.S.A.: California, Tejon Pass, 1200m, *Davis & Lightowlers* 67025 (E); Colorado: Paradox, Montrose Co., 1670m, *E. Walker* 170 (E); Idaho: Boise, c.800M, *J. Clark* 52 (E); Maryland: Columbia, *A. Ruth* 880 (E); Michigan: near Port Huron, 27 vi 1903, *C. Dodge* s.n. (E); Montana, 1066m, *Hamilton* 762 (E); Nevada: Nye Co., c.210m, *A. Heller* 9685 (E); N Carolina: Rowan County, *A. Radford* 44737 (E); Oregon: Klamath valley, *W. Cusick* 2844 (E).

AUSTRALIA: Canberra, A.C.T., Thredbo River, near Jindabyne, abundant as weed of disturbed and burnt areas near the river, *L. Adams* 1536 (K); Victoria: Melbourne, cow market, xi 1921, *O. Brien* s.n. (K).

NEW ZEALAND: South Island, Cromwell Gorge, *J. Hubbard* 253380 (K).

COMMENTS ON INFRA-SPECIFIC VARIATION

The most relevant varieties described within *B. tectorum* subsp. *tectorum* are:

var. *nudus* Klett & Richt., Fl. Leipz. 109 (1830) and var. glabratus Spenner, Fl. Friburg, 1: 152 (1825) – with glabrous spikelets, as in the Linnaean type specimen;

var. *hirsutus* Regel in Act. Hort. Petrop. 7: 600 (1880); var. *genuinus* Gren. & Godr., Fl. Fr. 3: 583 (1853); var. *pubescens* Schur., Enum. Pl. Transsilv. 805 (1866) – with pubescent spikelets; and var. *longipilus* (Kum. & Sendt.) Richt., Pl. Eur. 1: 114 (1890) – with very long hairs indeed;

var. *ponticus* (C. Koch) Ascherson & Graebner, Syn. Mitteleur. Fl. 2: 594 (1901) – with spikelets having only one fertile floret;

var. *grandiflorus* Hack. ex Fedtsch. in Bull. Jard. Bot. Pierre Grand 14, Suppl. 2: 89 (1915), nom. nud. – with very long spikelets.

In my opinion, varieties based on pubescence should not be recognized. Indumentum varies continuously from almost absent to dense with long hairs, and this pattern of variation occurs not only in the other *Genea* species as already mentioned, but in *Bromus* in general. Nor do I consider varieties based on the number of fertile florets as worth recognition, although I think it is possible that underlying this single-grained phenotype there is, at least sometimes, a real genotypic variation. The combination of this character with lush vegetative growth [e.g. in the type specimen of *B. scabriflorus* Opiz and in Afghanistan: N: Baghlan: N Salang, 2400m, *Freitag* 2707 (herb. Freitag!)] shows that at least sometimes the former is not a reduction due to phenotypic plasticity in less favourable environmental conditions. Also, some specimens of subsp. tectorum that grow in very poor conditions in SW Asia, often with subsp. *lucidus*, have 3 fertile florets.

The diagnostic features of the type specimen of *B. scabriflorus* based on my own observations are listed below:

Leaf blade length: 4.8–13cm
Panicle length: 11cm
Longest panicle branch in the lowermost panicle node: 6.8cm
No. of nodes in the panicle branch above: 3
No. of spikelets in the panicle branch above: 6
Panicle branches pubescence: many, very short hairs
Spikelet length: 1.4cm
No. of florets per spikelet: 7 (1–2 fertile)
Vein no. on lower glume: 1
Vein no. on upper glume: 3
2nd lemma length: 10.7–11.3mm
Outline of spikelet including awns: irregular
Anther length: 0.8mm
Callus on rachilla at the base of each fertile floret: fully developed
2nd awn length: 13–15.5mm
2nd palea length: 6.8–7.7mm

B. tectorum L. subsp. **lucidus** Sales in Fl. Veg. Mundi IX, 32 (1991). Type: as for *B. sericeus* Drobov.

Syn.: *B. sericeus* Drobov in Repert Spec. Nov. Regni Veg. 21: 39 (1925), non *B. sericeus* Tenore, Fl. Nap. Prod. 1(1): X (1811–15). Type: Syr Darya district, Tashkent, middle part of Keles basin, Kaplanbeck demarcated area. c.1500m, 4 v 1921, *Abolin* 7496 TAK!). Lectotype selected by Tsvelev, Grasses of Soviet Union 1: 326 (1984).

B. sericeus Drobov subsp. *fallax* H. Scholz in Willdenowia 19: 133 (1989), *nomen confusum* [the type specimen represents one of the many morphological variants between subsp. *lucidus* and the type subspecies]. Type: Sinai, auf Granitsand am Fusse des Dschebel Musa, 1500m, *Kneucker* 290 (holo. B!).

B. moeszii Pénzes in Magyar Bot. Lapok 33: 24 pl.10 (1934). Type: Iran, Auf Aker u. Strassen Graben bei [Daulatabad] Dolitabad, *Pichler* 18 (holo. G!).

Icon.: Bor, N. L. in Fl. Iraq, ed. Townsend & Guest 9: tab. 53 (1968).

Diagnostic features of the type specimen based on my own observations:
Leaf blade length: 2.8–5cm
Panicle length: 2.8–4.5cm
Longest panicle branch in the lowermost panicle node: 0.8–2.3cm
No. of nodes in the panicle branch above: 0–1
No. of spikelets in the panicle branch above: 1–2
Panicle branches pubescence: short erect hairs
Spikelet length: 2.6–2.9cm
No. of florets per spikelet: 10–11
Glume shape: ovate-oblong
Vein no. on lower glume: 3 (4,5)
Vein no. on upper glume: 7
2nd lemma length: 18.1–18.3mm
Top of spikelet including awns: irregular
Anther length: 1.2mm
Callus on rachilla at the base of each fertile floret: none or very incomplete
2nd awn length (second fertile floret from the base): 23.2–24mm
2nd palea length: 12.2–12.5mm.

Habitats. From sea level to 1900m, generally at higher altitudes in Iran, Afghanistan and often E Mediterranean, but in lowlands in Turkey, Saudi Arabia, Iraq and Kuwait; on more or less dry silt, usually over limestone, calcareous, clay, lava, gypsum and saline soil; in compact,stony or gravelly, loose drifted or fixed sandy soil; in desert and semi-desert wadis, steppe, very rarely in wet areas (probably introduced), such as muddy gravelly river banks; hill slopes, open flat valleys, as a weed in fields, rarely in gardens; often with *Halothamnus subaphyllus*, *Amygdalus*, *Artemisia*, *Astragalus glaucophyllus* and *Malcolmia grandiflora*.

Selection of material examined – a distribution map is given in Sales, 1991b fig. 5:

ASIA (+ CYPRUS). AFGHANISTAN: N: Samangan: Taschkurgan, 420m, *Freitag* 5062 (hb. Freitag); SW: Herat; Obeh, 'Hot Springs' valley, 1371m, *R. & E. Gibbons* 506 (E); SE: Kandahar: 60km W Kandahar, 900m, *Freitag* 503 (hb. Freitag). IRAN: W: Kordestan: Sanandaj, 1300m, *Jacobs* 6722 (W); E: between Dasht-e-Kavir and Dasht-e-Lut, 1250m, *Léonard* 5521 (BR); C: Semnan: SE of Shahrud, 830m, *Freitag* 15262 (hb. Freitag); S: Baluchistan: 100km S Zahedan to Khash, 1750m, *Rechinger* 54735 (E). IRAQ: DWD: 13km E K3, 680m, *Rawi et al.* 32959 (K); FPF: 20km to Khanqin, *Fanzi & Noovi* 39591 (K); LCA: Haswa, between Baghdad and Falluja, *Omar & Wedal* 47500 (K); MAM: Jarsang to Amadiya, *Kaim et al.* 41010 (K). JORDAN: Wadi Araba-Wadi Khalid (N Fenan), 350m, 9 iii 1986, *Kürschner* (E); Wadi Ram, *Davis* 9105 (E). KUWAIT: 6th Ring Road, near the Golf course, 40m, *Rawi et al.* 10936 (KT); Sobiyah, by the sea shore, *Rawi & El-Kholy* 12330 (KT); along the Salmi highway, 136km from Rikka, 200m, *Rawi et al.* 10650 (KT). PAKISTAN: W:

Quetta: Sariab, 1700m, *Rechinger* 28842 (W); Khanai, *V. Parkash* 16473 (RAW). SAUDI ARABIA: N: Wadi Ar-ar Project: Al-Barka, *Al-Sooqi* 3975 (RIY); Al-Harra, *Chaudhary & Al-Jouid* 10852 (E); N/C: c.30km W of Al Majma'ah, c.700m, *Podzorski* 921 (E). TURKEY: C7, Malatya, c.112m, *E. K. Balls* 2246 (E); C9, Siirt, Simak to Gizre, 610m, *Davis* 42684 (E). UZBEKSKAYA: Flora Bucharica, *Neustruev* 201 (LE).

ACKNOWLEDGEMENTS

This work was carried out with a The British Council and a Gulbenkian Foundation Studentship. I wish to express special thanks to my PhD supervisors Mr Ian Hedge (Royal Botanic Garden Edinburgh) and Dr Philip Smith (University of Edinburgh, Institute of Cell & Molecular Biology) for their encouragement and advice. I am in debt to the Regius Keeper of the Royal Botanic Garden, Edinburgh and the head of the Department of Botany, University of Edinburgh who gave me full use of their rich resources. Prof. Abílio Fernandes, Coimbra, encouraged me in the first place to study *Bromus*.

I am also grateful to the curators of the following herbaria: B, BG, BM, BR, C, COI, E, ELVE, FI, G, GB, GL, HUJ, K, KASSEL, KUH, KUWAIT, LE, LINN, LISE, LISU, M, MAF, O, OXF, P, PAD, PR, RAW, S, SOM, TARI, TCD, W, and WU.

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